DYNAMICS OF YELLOWSTONE CUTTHROAT TROUT AND LAKE TROUT IN THE YELLOWSTONE LAKE ECOSYSTEM: A CASE STUDY FOR THE ECOLOGY AND MANAGEMENT OF NON-NATIVE FISHES

by

John Michael Syslo

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ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

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ABSTRACT

The introduction of lake trout *Salvelinus namaycush* into Yellowstone Lake preceded the collapse of the native Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* population. As a system with a simple fish assemblage and several long-term data sets, Yellowstone Lake provided a unique opportunity to evaluate the ecology of a native salmonid in the presence of a non-native salmonid population undergoing suppression in a large natural lake. Diet data for Yellowstone cutthroat trout and lake trout were evaluated at varying densities to determine the effects of density on diet composition. Temporal diet shifts from 1996-1999 to 2011-2013 were likely caused by limitation of prey fish for lake trout. Diets, stable isotopes, and depth-related patterns in CPUE indicated lake trout > 300 mm consumed primarily amphipods, making them trophically similar to Yellowstone cutthroat trout from during 2011-2013. A lake trout removal program was initiated during 1995 to reduce predation on Yellowstone cutthroat trout. Abundance and fishing mortality were estimated for lake trout from 1998 through 2013 and Yellowstone cutthroat trout from 1986 through 2013. Density-dependence was evaluated by examining individual growth, weight, maturity, and pre-recruit survival as a function of abundance. In addition, a simulation model was developed for the lake trout-Yellowstone cutthroat trout system to determine the probability of Yellowstone cutthroat trout abundance persisting at performance metrics given potential reductions in lake trout abundance. Estimates of Yellowstone cutthroat trout abundance varied 5-fold and lake trout abundance varied 6-fold. Yellowstone cutthroat trout weight and pre-recruit survival decreased with increasing Yellowstone cutthroat trout abundance; however, individual growth and maturity were not related to abundance. Lake trout population metrics did not vary with lake trout abundance. Simulation model results were variable because of uncertainty in lake trout pre-recruit survival. Conservative estimates for required lake trout reductions were > 97% of 2013 abundance for a > 70% probability of Yellowstone cutthroat trout persistence at the performance metrics outlined in the Native Fish Conservation Plan. Lake trout removal will likely reduce lake trout abundance and result in Yellowstone cutthroat trout recovery if the amount of fishing effort exerted in 2013 is maintained for at least 15 years.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Non-native species have long been recognized as a driver of the global decline in biodiversity (Vitousek et al. 1997; Simberloff 2001) and are often ranked second to habitat loss and degradation as the most prevalent threat to freshwater biodiversity (Cambray 2003; Dextrase and Mandrak 2006). Non-native fishes have been implicated in the decline of many native freshwater fish populations through competition, predation, and hybridization (Cucherousset and Olden 2011). The negative effects demonstrated by non-native fishes has led to a proliferation in the implementation or consideration of control programs to slow dispersal, eradicate, or decrease the abundance of non-native fishes (Britton et al. 2011).

The lake trout *Salvelinus namaycush* is an apex predator native to northern North America that has been introduced to 15 countries around the world and extensively within the U. S. (Crossman 1995). High predation rates exerted by lake trout have negatively affected native fish species in ecosystems where they have been successfully introduced (Crossman 1995), including large lakes and reservoirs in eight western U.S. states (Martinez et al. 2009) where their presence has led to declines in native salmonid populations (Fredenberg 2002; Vander Zanden et al. 2003; Koel et al. 2005). Introductions of lake trout have also altered trophic dynamics in lakes and surrounding terrestrial ecosystems (Vander Zanden et al. 2003; Tronstad et al. 2010; Ellis et al. 2011).

Lake trout were discovered in Yellowstone Lake, Yellowstone National Park, in 1994 (Kaeding et al. 1996) after being introduced in the mid-to-late 1980s (Munro et al.

2005). Yellowstone Lake is the largest lake above 2,000 m elevation in North America and contains the largest population of nonhybridized Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* in the world (Gresswell and Varley 1988). The Yellowstone cutthroat trout is considered a “sensitive species” by the U.S. Forest Service and Bureau of Land Management and an imperiled species by state agencies in Idaho, Montana, Nevada, Utah, and Wyoming (Gresswell 2009). Yellowstone Lake represents nearly 80% of the remaining lacustrine habitat for Yellowstone cutthroat trout (Gresswell et al. 1994), which is a keystone species in the Greater Yellowstone Ecosystem. Yellowstone cutthroat trout spawning migrations have been documented in 68 of 124 tributary streams to Yellowstone Lake (Gresswell et al. 1994), with 4 mammal species and 16 bird species documented as predators of Yellowstone cutthroat trout (Bergum et al. in review).

The establishment of lake trout in Yellowstone Lake resulted in the addition of a fourth trophic level to the food web and a dramatic decline in Yellowstone cutthroat trout abundance (Koel et al. 2005; Tronstad et al. 2010). Notably, the number of Yellowstone cutthroat trout ascending Clear Creek to spawn declined from 55,000 individuals in 1987 to 500 in 2007 (Koel et al. 2012). The decline in Yellowstone cutthroat trout abundance resulted in a trophic cascade (Tronstad et al. 2010) and disruption of trophic linkages to non-piscine predators throughout the Yellowstone Lake basin (Crait and Ben-David 2006; Baril et al. 2013; Tiesberg et al. 2014). The dramatic change in Yellowstone cutthroat trout abundance and subsequent effects that spread throughout the Yellowstone

Lake basin provides a classic example of how a non-native apex piscivore can alter a freshwater ecosystem.

In addition to altering food-web structure, non-native piscivores can compete with native prey species because most piscivorous fish species exhibit ontogenetic diet shifts (Juanes et al. 2002). Therefore, not only do non-native piscivores restructure ecosystems through high predation rates, but they can compete with native fishes before switching to piscivory (McHugh et al. 2008). Additionally, dietary shifts (i.e., prey switching) are necessary to sustain predator biomass in systems where non-native piscivores reduce prey abundance (McMahon and Bennett 1996; Roseman et al. 2014). Thus, the trophic niche of non-native lake trout can change through time and competition with native species can become an important interaction in addition to predation.

The collapse of the Yellowstone cutthroat trout population and coinciding increase in lake trout abundance provided a rare opportunity to evaluate feeding ecology of a native prey and non-native piscivore following the restructuring of a large lentic ecosystem. The objectives of Chapter 2 were to assess trophic overlap and temporal diet shifts for Yellowstone cutthroat trout and lake trout following the Yellowstone cutthroat trout population collapse and the lake trout population increase. To evaluate trophic overlap, I examined diet contents, stable isotopes, and depth-related patterns in catch per unit effort (CPUE) for Yellowstone cutthroat trout and lake trout from 2011 through 2013. Diets assessed from 2011 through 2013 were compared to previous studies for lake trout and Yellowstone cutthroat trout to evaluate whether diet shifts were responsible for any observed trophic similarity and whether diet shifts provided a potential mechanism for density-dependent compensation in either population (see below).

To reduce predation on Yellowstone cutthroat trout, a lake trout removal program was initiated during 1995 (McIntyre et al. 1995). The lake trout suppression program in Yellowstone Lake is the longest ongoing lake trout removal program in the western USA (Martinez et al. 2009) and one of few examples of a long-term mechanical-removal program for a non-native fish in a large, natural lake. Therefore, Yellowstone Lake provides an important case study for other programs aiming to recover native species through mechanical removal of non-native fishes.

Reports of mechanical removal for non-native fishes resulting in native fish population recovery are sparse (Weidel et al. 2007) and ecological complexity can make efficacy difficult to demonstrate or predict (Coggins et al. 2011; Franssen et al. 2014). Following the implementation of removal efforts, native and non-native populations are typically monitored to determine whether responses in abundance are evident (Franssen et al. 2014). Although monitoring is a critical component of non-native fish removal programs, population models are required to predict the reduction in non-native fishes required for the persistence of native fish populations at levels specified by management objectives (Peterson et al. 2008). Models also provide the ability to predict efficacy while accounting for multiple factors affecting abundance, including density-dependent population regulation (i.e., compensation), environmental variation, and the effects of bycatch on native fish populations.

Compensation resulting from density-dependent population regulation contributes to the ability of fish populations to recover from decreased abundance (Rose et al. 2001). The pre-recruit life stage can exhibit strong density-dependence (Myers et al. 1999). However, density-dependence in recruited life-stages can also regulate population growth through changes in growth, maturity schedules, and body condition (Trippel 1995; Lorenzen and Enberg 2002; Vicenzi et al. 2008), which subsequently influence fecundity. Compensatory density-dependence is pervasive among fish populations (Rose et al. 2001), but can be difficult to evaluate because of the requirement for long-term demographic data from periods with contrasting abundance (Johnston and Post 2009; Catalano and Allen 2011).

The collapse of the Yellowstone cutthroat trout population and coinciding increase in lake trout abundance provided a unique opportunity to study population dynamics at varying densities. The objectives of Chapter 3 were to use long-term data to assess Yellowstone cutthroat trout and lake trout population dynamics as a function of abundance and to construct a simulation model to assess the response of Yellowstone cutthroat trout to potential reductions in lake trout abundance resulting from continued mechanical removal. First, I used long-term monitoring and catch data to develop statistical catch-at-age (SCA) models to estimate abundance and fishery characteristics (i.e., catchability and mortality) for Yellowstone cutthroat trout and lake trout. Second, I evaluated the effects of density and environmental variation on weight, individual growth, maturity schedule, and pre-recruit survival for Yellowstone cutthroat trout and lake trout. Third, the information from the previous steps was used to develop a simulation model of the Yellowstone cutthroat trout – lake trout system to assess the decrease in lake trout abundance required for Yellowstone cutthroat trout to increase to levels specified by management objectives. The simulation model included density-dependent compensation, environmental variation, and the effect of bycatch on the Yellowstone cutthroat trout population.

Finally, Chapter 4 provides conclusions drawn from the research conducted in Chapters 2 and 3. As a note, Chapters 2 and 3 were developed for publication; therefore, I use the pronoun “we” throughout the chapters to acknowledge the contributions of co-authors and the chapters vary slightly with regard to punctuation and capitalization.

CHAPTER TWO

TROPHIC OVERLAP AND TEMPORAL DIET SHIFTS FOR A NONNATIVE AND A NATIVE SALMONID IN YELLOWSTONE LAKE, YELLOWSTONE NATIONAL PARK

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

Author: John M. Syslo

Contributions: Conceived the study, collected and analyzed data, and wrote the manuscript.

Co-Author: Christopher S. Guy

Contributions: Assisted with study design and development of study questions, discussed the results and implications, and edited the manuscript.

Co-Author: Todd M. Koel

Contributions: Assisted with developing study questions, assisted with sampling, obtained funding, and commented on the manuscript.

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Abstract

Nonnative piscivorous fishes have altered freshwater ecosystems throughout the world. In addition to exerting high predation rates, nonnative piscivores can compete with native fishes as a result of ontogenetic diet shifts or temporal diet shifts (i.e., prey switching) resulting from depleted prey populations. Feeding ecology has implications for ecological interactions and population dynamics (i.e., density-dependence); therefore, diet studies are necessary to determine the effects of nonnative piscivores on native fish populations. The introduction of Lake Trout *Salvelinus namaycush* into Yellowstone Lake, Yellowstone National Park, preceded the collapse of the native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* population. We assessed diets, stable isotopes (i.e., $\delta^{13}C$ and $\delta^{15}N$), and depth-related patterns in catch per unit effort (CPUE) for Yellowstone Cutthroat Trout and Lake Trout from 2011 through 2013 to evaluate trophic overlap. We also compared diets to studies conducted during previous periods with contrasting Yellowstone Cutthroat Trout and Lake Trout CPUE to evaluate diet shifts related to density. Diets, stable isotopes, and depth-related patterns in CPUE indicated Lake Trout > 300 mm were trophically similar to Yellowstone Cutthroat Trout from 2011 through 2013 as a result of temporal diet shifts resulting from limited prey fish. Lake Trout shifted from a diet dominated by Yellowstone Cutthroat Trout during the early stages of invasion to a diet dominated by amphipods following an increase in Lake Trout abundance and a decline in Yellowstone Cutthroat Trout prey. Yellowstone Cutthroat Trout diet was dominated by zooplankton during a period when CPUE of Yellowstone Cutthroat Trout was high and dominated by amphipods when CPUE was

reduced. The changing trophic dynamics observed for Yellowstone Cutthroat Trout and Lake Trout provide a classic example of how a nonnative apex piscivore can alter a freshwater ecosystem.

Introduction

Yellowstone Lake, Yellowstone National Park, contains the largest population of nonhybridized Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in the world (Gresswell and Varley 1988). The Yellowstone Cutthroat Trout is considered a keystone species in the greater Yellowstone Ecosystem, with 4 mammal species and 16 bird species documented consuming Yellowstone cutthroat trout (Bergum et al. in review). In 1994, Lake Trout *Salvelinus namaycush* were discovered in Yellowstone Lake (Kaeding et al. 1996), and the effect on Yellowstone cutthroat trout has been substantial (Koel et al. 2005). For example, the number of Yellowstone Cutthroat Trout ascending Clear Creek to spawn declined from 55,000 individuals in 1987 to 500 in 2007 (Koel et al. 2012). The decline in Yellowstone Cutthroat Trout abundance resulted in a four-level trophic cascade (Tronstad et al. 2010) and disruption of trophic linkages to non-piscine predators throughout the Yellowstone Lake basin (Crait and Ben-David 2006; Baril et al. 2013; Tiesberg et al. 2014). The drastic change in Yellowstone Cutthroat Trout abundance and subsequent effects that spread throughout the Yellowstone Lake basin provides a classic example of how a nonnative apex piscivore can alter a freshwater ecosystem.

Nonnative piscivorous fishes have altered freshwater ecosystems throughout the world (Cucherousset and Olden 2011). The most dramatic changes occur when predator introductions cause the alteration of food-web structure through the addition of a novel trophic level (Eby et al. 2006; Tronstad et al. 2010). The imposition of top-down regulation on native fish populations through predation can ultimately result in trophic cascades within water bodies (Tronstad et al. 2010; Ellis et al. 2011).

In addition to altering food-web structure, nonnative piscivores can compete with native prey species because most piscivorous fish species exhibit ontogenetic diet shifts (Juanes et al. 2002). Additionally, prey switching is necessary to sustain predator biomass in systems where nonnative piscivores reduce prey abundance (McMahon and Bennett 1996; Roseman et al. 2014). Thus, the trophic niche of the nonnative predator (such as Lake Trout) can change through time and competition with native species can become an important interaction in addition to predation.

The Lake Trout is a large-bodied apex piscivore that has been introduced to 15 countries around the world and extensively within the United States (Crossman 1995). The predatory demand of nonnative Lake Trout populations can exceed the available prey supply even before Lake Trout increase to high densities (Martinez et al 2009), resulting in declines in native fish populations in water bodies where the species has been introduced (Crossman 1995; Ellis et al. 2011). In the absence of abundant prey fish, Lake Trout often feed on lower trophic levels (Pazzia et al. 2002) and can become cannibalistic to increase energy intake (Martin and Olver 1980).

Cannibalism is considered an important factor regulating juvenile survival and Lake Trout population growth rate (Evans and Willox 1991; Richards et al. 2004). In addition to cannibalism, Lake Trout population growth rate can be regulated by diet. For example, lake trout populations feeding on invertebrates have lower individual growth rates than piscivorous populations (Matuszek et al. 1990; Madenjian et al. 1998; Pazzia et al. 2002). Diet ultimately affects reproductive output because length and weight are related to fecundity.

Diet shifts can also affect the population dynamics of the native prey species. For example, declines in density of the native prey species can result in increased per-capita prey availability and an increase in optimal prey types in the diet (Martinussen et al. 2011; Rudstam et al. 2011). The incorporation of optimal prey types in the diet can cause changes in individual growth, body condition, and maturity-at-age (Trippel 1995; Rudstam et al. 2011), leading to increased population growth rate at reduced abundance (Rose et al. 2001).

Trophic overlap and temporal diet shifts have implications for ongoing efforts to increase Yellowstone Cutthroat Trout abundance through the mechanical removal of Lake Trout in Yellowstone Lake. The Lake Trout removal program was initiated during 1995 with the purpose of reducing Lake Trout abundance to decrease predation on Yellowstone Cutthroat Trout. However, Lake Trout abundance continued to increase through 2009 despite the removal of 830,000 fish during the period (Syslo et al. 2011; Koel et al. 2012). If Lake Trout occupy a similar trophic position to Yellowstone Cutthroat Trout, interspecific competition could reduce the likelihood of Yellowstone Cutthroat Trout recovery. Additionally, diet shifts can provide potential regulatory mechanisms for Lake Trout and Yellowstone Cutthroat Trout abundances in Yellowstone Lake through cannibalism or changes in reproductive output.

Our objectives were to assess trophic overlap and temporal diet shifts for Yellowstone Cutthroat Trout and Lake Trout following the Lake Trout population increase and Yellowstone Cutthroat Trout population collapse. To evaluate trophic overlap, we examined diet contents, stable isotopes (i.e., $\delta^{13}C$ and $\delta^{15}N$), and depth-related patterns in CPUE for Yellowstone Cutthroat Trout and Lake Trout from 2011 through 2013. Given ontogenetic diet shifts, we predicted Yellowstone Cutthroat Trout and small (i.e., nonpiscivorous) Lake Trout would exhibit the greatest degree of trophic overlap and large (i.e., piscivorous) Lake Trout would not exhibit trophic overlap with Yellowstone Cutthroat Trout. We used CPUE to characterize Yellowstone Cutthroat Trout and Lake Trout relative abundance through time and compared diets assessed from 2011 through 2013 to previous studies for Yellowstone Cutthroat Trout (i.e., 1989) and Lake Trout (i.e., 1996 – 1999). Additionally, a bioenergetics model was used to estimate consumption by Lake Trout from 2011 through 2013 for comparison to the 1996 – 1999 study. We predicted Yellowstone Cutthroat Trout diet would include more bioenergetically favorable prey items when Yellowstone Cutthroat Trout CPUE was low relative to when Yellowstone Cutthroat Trout CPUE was high. We predicted Lake Trout diet would include greater proportions of other fishes, including conspecifics, and invertebrates when Lake Trout CPUE was high relative to when Lake Trout CPUE was low. Given the Yellowstone Cutthroat Trout decline and Lake Trout increase, we predicted consumption of Yellowstone Cutthroat Trout by Lake Trout from 2011 through 2013 would decline relative to 1996 – 1999.

Study Area

Yellowstone Lake (Figure 2.1) is at an elevation of 2,357 m, has a surface area of 34,020 ha, 239 km of shoreline, a mean depth of 48.5 m (Kaplinski 1991), and a maximum depth of 133 m (Morgan et al. 2003). The lake is typically ice covered from mid-December until late May or early June. Thermal stratification typically occurs in late July and can last into September, with summer surface water temperature reaching 17°C and a thermocline at about 15 m (Koel et al. 2007).

The lake is categorized as oligo-mesotrophic (Theriot et al. 1997), with diatoms dominating the phytoplankton assemblage throughout the year (Benson 1961; Tronstad et al. 2010). The zooplankton community consists primarily of the rotifer *Conochilus unicornis*, *Diaptomus* and *Cyclops* Copepods, and *Daphnia* spp. (Benson 1961). The benthic macroinvertebrate assemblage is dominated by the amphipods *Hyallela azteca* and *Gammarus lacustris* (Benson 1961). *G. lacustris* occurs in a wider range of depths than *H. azteca* and composes a larger portion of the historic Yellowstone Cutthroat Trout diet (Benson 1961). The fish assemblage in the lake consists of two native species, Yellowstone Cutthroat Trout and Longnose Dace *Rhinichthys cataractae*, and three nonnative species in addition to Lake Trout, Longnose Sucker *Catostomus catostomus*, Redside Shiner *Richardsonius balteatus*, and Lake Chub *Couesius plumbeus* (Gresswell and Varley 1988).

Methods

Sampling

Yellowstone Cutthroat Trout Assessment Netting. Gill nets were used to assess the Yellowstone Cutthroat Trout population at 11 sites throughout the lake in mid-September from 1978 through 2013 (Kaeding and Koel 2011). At each site, five sinking experimental gill nets were set overnight perpendicular to shore. Nets were set about 100 m apart with the near-shore end about 1.5-m deep. Nets were 1.5-m deep and 38-m long, consisting of 7.6-m panels of 19, 25, 32, 38, and 51-mm bar measure. All fish caught in Yellowstone Cutthroat Trout assessment netting were measured for total length (TL; nearest mm). Weight (nearest g), sex, and maturity were recorded for incidental Yellowstone Cutthroat Trout mortalities.

Lake Trout Assessment Netting. A sampling program to assess the Lake Trout population was developed in 1997 (Ruzycki et al. 2003). Multiple depth strata were sampled during Lake Trout assessment netting; therefore, Lake Trout assessment netting also sampled the Yellowstone Cutthroat Trout population. Sixteen sites throughout the lake were sampled during early August with six experimental gill nets per site. At each site, a small-mesh and large-mesh sinking gill net were set overnight at each of three depth strata (epilimnion [3 – 10 m], metalimnion [10 – 30 m], and hypolimnion [> 40 m]). Small-mesh gill nets were 2-m deep and 76-m long, consisting of 13.7-m panels of 19, 25, 32, 38, 44, and 51-mm bar measure. Large-mesh gill nets were 3.3-m deep and 68.6-m long, consisting of 13.7-m panels of 57, 64, 70, 76, and 89-mm bar measure. Gill nets were set perpendicular to shore and nets within a stratum were set parallel about 100 m apart. The shallow stratum (i.e., 3 – 10 m) was not sampled in 1998 to avoid Yellowstone Cutthroat Trout incidental mortality (Ruzycki 2004). Lake Trout assessment netting was inconsistent from 1999 through 2009 and a new protocol was developed in 2010 and implemented through 2013. Lake Trout assessment netting from 2010 through 2013 was similar to the program developed in 1997 (i.e., net specifications and depth strata) but included 24 sites per year and the shallow stratum was not sampled during 2011. All fish sampled in Lake Trout assessment netting were measured for TL. Weight (nearest g), sex, maturity, and gonad weight were recorded for Lake Trout and incidental Yellowstone Cutthroat Trout mortalities. In 2013, sagittal otoliths were sampled from 10 Lake Trout per 1-cm length group for aging (see Syslo et al. 2011 for description of aging methods).

Lake Trout Suppression Netting. Sinking gill nets were used to remove Lake Trout from 1994 through 2013 during the ice-free season (i.e., late May through October). Suppression netting consisted of 25, 32, 38, 44, 51, 57, and 64-mm bar-measure gill nets that were 90 m long and 3.3 m deep. Gill nets were typically set at depths greater than 20 m to avoid Yellowstone Cutthroat Trout bycatch. Gill net soak time varied from 1 to 7 nights. Trap nets were used from 2010 through 2013 to target Lake Trout (i.e., > 450 mm TL) from late May through August. Eight to ten trap nets were deployed at fixed locations throughout Yellowstone Lake each year. Trap net leads were 180 – 305-m long and 9 – 15-m deep with mesh sizes varying from 76 – 178-mm bar measure (Koel et al. 2012). Trap net pots were 6-m wide, 6-m long, and 6 – 12-m deep with mesh sizes varying from 51 – 57-m3m bar measure (Koel et al. 2012). Trap net soak times varied from 1 to 4 nights.

Diet. Yellowstone Cutthroat Trout and Lake Trout diets were sampled from all netting types in 2011. Sampling of Lake Trout and Yellowstone Cutthroat Trout diets was stratified by season: pre-stratification (before 1 August), stratification (1 August – 20 September), and post-stratification (after 20 September). To account for ontogenetic diet shifts, an attempt was made to sample at least 15 individuals of each species from 50-mm length classes starting at 150 mm during each season. About 50% of stomachs from Lake Trout > 400 mm were empty in 2011; therefore, diets from Lake Trout > 400 mm were sampled again in 2013. Stomach contents were primarily sampled from assessment netting during the stratified season; however, stomachs from large Lake Trout (i.e., > 450 mm TL) were also obtained from trap nets to augment sample sizes from Lake Trout assessment netting. During the pre- and post-stratified seasons, stomachs were obtained by subsampling fish sampled in suppression netting (i.e., gill nets and trap nets). An attempt was made to only sample fish from gill nets set for one night. Stomach contents were sampled from as many gill netting areas (Figure 2.1) as possible during each season. Each time a gill net was lifted in a gill netting area that had not been previously sampled that season, the first three Yellowstone Cutthroat Trout or Lake Trout within each 50-mm length class were sampled. Trap nets were soaked for only one night prior to sampling fish for stomach contents. When trap nets were lifted, the first three fish within each 50-mm length class were sampled from each net.

Stomachs and stomach contents were removed from dead Lake Trout and Yellowstone Cutthroat Trout in the laboratory. Stomach contents from live Yellowstone Cutthroat Trout were obtained by gastric lavage using acrylic tubes (Quist et al. 2002). Tubes were about 375-mm long with 1-mm thick walls and inner diameters of 8, 11, 14, 18, and 24 mm. The largest tube diameter that could be inserted into the esophagus was selected for each Yellowstone Cutthroat Trout. After the tube was inserted, a small amount of distilled water was added, the tube was sealed with the hand, and the fish was inverted several times. The tube was removed while the fish was in a vertical position and stomach contents were dislodged into a tray. Lavage was repeated until prey items were no longer produced. Stomach contents were fixed in 10% buffered formalin and preserved in 70% ethanol.

Prey items were identified to family or order for invertebrates and to species for fish. Prey items were separated by taxon and the blotted wet weight was recorded for each prey category (nearest 0.01 g). Prey fish were measured for TL when possible. Lake Trout prey were not identified in Lake Trout stomachs (see Results); therefore, we assumed unidentified digested salmonids were Yellowstone Cutthroat Trout when estimating weight at ingestion. For digested Yellowstone Cutthroat Trout and unidentified salmonids, vertebral column length or standard length were converted to TL at ingestion using existing regression equations for Yellowstone Cutthroat Trout (Ruzycki and Beauchamp 1997). Total length at ingestion was converted to wet weight (g) using a weight-length regression for Yellowstone Cutthroat Trout sampled in Yellowstone Cutthroat Trout assessment netting in 2011 ($r^2 = 0.98$, $N = 968$, $P < 0.01$):

$$W = 0.000006 \times TL^{3.090}.$$

Recovery of stomach contents can vary from 60% to 90% by weight using stomach tubes (Quist et al. 2002). Therefore, lavage was performed on a subset ($N = 16$) of incidental mortalities to assess recovery of prey items. Mean proportion by weight was estimated by prey type among samples obtained using gastric lavage and among samples of total stomach contents (i.e., gastric lavage combined with remaining stomach contents). Mean proportion by weight for prey types obtained using gastric lavage and total stomach contents only differed by 0.00 – 0.04, indicating gastric lavage produced a representative sampling of Yellowstone Cutthroat Trout diet. Yellowstone Cutthroat Trout diet was quantified as proportion by volume in a previous study (Jones et al. 1990). Therefore, both weight and volume were measured for Yellowstone Cutthroat Trout prey types for a subset of stomachs sampled in 2011 to develop weight to volume conversions. Regression slopes for weight as a function of volume were not different than 1.0 (J.M. Syslo; unpublished data); therefore, diets from 1989 and 2011 were able to be compared.

Stable Isotopes. The analysis of diets provides high taxonomic resolution when evaluating trophic position; however, diets can be temporally variable (Garvey and Chipps 2012). Stable isotope ratios (i.e., carbon [$\delta^{13}C$] and nitrogen [$\delta^{15}N$]) can be used to provide a measure of feeding habits that represents long-term feeding behavior (Garvey and Chipps 2012). Consumer $\delta^{15}N$ increases relative to the food source, providing a measure of trophic position (Minigawa and Wada 1984). In contrast, $\delta^{13}C$ of consumers are similar to ratios in their prey, providing an indication of food origin. Specifically, $\delta^{13}C$ values tend to be greatest (i.e., less negative) in littoral zones, decrease in pelagic zones, and highly negative in profundal zones (Vander Zanden and Rasmussen 1999). The combination of diet and stable isotope analyses provides a powerful approach to assessing trophic position (Clarke et al. 2005; Feiner et al. 2013).

Tissue samples were collected from recently deceased Yellowstone Cutthroat Trout and Lake Trout sampled in Lake Trout Assessment netting during 2011 and 2013. An attempt was made to sample five fish of each species from each 50-mm length class starting at 150 mm. A tissue plug was removed from the dorsal musculature using a 4-mm biopsy punch. Amphipods were sampled to evaluate whether baseline $\delta^{15}N$ for primary consumers varied between the profundal and littoral zone (Vander Zanden and Rasmussen 1999; Post 2002). Amphipods were used because they are widely distributed throughout the lake, occupy a wide range of depths (i.e., 0-45 m), and are an important prey item for fishes in Yellowstone Lake (Benson 1961). Amphipods were sampled from macrophytes attached to gill nets at each depth stratum and site where they were detected in Lake Trout Assessment netting in 2013.

Fish tissue samples and amphipods were placed in a portable cryogenic freezer (model CX100; Taylor Wharton, Theodore, AL, USA) during collection. Samples were freeze-dried for 18 h using a Labconco Freezone 1 (Labconco Corporation, Kansas City, MO, USA) and ground to a fine powder with a mortar and pestle. About 1 mg of the ground sample was placed into a tin capsule and analyzed at the University of California-Davis Stable Isotope Facility with a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire UK). Stable isotope ratios were calculated as:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \cdot 1000,$$

where $R_{sample} = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ of the sample and $R_{standard} = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ of the international standard (Vander Zanden and Rasmussen 1999). The international standard for carbon was Vienna PeeDee Belemnite and the standard for nitrogen was atmospheric nitrogen.

Thermal Regime. Daily temperature profiles were measured for use in bioenergetics modeling (see below). Profiles were measured in the center of the West Thumb Basin from late May through October using a vertical temperature logger array. Temperature loggers were placed along a steel cable every 1 m from depths between 1 m and 20 m and every 10 m at depths > 20 m.

Trophic Overlap

Diet. Mean proportion by weight (*MW*) was estimated by season for each prey type in Lake Trout and Yellowstone Cutthroat Trout diets from 2011 through 2013 (Chipps and Garvey 2007). Mean proportion by weight was calculated for three Yellowstone Cutthroat Trout length classes (160 – 300 mm, 301 – 475 mm, and 476 – 575 mm) and four Lake Trout length classes (160 – 300 mm, 301 – 475 mm, 476 – 575 mm, and 576 – 920 mm) to account for ontogenetic variation in diet. Schoener's index (*D*) was used to estimate diet overlap between Yellowstone Cutthroat Trout and Lake Trout (Schoener 1968):

$$D = 1 - 0.5\left(\sum_{i=1}^{n} |p_{ij} - p_{ik}|\right),$$

where i indicates prey item, p_{ij} indicates proportion prey item i is of diet for species j, and p_{ik} indicates proportion prey item i is of diet for species k. Schoener's index was estimated between each Yellowstone Cutthroat Trout and Lake Trout length class by season. Values of $D \geq 0.60$ were considered significant (Wallace 1981).

Stable Isotopes. Amphipod $\delta^{15}N$ was regressed as a linear function of $\delta^{13}C$ and the regression model was used to correct $\delta^{15}N$ for Yellowstone Cutthroat Trout and Lake Trout. For each fish, the regression equation was used to calculate $\delta^{15}N$ at the observed $\delta^{13}C$ value (Vander Zanden and Rasmussen 1999; Post 2002). Corrected $\delta^{15}N$ and $\delta^{13}C$ were compared among species length class combinations using one way analysis of variance ($\alpha = 0.05$) and Tukey's multiple comparison test.

Relative Abundance. Catch per unit effort (i.e., number of fish per 100-m of net set for 1 night) of Yellowstone Cutthroat Trout and Lake Trout sampled in Lake Trout assessment netting was used to determine vertical distribution by species. Mean CPUE was estimated by length class and depth stratum for Lake Trout and Yellowstone Cutthroat Trout from 2010 – 2013. Catch per unit effort data from Lake Trout assessment netting in 2011 were omitted because the epilimnion was not sampled (see above).

Temporal Shifts

Relative Abundance. Catch per unit effort of Yellowstone Cutthroat Trout in Yellowstone Cutthroat Trout assessment netting (1978 – 2013) and Lake Trout in Lake

Trout assessment netting (1997, 2010, 2012, and 2013) was used to assess relative abundance through time. Lake Trout CPUE for 2010, 2012, and 2013 was considered to represent the relative abundance during the period of diet sampling (i.e., 2011 and 2013). Mean CPUE was estimated among sites by length class (see above) and year.

Diet. Temporal comparisons were qualitative rather than statistical because only summary values were available for previous diet studies. Yellowstone Cutthroat Trout diet was only evaluated during the stratified season in 1989 and was not evaluated by length class (Jones et al. 1990). Therefore, Yellowstone Cutthroat Trout diet data from the 2011 stratified season were pooled among length classes to compare to 1989 diet data. Lake Trout diet during 1996 – 1999 was evaluated by age 3 – 4 (373 – 444 mm; TL), age 5 – 8 (421 – 599 mm), and age ≥ 9 (> 600 mm) categories (Ruzycki et al. 2003). The corresponding categories in 2011 – 2013 were age 1 – 4 (160 – 475 mm; TL), age 5 – 7 (476 – 575 mm), and age ≥ 8 (576 – 920 mm).

Bioenergetics. Consumption was estimated for age 2 – 17 Lake Trout using Fish Bioenergetics 3.0 (Hanson et al. 1997). Data requirements included age-specific estimates of individual growth in weight, energy losses from spawning, seasonal diet proportions, prey energy densities, and thermal history. Day 1 of model simulations was 20 May, corresponding to the average date of ice-off.

For each age, growth in weight for each age was estimated from age-length and length-weight models. Lake Trout TL at age was described by the von Bertalanffy growth equation for Lake Trout sampled in Lake Trout assessment netting ($N = 479$):

$$\mathrm{TL}_t = 861\left[1 - e^{-0.147(t+0.502)}\right],$$

where TL_t is total length at age t (years). Total length at age was converted to weight at age (W; Table 1) using an equation for Lake Trout sampled in Lake Trout assessment netting ($N = 422$):

$$W = 0.000002 \text{ x } \mathrm{TL}^{3.23}.$$

Spawning losses were simulated on 1 September by reducing body weight by the average age-specific gonadosomatic index (GSI) among mature males and females (Table 2.1). Age at first maturity was 4 years for males and 6 years for females (Syslo et al. 2011). Male GSI was assumed to equal 3.3 % for mature Lake Trout (Ruzycki et al. 2003) and female GSI varied from 8.8% at age 6 to 15.8% at age 17 (J. M. Syslo; unpublished data). Male and female Lake Trout were assumed to spawn every year.

Lake Trout diet was pooled among the 160 – 300-mm and 301 – 475-mm length classes because fish composed a negligible proportion of diet for both length classes. Estimates of Lake Trout diet proportions by weight were available for the pre-stratified, stratified, and post-stratified seasons. Diet for the ice-covered season was simulated by linear interpolation between the post-stratified and pre-stratified seasons (Ruzycki et al. 2003). Literature values were used for prey energy densities (see Table 2.2) and 15% of invertebrate prey and 3% of fish prey was assumed to be indigestible (Beauchamp et al. 2007).

Thermal history was calculated by length class using daily temperature profiles and Lake Trout depth distributions. Temperature profiles were available from late May through October (see above). The temperature observed immediately after ice-off (i.e., 3.5°C) was used for the environmental temperature for Lake Trout through the ice-covered season. Lake Trout depth distribution for the stratified season was estimated from Lake Trout assessment netting. Depth distributions during the pre-stratified and post-stratified seasons were estimated using the depths of Lake Trout sampled in suppression netting (i.e., gill nets and trap nets).

Results

Trophic Overlap

Yellowstone Cutthroat Trout Diet. Amphipods composed greater than 0.60 of the diet for Yellowstone Cutthroat Trout in all length classes during all seasons in 2011 (Table 2.3). During the pre-stratified season, chironomids composed the second greatest proportion of diet for all Yellowstone Cutthroat Trout length classes (Table 2.3). During the stratified season, the second greatest proportion of diet was composed of cladocerans for 160 – 300 mm Yellowstone Cutthroat Trout, with cladocerans and insects composing the second greatest proportion of diet for 301 – 475-mm Yellowstone Cutthroat Trout. Yellowstone Cutthroat Trout in the 476 – 575-mm length class consumed amphipods almost exclusively during the stratified season (Table 2.3). During the post-stratified season, cladocerans composed the second greatest proportion of diet for 301 – 475 and 476 – 575-mm Yellowstone Cutthroat Trout (Table 2.3).

Lake Trout Diet. From 2011 through 2013, amphipods composed a greater proportion of diet than any other prey type for all Lake Trout length classes and seasons with the exception of 160 – 300-mm Lake Trout during the pre-stratified season (Table

2.4). Copepods composed 0.28 to 0.57 of the diet for 160 – 300-mm Lake Trout and cladocerans composing up to 0.32 of the diet for 301 – 475-mm Lake Trout (Table 2.4). The proportion of fish in Lake Trout diet increased through the year (Table 2.4.). Yellowstone Cutthroat Trout composed 0.03 to 0.21 of the diet for Lake Trout ≥ 476 mm and unidentified salmonids composed up to 0.12 of Lake Trout diet (Table 2.4). Cyprinids composed < 0.01 of Lake Trout diet and Longnose Suckers were not observed in the Lake Trout diet (Table 2.4). Lake Trout eggs composed 0.07 to 0.16 of the diet for 301 – 475, 476 – 575, and 576 – 920-mm Lake Trout during the post-stratified season (Table 2.4). A total of 67 salmonids were identified in Lake Trout diets. Fifty-five salmonids were identified as Yellowstone Cutthroat Trout and no Lake Trout were identified in Lake Trout diets.

Diet Overlap. Schoener's diet overlap (*D*) was greater than 0.60 for half of the species length class comparisons (Table 2.5). Schoener's diet overlap was less than 0.60 between 160 – 300-mm Lake Trout and all Yellowstone Cutthroat Trout length classes in all seasons (Table 2.5) and exceeded 0.60 between Lake Trout in the 476 – 575-mm length class and all Yellowstone Cutthroat Trout length classes in all seasons (Table 2.5). Diet overlap was greatest during the pre-stratified season (Table 2.5).

Stable Isotopes. A significant negative relationship between amphipod $\delta^{13}C$ and $\delta^{15}N$ values provided a baseline to standardize $\delta^{15}N$ (Figure 2.2). Significant differences were detected among species length-class combinations for $\delta^{13}C$ and standardized $\delta^{15}N$ (ANOVA: $F = 8.05$; df = 6, 108; $P < 0.01$ for both tests). Values of $\delta^{13}C$ were significantly smaller (i.e., more negative) for 160 – 300-mm Lake Trout than for all Yellowstone Cutthroat Trout length classes (Figure 2.3) and $\delta^{15}N$ was significantly greater for 160 – 300-mm Lake Trout than for all Yellowstone Cutthroat Trout length classes (Figure 2.4). Lake trout ≥ 301 mm had similar $\delta^{13}C$ and $\delta^{15}N$ to 160 – 475-mm Yellowstone Cutthroat Trout (Figures 2.3 and 2.4). Values of $\delta^{13}C$ and $\delta^{15}N$ were similar among length classes of Lake Trout and among length classes of Yellowstone Cutthroat Trout (Figures 2.3 and 2.4).

Relative Abundance. Mean CPUE for all Yellowstone Cutthroat Trout length classes was greatest at depths < 10 m and declined with increasing depth (Figure 2.5). Mean CPUE for Lake Trout was greatest in the 11 – 30-m depth for all length classes (Figure 2.5). Catch per unit effort for 160 – 300-mm Lake trout was greater at depths > 40 m than in the < 10 m depth stratum. For Lake trout ≥ 301 mm, CPUE was greater in the < 10 m depth stratum than at depths > 40 m.

Temporal Shifts

Yellowstone Cutthroat Trout. Catch per unit effort in Yellowstone Cutthroat Trout assessment netting from 1978 through 2013 was variable for 160 – 300-mm Yellowstone Cutthroat Trout, declined for 301 – 475-mm Yellowstone Cutthroat Trout, and increased for 476 – 575-mm Yellowstone Cutthroat Trout (Figure 2.6). Catch per unit effort for 160 – 300-mm Yellowstone Cutthroat Trout was greater in 2011 than any other year and was 2.8 times greater than in 1989 (Figure 2.6). For 301 – 475-mm Yellowstone Cutthroat Trout, CPUE declined by 90% from 1989 through 2011 (Figure

2.6). Catch per unit effort for 476 – 575-mm Yellowstone Cutthroat Trout was 10 times greater in 2011 compared to 1989 (Figure 2.6); however, fish in the length class represented a small proportion of the overall relative abundance. Yellowstone Cutthroat Trout shifted from a diet dominated by cladocerans in 1989 to a diet dominated by amphipods in 2011. Amphipods increased from 0.08 of Yellowstone Cutthroat Trout diet during the stratified season in 1989 to 0.79 in 2011 (Figure 2.7). The proportion of diet composed of cladocerans declined from 0.80 during the stratified season in 1989 to 0.11 in 2011 (Figure 2.7).

Lake Trout. Compared to 1997, mean CPUE was six times greater for 160 – 300-mm Lake Trout, three times greater for 301 – 475-mm Lake Trout, four times greater for 476 – 575-mm Lake Trout, and similar for 576 – 920-mm Lake Trout from 2010 through 2013 (Figure 2.8). Lake trout age classes that predominately consumed Yellowstone Cutthroat Trout in 1996 – 1999 consumed mostly amphipods from 2011 through 2013 (Figure 2.9). Per-capita consumption of Yellowstone Cutthroat Trout biomass by Lake Trout varied from 1.5 to 2.5 kg/year for ages 5 – 8 and from 4 – 8 kg/year for ages ≥ 8 from 1996 through 1999 (Figure 2.10). From 2011 through 2013, per-capita consumption of combined Yellowstone Cutthroat Trout and unidentified salmonid biomass varied from 0.4 – 0.6 kg/year for ages 5 – 7 and 1.4 – 2.2 kg/year for ages ≥ 8 (Figure 2.10). Per-capita consumption of Yellowstone Cutthroat Trout individuals by Lake Trout was 13/year for ages 3 – 4, 42/year for ages 5 – 8, and 41/year for ages ≥ 9 from 1996 through 1999 (Figure 2.10). From 2011 through 2013, per-capita consumption of combined Yellowstone Cutthroat Trout and unidentified salmonid individuals was 0.1/year for ages 3 – 4, varied from 8.6 – 9.3/year for ages 5 – 7, and varied from 19.6 to 31.8/year for ages ≥ 8 (Figure 2.10).

Discussion

The collapse of the Yellowstone Cutthroat Trout population and coinciding increase in Lake Trout abundance provided a rare opportunity to evaluate the feeding ecology of a native prey and non-native piscivore following the restructuring of the food web in a large lentic ecosystem. Following the Yellowstone Cutthroat Trout population collapse, Yellowstone Cutthroat Trout and Lake Trout exhibited diet shifts that resulted in a high degree of trophic overlap between species. Trophic overlap was a function of a shared reliance on amphipods for Yellowstone Cutthroat Trout and Lake Trout greater than 300 mm. Not only do Lake Trout pose a threat to Yellowstone Cutthroat Trout through predation, but our results indicate competition could become an additional stressor for the Yellowstone Cutthroat Trout population if amphipods are limiting.

We were not able to quantify amphipod availability; however, amphipods are likely a preferred prey item for Yellowstone Cutthroat Trout and amphipod abundance may be reduced when fish abundance is high. Previous studies indicated greater amphipod density occurred in areas where Yellowstone Cutthroat Trout abundance was reduced through exploitation (Benson 1961). We surmise the shift from zooplanktivory to benthic amphipods observed for Yellowstone Cutthroat Trout was the result of increased amphipod availability following the Yellowstone Cutthroat Trout population decline.

Similar diet shifts from zooplanktivory toward increased consumption of benthic amphipods occurred with increased availability of the amphipod *Diporeia* spp. for Bloater *Coregonus hoyi*, Alewife *Alosa pseudoharengus*, and Slimy Sculpin *Cottus cognatus* in Lake Michigan (Hondorp et al. 2005). Additionally, the occurrence of *Diporeia* spp. in diets of Lake Whitefish *Coregonus clupeaformis* decreased and planktivory increased when abundance of *Diporeia* spp. declined from 1980 through 1999 in Lake Michigan, corresponding to a decrease in Lake Whitefish body condition and growth (Pothoven et al. 2001). In Lake Michigan, *Diporeia* spp. contain greater energy density than other macroinvertebrates (Gardner et al. 2005) and availability of *Diporeia* spp. influences fish body condition, distribution, and abundance (Pothoven et al. 2001; Hondorp et al. 2005). The large proportion of Yellowstone Cutthroat Trout and Lake Trout diets composed by amphipods from 2011 through 2013 indicates amphipods may be a keystone species in the Yellowstone Lake food web, similar to *Diporeia* spp. in Lake Michigan.

The large proportion of Lake Trout diet composed of amphipods likely indicated prey fish were limiting for Lake Trout in Yellowstone Lake from 2011 through 2013. Piscivory is necessary for Lake Trout to maintain high individual growth rates and body condition (Pazzia et al. 2002). To support the individual growth rate observed from 2011 through 2013, Lake Trout in piscivorous length classes in Yellowstone Lake fed at a higher proportion of maximum consumption ($pC_{\max}$; 0.60 – 0.67) than nonnative populations that were more piscivorous. For example, $pC_{\max}$ was about 0.31 for nonnative Lake Trout in piscivorous length classes in Bear Lake, Idaho – Utah (Ruzycki et al. 2001) and varied from 0.41 – 0.65 in Lake Chelan (Schoen et al. 2012).

In addition to dietary shifts toward benthic amphipods, a change in the size of prey consumed by Lake Trout in Yellowstone Lake was likely caused by prey limitation. Lake Trout typically select for larger individuals of a given prey species when prey are abundant and consume smaller individuals after larger fish are depleted (Matuszek et al. 1990; Rand and Stewart 1998). In Yellowstone Lake, declines in consumption of Yellowstone Cutthroat Trout and unidentified salmonid individuals were less than declines in consumption of biomass because the average prey was smaller from 2011 through 2013 than 1996 through 1999. For example, the annual biomass of Yellowstone Cutthroat Trout and unidentified salmonids consumed by Lake Trout considered fully piscivorous (i.e., age ≥ 9) declined 67%, whereas the number of individuals consumed only declined 32%.

Prey limitation for Lake Trout in Yellowstone Lake is further supported when considering the high efficiency characterizing Lake Trout predation. For example, Lake Trout maintained relatively constant consumption rates across a 100-fold difference in prey densities in the Great Lakes (Eby et al. 1995). In Lake Pend Oreille, Idaho, Kokanee composed 88% of the diet for nonnative Lake Trout despite an 80 to 90% reduction in Kokanee abundance (Clarke et al. 2005). The observed decrease of Yellowstone Cutthroat Trout in Lake Trout diets indicates fish prey availability was substantially reduced for Lake Trout in Yellowstone Lake.

To maintain piscivorous diets, Lake Trout can switch prey species following declines in preferred prey (Rand and Stewart 1998). Lake Trout are opportunistic predators and consume prey fish species in proportion to their relative abundance in the environment (Elrod and O'Gormon 1991). Nonnative Lake Trout in Lake Chelan, Washington, consumed several different prey species (salmonids, cyprinids, Threespine Stickleback *Gasterosteus aculeatus*, and Burbot *Lota lota*), following the decline of a preferred prey species (Kokanee *Oncorhynchus nerka*, Schoen et al. 2012). Following the collapse of the Kokanee population in Flathead Lake, Montana (Spencer et al. 1991), Lake Trout consumed a variety of salmonid species and Yellow Perch *Perca flavescens* (Beauchamp et al. 2006). Fishes other than Yellowstone Cutthroat Trout did not compose a substantial proportion of Lake Trout diet from 2011 through 2013 in Yellowstone Lake. The lack of alternative prey fish in Lake Trout diet may be a function of the simple fish assemblage in Yellowstone Lake.

Given the lack of alternative prey fish species in Yellowstone Lake, we expected to observe cannibalism for Lake Trout. However, Lake Trout prey were not observed in Lake Trout diets. Although density-dependent stock-recruitment relationships for Lake Trout in the native range are frequently attributed to cannibalism of Lake Trout in the juvenile life stage (Evans and Willox 1991; Richards et al. 2004), observed incidences of cannibalism primarily involved predation on stocked juvenile Lake Trout (Bronte et al. 1995; Plosilla 1977). Cannibalism of wild Lake Trout juveniles may be less prevalent because wild juveniles typically occupy greater depths than piscivorous Lake Trout length classes (Martin and Olver 1980). Incidences of cannibalism observed in the nonnative range of Lake Trout vary by lake. In Flathead Lake, Montana, cannibalism was considered an important mechanism for population regulation (Beauchamp et al. 2006). Similarly, Lake Trout cannibalism was substantial in Lake Chelan, Washington, where 84% of the diet for Lake Trout greater than 551 mm was composed of Lake Trout during thermal stratification (Schoen et al. 2012). In contrast, cannibalism was not observed in four Colorado reservoirs where predatory demand of stocked Lake Trout exceeded the forage base (Johnson and Martinez 2002).

Cannibalism did not provide a mechanism for population regulation of Lake Trout in Yellowstone Lake; however, diet shifts toward lower trophic levels may ultimately result in decreased Lake Trout population growth rate through decreased individual growth rate, body condition, and fecundity. In contrast, the increase in consumption of a preferred prey (amphipods) for Yellowstone Cutthroat Trout may lead to increased population growth rate through increased individual growth and body condition. Dietary shifts for Yellowstone Cutthroat Trout and Lake Trout likely have implications for the success of Lake Trout removal and Yellowstone Cutthroat Trout recovery in Yellowstone Lake, and future research should evaluate Yellowstone Cutthroat Trout and Lake Trout population characteristics to determine whether diet shifts have the potential to affect population growth rates (Chapter 3).

Nonnative piscivorous fishes have altered freshwater ecosystems throughout the world (Eby et al. 2006; Cucherousset and Olden 2011). Examining the feeding habits of nonnative fishes is critical for determining the ecological effects of species introductions, and diet studies are commonly conducted for nonnative fishes to evaluate trophic overlap or the effects of piscivory on native fishes (Ruzycki et al. 2001; Clarke et al. 2005; Schoen et al. 2012); however, studies documenting long-term changes in feeding ecology are rare. We used a combination of historical fish abundance and diet studies, stable isotope analysis, and bioenergetics modeling to evaluate changes in prey consumption through time in a rapidly evolving food web following nonnative species introduction. Evaluating feeding ecology following the establishment of nonnative Lake Trout and the decline of a native Yellowstone Cutthroat Trout population allowed us to identify trophic overlap and temporal diet shifts as potentially important processes with implications for managing a nonnative piscivore in a large natural lake. Diet shifts for Yellowstone Cutthroat Trout and Lake Trout highlight the drastic changes that can occur in simple food webs following the establishment of a nonnative apex piscivore.

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Tables and Figures

Table 2.1. Age-specific weight, gonadosomatic index (GSI; average of male and female), diet length class, and proportion of physiological maximum consumption rate (pC_{max}) used in bioenergetics simulations for Lake Trout in Yellowstone Lake, Yellowstone National Park (following Schoen et al. 2012).

Age (years)	Weight (g)	GSI (%)	Length class (TL; mm)	pC_{max}
2	135	0.0	160 – 475	0.933
3	323	0.0	160 – 475	0.886
4	585	1.7	160 – 475	0.858
5	907	1.7	476 – 575	0.670
6	1,268	6.1	476 – 575	0.688
7	1,651	6.6	476 – 575	0.673
8	2,040	5.8	576 – 920	0.624
9	2,423	7.7	576 – 920	0.635
10	2,791	6.7	576 – 920	0.639
11	3,138	8.8	576 – 920	0.631
12	3,460	7.8	576 – 920	0.625
13	3,756	9.4	576 – 920	0.619
14	4,024	9.6	576 – 920	0.615
15	4,267	9.6	576 – 920	0.610
16	4,484	9.6	576 – 920	0.606
17	4,677	9.6	576 – 920	0.602

Table 2.2. Energy density for prey organisms used in bioenergetics simulations for Lake Trout in Yellowstone Lake, Yellowstone National Park.

Prey item	Surrogate	Energy density (J/g)	Source
Amphipoda		4,429	Cummins and Wuycheck (1971)
Zooplankton	*Daphnia* spp.	3,812	Luecke and Brandt (1993)
Chironomidae		2,742	Cummins and Wuycheck (1971)
Hirudinea (leech)		4,743	Hanson et al. (1997)
Other invertebrates[a]		2,420	Cummins and Wuycheck (1971) Cianco et al. (2007)
Lake Trout eggs	Salmonid eggs	6,117	Cummins and Wuycheck (1971)
Yellowstone Cutthroat Trout	*Oncorhynchus mykiss*	5,764	Hanson et al. (1997)
Unidentified Salmonid	*Oncorhynchus mykiss*	5,764	Hanson et al. (1997)
Cyprinid	*Notropis atherinoides*	5,108	Bryan et al. (1996)
Unidentified fish	*Oncorhynchus mykiss*	5,764	Hanson et al. (1997)

[a] Includes a weighted average for Diptera, Ephemeroptera, Plecoptera, Trichoptera, Hymenoptera, Coleoptera, Gastropoda, Mollusca, and Oligochaeta.

Table 2.3. Proportion of diet by weight for Yellowstone Cutthroat Trout prey (Cla = cladoceran; Cop = copepod; Amp = amphipod; Lee = leech; Chi = chironomid; Ins = insects; Mol = mollusk; Egg = Lake Trout egg; Yel = Yellowstone Cutthroat Trout; Sal = unidentified salmonid; Cyp = cyprinid; Fis = unidentified fish) by season and length class in Yellowstone Lake, Yellowstone National Park in 2011.

		Prey items											
Length class	*N*	Cla	Cop	Amp	Lee	Chi	Ins[a]	Mol	Egg	Yel	Sal	Cyp	Fis
Pre-stratified													
160–300	12	0	0.06	0.84	0	0.09	0	0	0	0	0	0	0
301–475	26	0.02	0.08	0.76	0	0.12	0.03	0	0	0	0	0	0
476–575	33	0	0	0.81	0	0.16	0	0	0	0	0	0	0
Stratified													
160–300	41	0.27	0	0.60	0	0.01	0.12	0	0	0	0	0	0
301–475	36	0.10	0	0.74	0	0.06	0.10	0	0	0	0	0	0
476–575	60	0.01	0	0.96	0	0	0.03	0	0	0	0	0	0
Post-stratified													
160–300	7	0	0	0.99	0	0	0	0	0	0	0	0	0
301–475	27	0.26	0.02	0.72	0	0	0	0	0	0	0	0	0
476–575	25	0.22	0	0.72	0	0	0.06	0	0	0	0	0	0

[a] Includes Ephemeroptera, trichoptera, plectoptera, and nonchironomid dipterans

Table 2.4. Proportion of diet by weight for Lake Trout prey (Cla = cladoceran; Cop = copepod; Amp = amphipod; Lee = leech; Chi = chironomid; Ins = insects; Mol = mollusk; Egg = Lake Trout egg; Yel = Yellowstone Cutthroat Trout; Sal = unidentified salmonid; Cyp = cyprinid; Fis = unidentified fish) by season and length class in Yellowstone Lake, Yellowstone National Park from 2011 through 2013.

		Prey items											
Length class	*N*	Cla	Cop	Amp	Lee	Chi	Ins[a]	Mol	Egg	Yel	Sal	Cyp	Fis
Pre-stratified													
160–300	46	0	0.57	0.35	0.07	0.01	0	0	0	0	0	0	0
301–475	81	0	0.12	0.70	0.04	0.12	0	0	0	0	0.01	0	0.01
476–575	54	0	0.06	0.71	0.11	0.08	0	0	0	0.03	0	0	0.02
576–920	66	0	0	0.81	0.06	0.07	0	0	0	0.06	0.01	0	0
Stratified													
160–300	64	0.04	0.28	0.43	0.14	0.08	0.02	0	0	0.02	0	0	0
301–475	53	0.29	0.05	0.32	0.21	0.13	0.01	0	0	0	0	<0.01	0
476–575	46	0.04	0	0.59	0.13	0	0	0.01	0	0.20	0	0	0.02
576–920	49	0	0	0.55	0.04	0	0	0	0	0.21	0.10	<0.01	0.09
Post-stratified													
160–300	18	0.06	0.35	0.45	0.15	0	0	0	0	0	0	0	0
301–475	87	0.32	0.12	0.46	0.02	0	0	0	0.07	0	0	0	0
476–575	50	0.06	0.02	0.60	0.02	0	0	0	0.16	0.06	0.02	0	0.06
576–920	50	0	0	0.57	0	0	0.02	0	0.08	0.20	0.12	<0.01	0

[a] Includes Ephemeroptera, trichoptera, plectoptera, and nonchironomid dipterans

Table 2.5. Schoener's index of diet overlap for Lake Trout and Yellowstone Cutthroat Trout length classes by season in Yellowstone Lake, Yellowstone National Park, from 2011 through 2013. Values greater than 0.60 (bold) were considered significant.

Cutthroat Trout length class	Lake Trout length class 160–300	301–475	476–575	576–920
Pre stratified season				
160–300	0.42	**0.85**	**0.84**	**0.87**
301–475	0.44	**0.89**	**0.85**	**0.83**
476–575	0.36	**0.82**	**0.79**	**0.88**
Stratified season				
160–300	0.50	**0.61**	**0.63**	0.56
301–475	0.54	0.49	**0.63**	0.56
476–575	0.45	0.34	**0.60**	0.56
Post-stratified season				
160–300	0.45	0.47	**0.60**	0.57
301–475	0.52	**0.76**	**0.67**	0.57
476–575	0.50	**0.69**	**0.65**	0.59

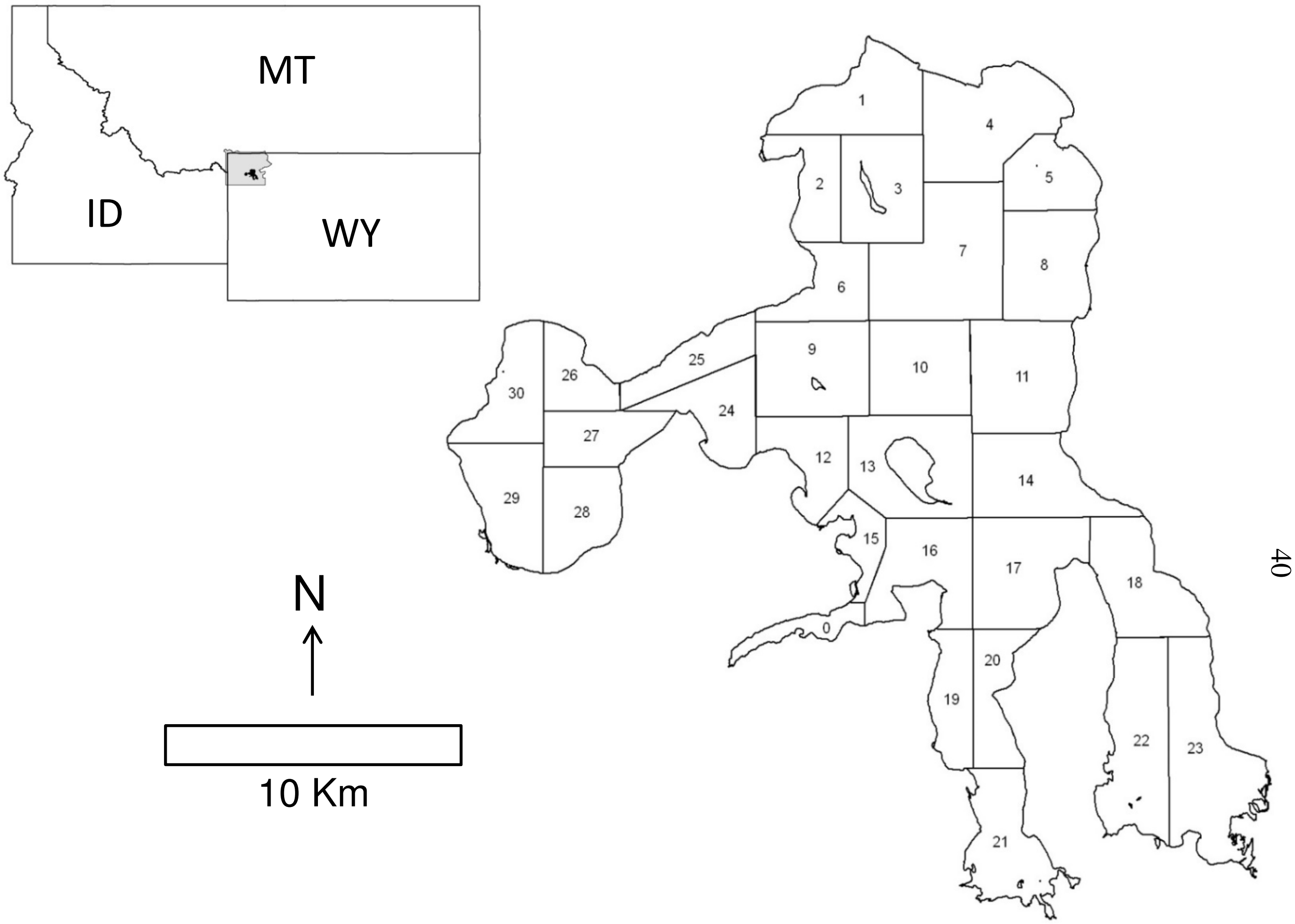

Figure 2.1. Map of Yellowstone Lake, Yellowstone National Park, depicting gill netting areas.

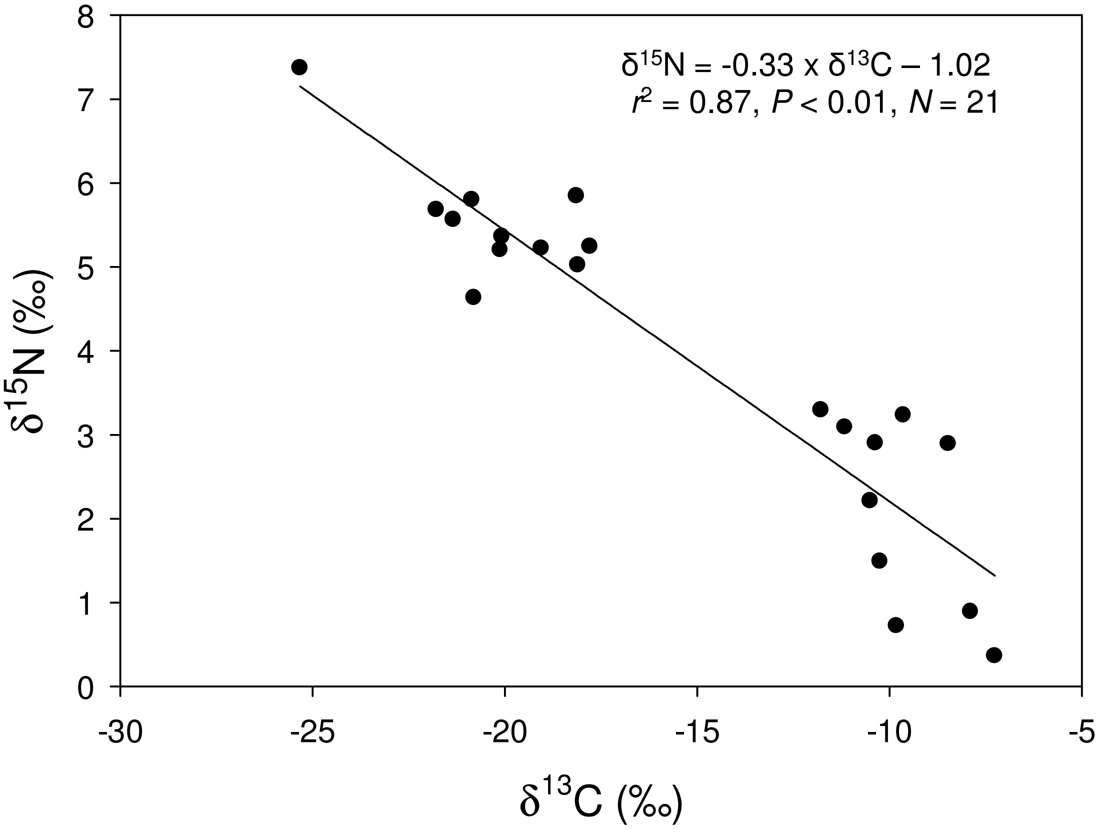

Figure 2.2. Regression of $\delta^{15}N$ as a function of $\delta^{13}C$ for amphipods sampled in Yellowstone Lake, Yellowstone National Park.

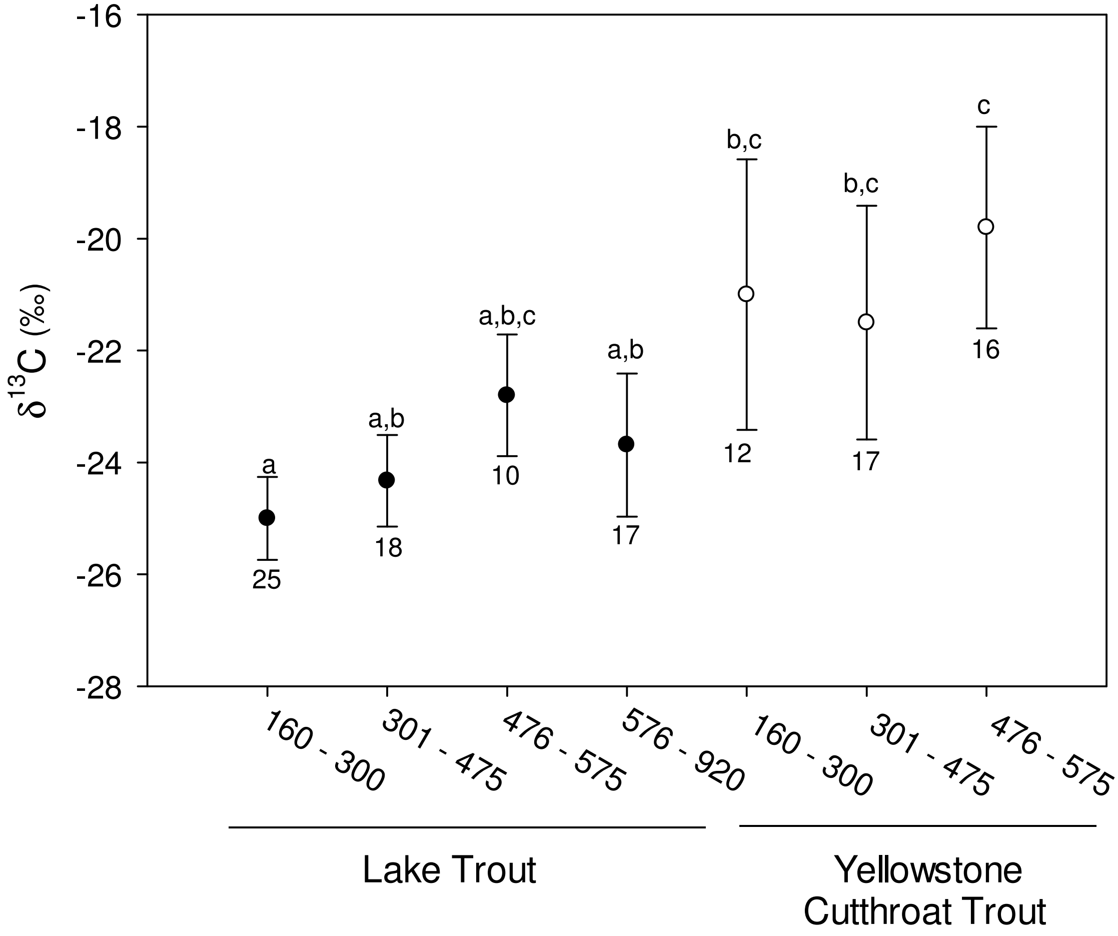

Figure 2.3. Mean $\delta^{13}C$ for length classes (mm) of Lake Trout (solid circles) and Yellowstone Cutthroat Trout (open circles) in Yellowstone Lake, Yellowstone National Park. Error bars delineate 95% confidence intervals. Means with different letters are significantly different ($\alpha = 0.05$). Numbers below bars are sample sizes.

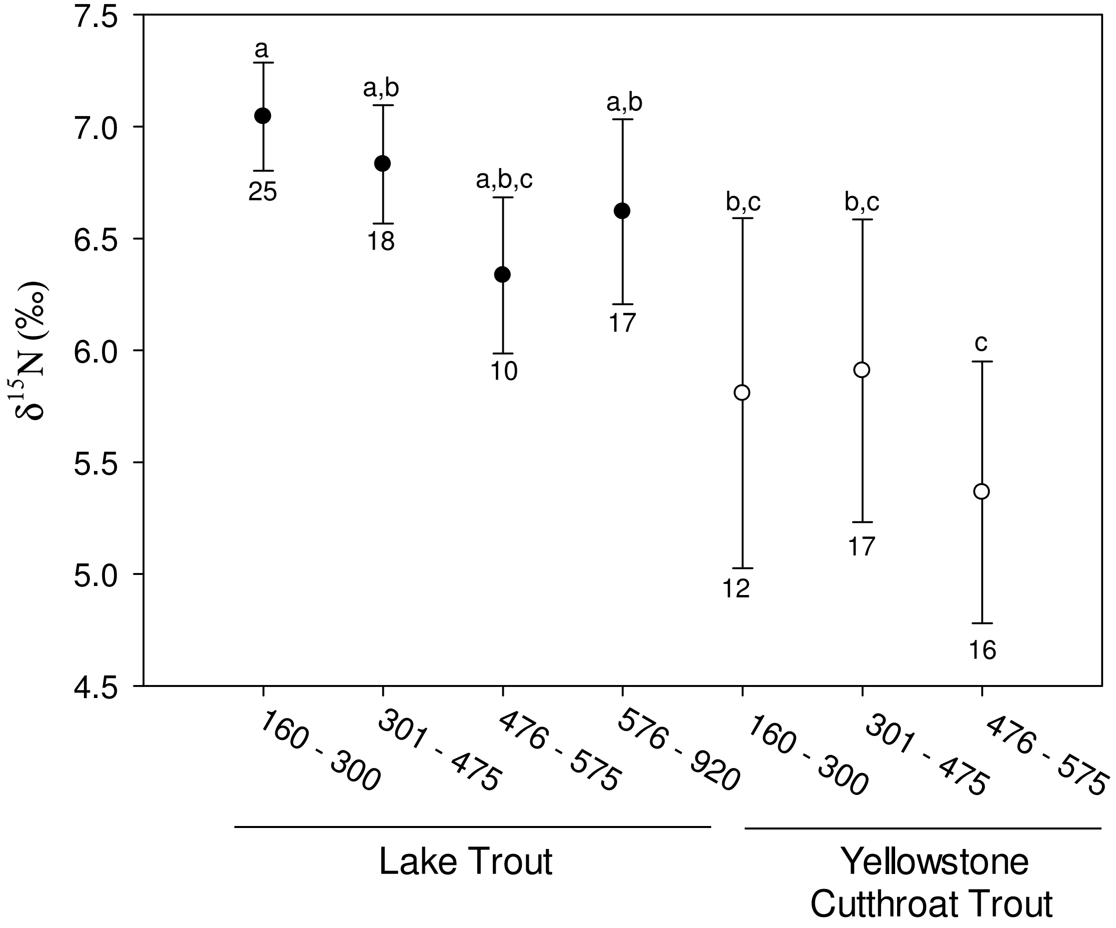

Figure 2.4. Mean $\delta^{15}N$ for length classes (mm) of Lake Trout (LKT, solid circles) and Yellowstone Cutthroat Trout (YCT, open circles) in Yellowstone Lake, Yellowstone National Park. Error bars delineate 95% confidence intervals. Means with different letters are significantly different ($\alpha = 0.05$). Numbers below bars are sample sizes.

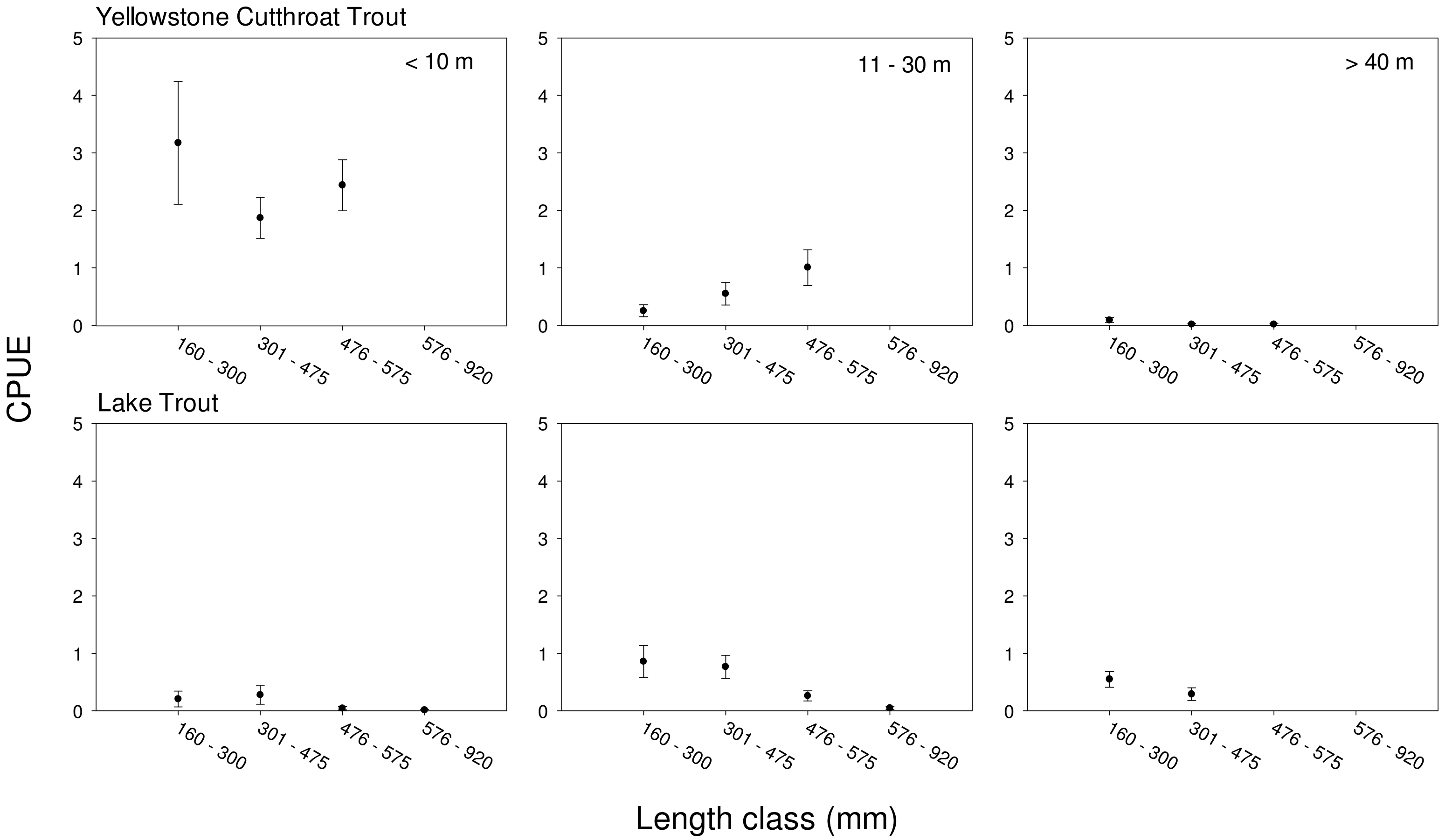

Figure 2.5. Mean catch per unit effort (CPUE) of Yellowstone Cutthroat Trout (upper panel) and Lake Trout (lower panel) length classes by depth stratum (left panel = < 10 m, center panel = 11 – 30 m, and right panel > 40 m) from Lake Trout assessment netting in Yellowstone Lake, Yellowstone National Park, from 2010 through 2013 pooled. Error bars delineate 95% confidence intervals.

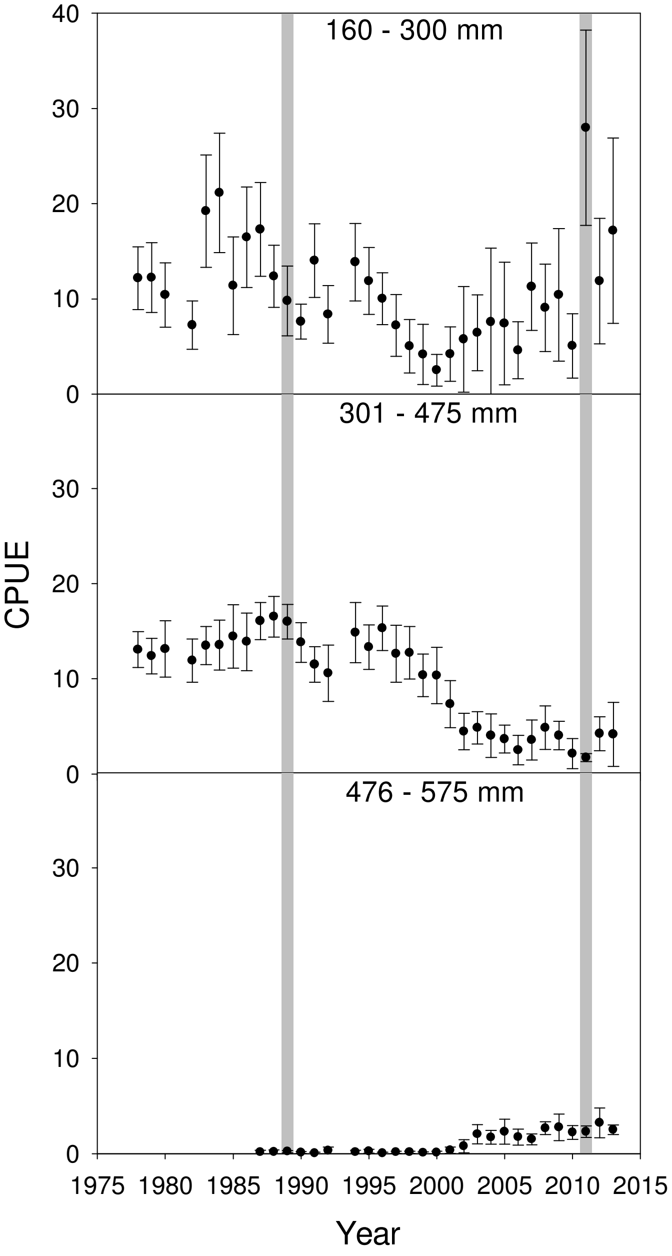

Figure 2.6. Mean Yellowstone Cutthroat Trout catch per unit effort (CPUE) by length class in Yellowstone Cutthroat Trout assessment netting from 1978 through 2013 in Yellowstone Lake, Yellowstone National Park. Error bars delineate 95% confidence intervals and grey vertical bars delineate years with diet data.

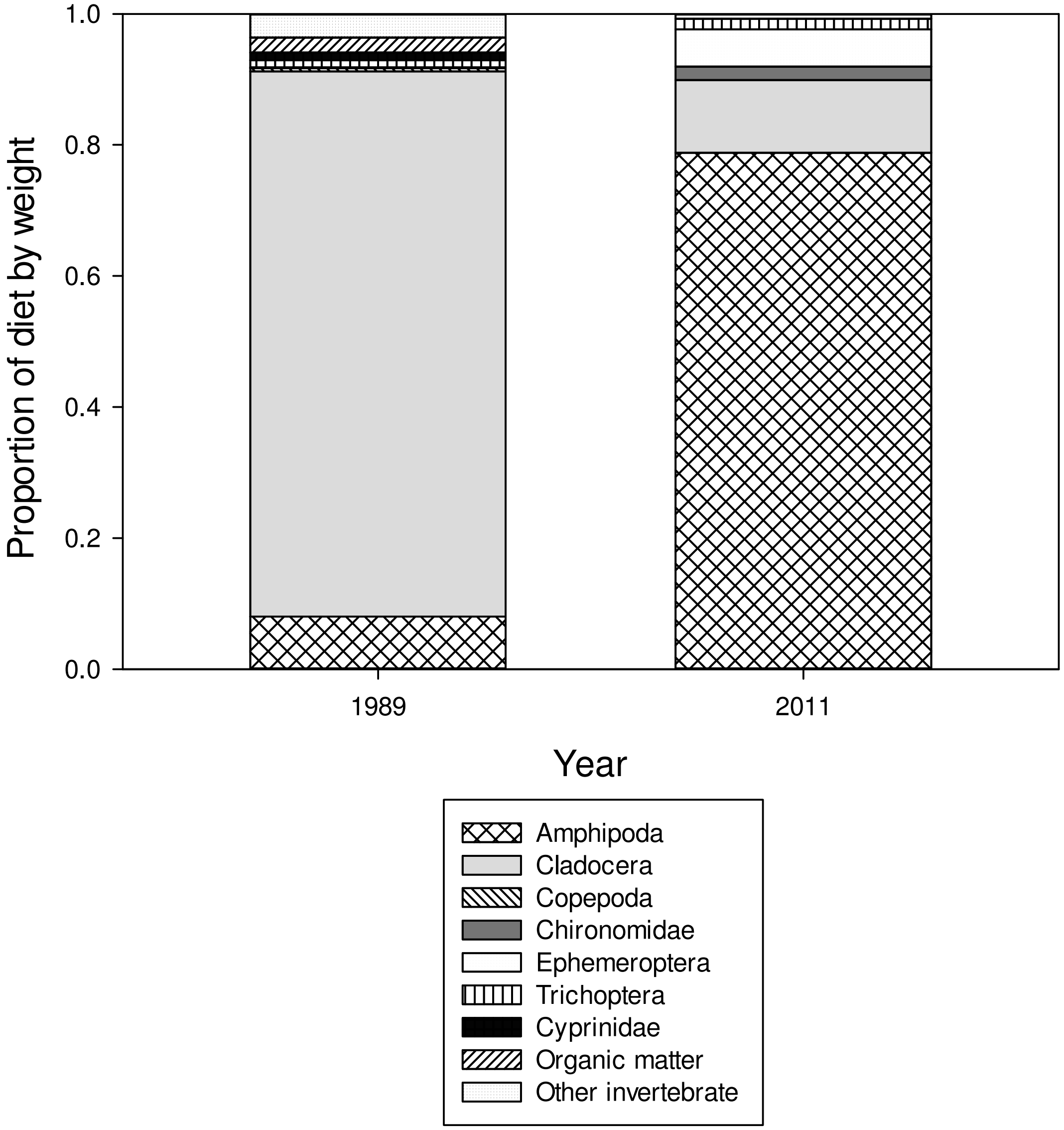

Figure 2.7. Proportion of diet by weight in 1989 (*N*=132; Jones et al. 1990) and 2011 (*N* = 267) for all length classes pooled during the stratified season for Yellowstone Cutthroat Trout in Yellowstone Lake, Yellowstone National Park.

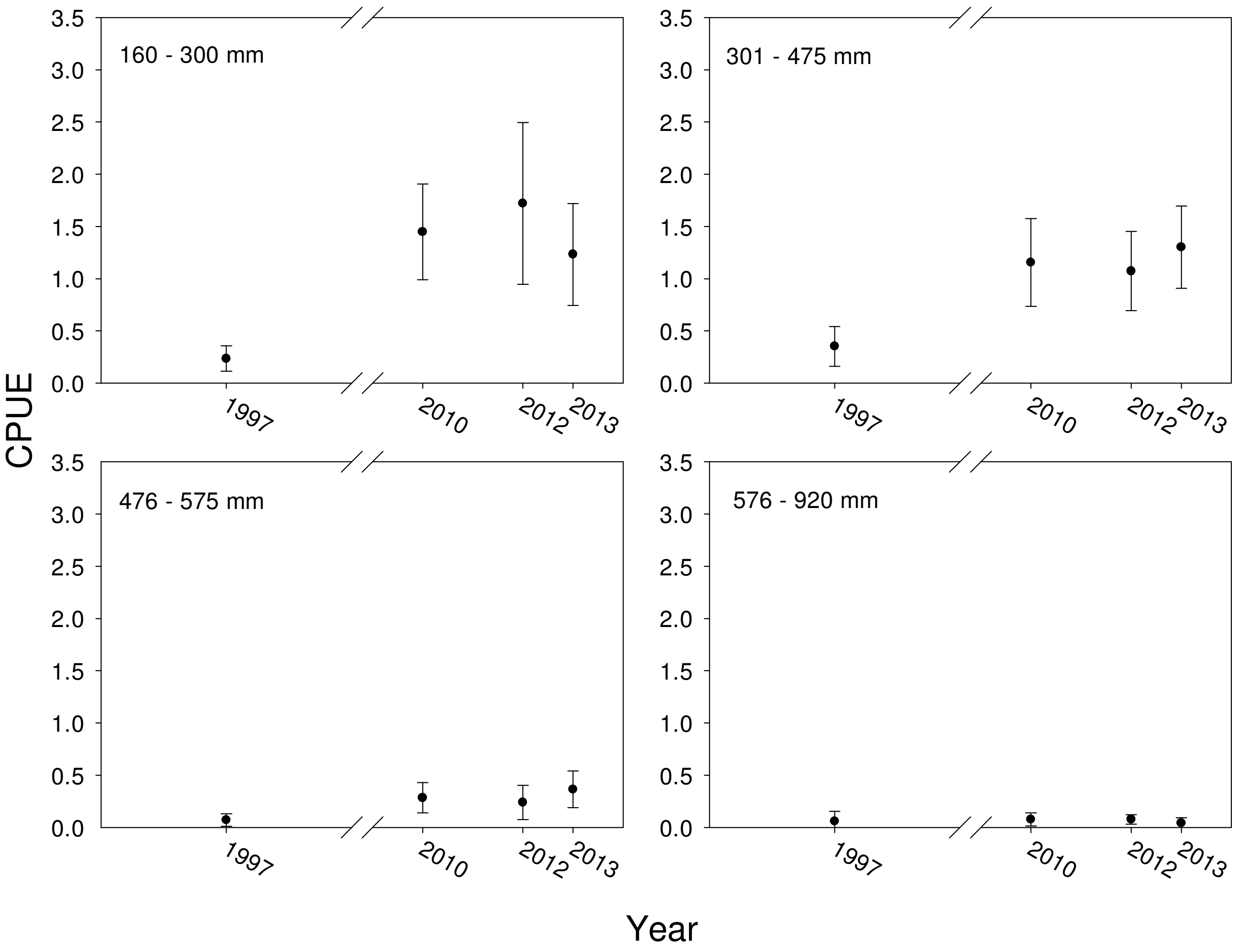

Figure 2.8. Lake trout catch per unit effort (CPUE) by length class in Lake Trout assessment netting from 1997 through 2013 in Yellowstone Lake, Yellowstone National Park. Error bars delineate 95% confidence intervals.

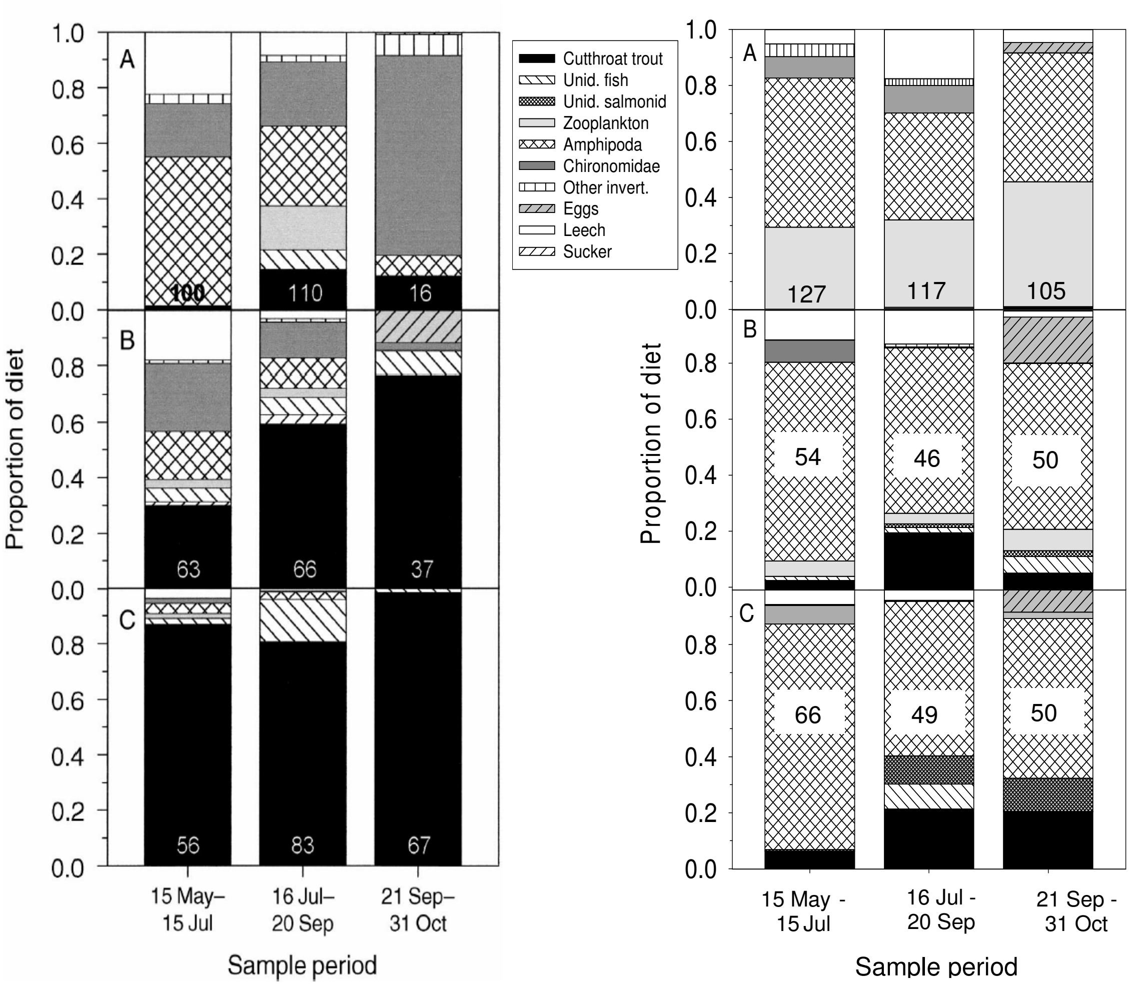

Figure 2.9. Mean proportion of Lake Trout diet by weight in 1996 – 1999 (left panel) and 2011 – 2013 (right panel) by age class (left panel: A 3 – 4, B 5 – 8, C 9 – 23; right panel: A 2 – 4, B 5 – 7, C 8 – 17) during three periods of thermal stratification. Sample sizes are indicated by numbers in bars. (Left panel reprinted from Ruzycki et al. [2003] with permission from Ecological Society of America).

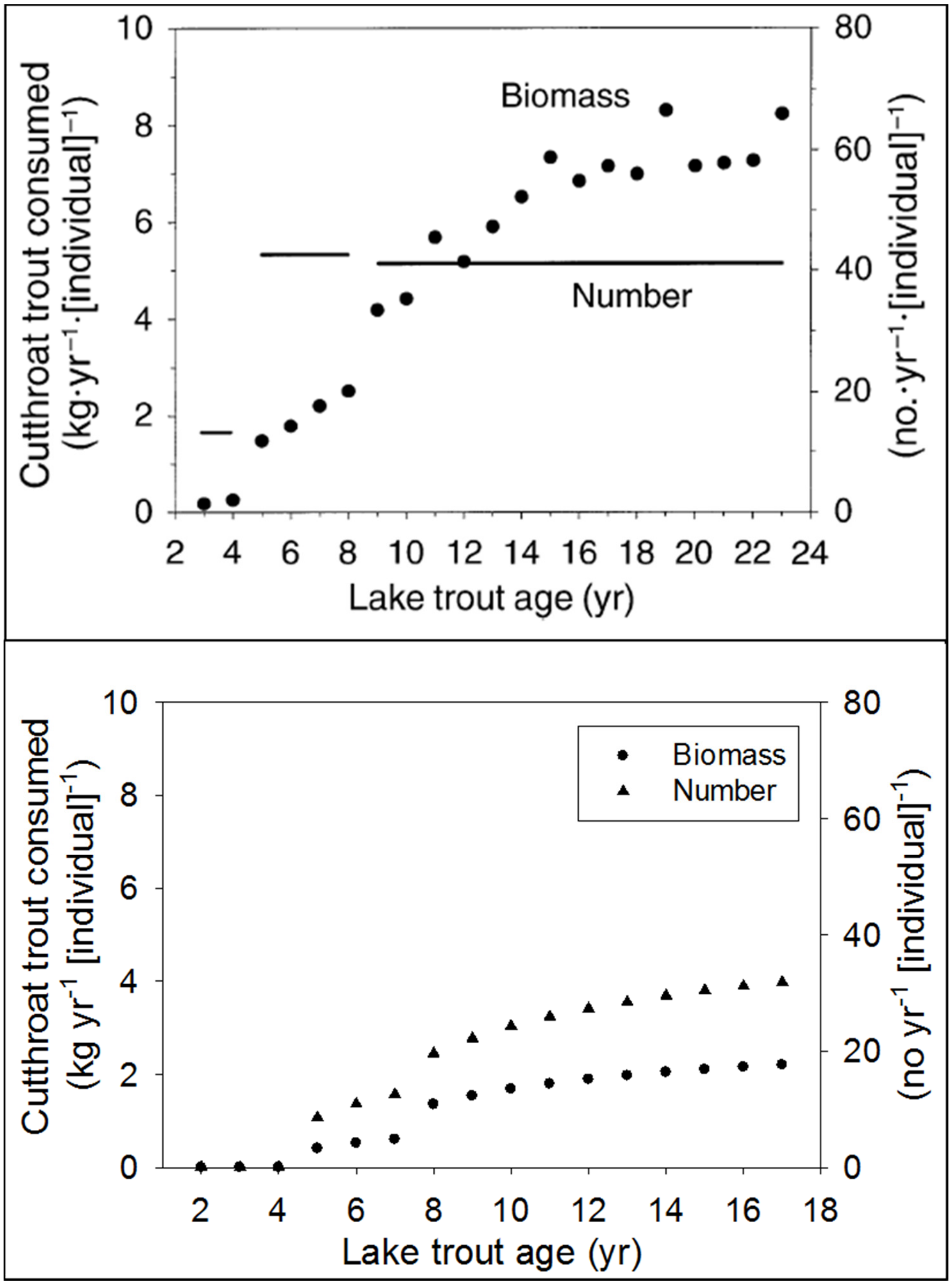

Figure 2.10. Per-capita consumption of Yellowstone Cutthroat Trout biomass (circles) and number (top panel: lines; bottom panel: triangles) by Lake Trout age in Yellowstone Lake, Yellowstone National Park, during 1996 –1999 (top panel) and 2011 – 2013 (bottom panel) estimated using bioenergetics models. Estimates for 2011 – 2013 include unidentified salmonids (see Methods). (Top panel reprinted from Ruzycki et al. [2003] with permission from Ecological Society of America).

References

Al-Chokhachy, R., M. Peacock, L. G. Heki, and G. Thiede. 2009. Evaluating the reintroduction potential of Lahonton cutthroat trout in Fallen Leaf Lake, California. North American Journal of Fisheries Management 29:1296-1313.

Baril, L. M., D. W. Smith, T. Drummer, and T. M. Koel. 2013. Implications of cutthroat trout declines for breeding ospreys and bald eagles at Yellowstone Lake. Journal of Raptor Research 17:234-235.

Beauchamp, D. A., M. W. Kershner, N. C. Overman, J. Rhydderch, J. Lin, and L. Hauser. 2006. Trophic interactions on nonnative lake trout and lake whitefish in the Flathead Lake foodweb. Report to the Confederated Salish-Kootenai Tribes.

Beauchamp, D. A., D. H. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Benson, N. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Service Fishery Research Report 56.

Bergum, D. J., K. A. Gunther, and L. M. Baril. In review. Impacts of Yellowstone cutthroat trout decline on mammals and birds in Yellowstone National Park.

Bronte, C. R., S. T. Schram, J. H. Slegeby, and B. L. Swanson. 1995. Density-independent survival of wild lake trout in the Apostle Islands area of Lake Superior. Journal of Great Lakes Research 21:246-252.

Bryan, S. D., C. A. Soupir, W. G. Duffy, and C. E. Freiburger. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. Journal of Freshwater Ecology 11:153-161.

Chipps, S. R., and J. E. Garvey. 2007. Assessment of diets and feeding patterns. Pages 473-514 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Cianco, J. E., M. A. Pascual, and D. A. Beauchamp. 2007. Energy density of Patagonian aquatic organisms and empirical predictions based on water content. Transactions of the American Fisheries Society 136:1415-1422.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:267-277.

Crait, J. R., and M. Ben-David. 2006. River otters in Yellowstone Lake depend on a declining cutthroat trout population. Journal of Mammalogy 87:485-494.

Crossman, E. J. 1995. Introduction of the lake trout (Salvelinus namaycush) in areas outside its native distribution: a review. Journal of Great Lakes Research 21:17-29.

Cucherousset, J., and J. Olden. 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36:215-230.

Cummins, K. W., and J.C. Wuycheck. 1971. Caloric equivalents and investigations in ecological energetics. Mitteilungen international Vereinigung fur theorische und angewandte Limnologie 18:1-151.

Dux, A. M., C. S. Guy, and W. A. Fredenberg. 2011. Spatiotemporal distribution and population characteristics of a nonnative lake trout population, with implications for suppression. North American Journal of Fisheries Management 31:187-196.

Eby, L. A., L. G. Rudstam, and J. F. Kitchell. 1995. Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1564-1571.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. Trends in Ecology and Evolution 21:576-584.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray, and B. S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences 108:1070-1075.

Elrod, J. H., and R. O'Gorman. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979-1987. Transactions of the American Fisheries Society 120:290-302.

Evans, D. O., and C. C. Willox. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycush*, by stocking of non-native stocks. Canadian Journal of Fisheries and Aquatic Sciences 48:134-147.

Feiner, Z. S., J. A. Rice, A. J. Bunch, and D. D. Aday. 2013. Trophic niche and diet overlap between invasive white perch and resident white bass in a southeastern reservoir. Transactions of the American Fisheries Society 142:912-919.

Gardner, W. S., T. F. Nalepa, W. A. Frez, E. A. Cichoki, and P. F. Landrum. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. Canadian Journalof Fisheries and Aquatic Sciences 42:1827-1832.

Garvey, J. E., and S. R. Chipps. 2012. Diets and energy flow. Pages 733 – 779 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries Techniques, 3rd edition. American Fisheries Society, Bethesda, MD.

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.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wsiconsin System, Sea Grant Institute,WISCU-T-97-001, Madison.

Hondorp, D. W., S. A. Pothoven, and S. B. Brandt. 2005. Influence of Diporeia density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. Transactions of the American Fisheries Society 134:588-601.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:127-143.

Jones, R.D., R. Andrascik, D.G. Carty, E.M. Colvard, R. Ewing, W.R.Gould, R.E. Gresswell, D.L. Mahoney, T. Olliff, and S.E. Relyea. 1990. Fishery and aquatic management program. U.S. Fish and Wildlife Service, Technical Report for 1989, Yellowstone National Park, Wyoming.

Juanes, F., J. Buckel, and F. S. Scharf. 2002. Feeding ecology of piscivorous fishes. Pages 267-283 *in* P. J. Hart and J. D. Reynolds, editors. Handbook of fish biology and fisheries. Blackwell, Hoboken, New Jersey.

Kaeding, L. R., and T. M. Koel. 2011. Age, growth, maturity, and fecundity of Yellowstone cutthroat trout. Northwest Science 85:431-444.

Kaplinski, M. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wyoming. Master's thesis, Northern Arizona University, Flagstaff.

Koel, T., P. Bigelow, P. Doepke, B. Ertel, and D. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries 30:10-19.

Koel, T.M., J. L. Arnold, P.E. Bigelow, P.D. Doepke, B.D. Ertel, and M.E. Ruhl. 2007. Yellowstone fisheries and aquatic sciences annual report, 2006. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2007-04. Available from www.nps.gov/yell/planyourvisit/fishreports.htm.

Koel, T. M., J. L. Arnold, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2012. Yellowstone fisheries and aquatic sciences annual report, 2011. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2012-03. Available from www.nps.gov/yell/planyourvisit/fishreports.htm.

Luecke, C., and D. Brandt. 1993. Estimating the energy density of Daphnid prey for use with rainbow trout bioenergetics models. Transactions of the American Fisheries Society 122:386-389.

Martin, N., and C. H. Olver. 1980. The lake Charr, Salvelinus namaycush. Pages 205-277 *in* E. Balon, editor. Charrs: salmonid fishes of the genus *Salvelinus*. Kluwer Boston, Inc., Hingham, Massachusetts.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western Lake Trout Woes. Fisheries 34:424-442.

Martinussen, P. A., G. Robertsen, and S. Einum. 2011. Density-dependent diet composition of juvenile Atlantic salmon (*Salmo salar*). Ecology of Freshwater Fish 20:384-392.

Matuszek, J. E., B. J. Shuter and J. M. Casselman. 1990. Changes in lake trout growth and abundance after introduction of cisco into Lake Opeongo, Ontario. Transactions of the American Fisheries Society 119:718-729.

McMahon, T. E., and D. H. Bennett. 1996. Walleye and northern pike: boost or bane to Northwest fisheries? Fisheries 21:6-13.

Minigawa, M., and E. Wada. 1984. Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. Geochimica et Cosmochimica Acta 48:1135-1140.

Morgan, L.A., W.C. Shanks III, D.A. Lovalvo, S.Y. Johnson, W.J. Stephenson, K.L. Pierce, S.S. Harlan, C.A. Finn, G. Lee, M. Webring, B. Schulze, J. Dühn, R. Sweeney, and L. Balistrieri. 2003. Exploration and discovery in Yellowstone Lake: results from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. Journal of Volcanology and Geothermal Research 12:221-242.

Pazzia, I., M., Trudel, M. Ridgeway, and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Science 59:1593-1605.

Plosila, D. S. 1977. Relationship of strain and size of stocking to survival of lake trout in Adirondack lakes. New York Fish and Game Journal 24:1-24. Post., D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Pothoven, S. A., T. F. Nalepa, P. J. Schneeberger, and S. B. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21:876-883.

Quist, M. C., C. S. Guy, R. J. Bernot, and J. L. Stephen. 2002. Efficiency of removing food items from walleyes using acrylic tubes. Journal of Freshwater Ecology 17:179-184.

Rand, P. S., and D. J. Stewart. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: a test of bioenergetics model prediction. Canadian Journal of Fisheries and Aquatic Sciences 55:307-317.

Richards, J. M., M. J. Hansen, C. R. Bronte, and S. P. Sitar. 2004. Recruitment dynamics of the 1971-1991 year-classes of lake trout in Michigan waters of Lake Superior. North American Journal of Fisheries Management 24:475-489.

Rose, K. A., J. H. Cowan Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293-327.

Roseman, E. F., J. S. Schaeffer, E. Bright, and D. G. Fielder. 2014. Angler-caught piscivore diets reflect fish community changes in Lake Huron. Transactions of the American Fisheries Society 143:1419-1433.

Rudstam, L. G., T. E. Brooking, S. D. Krueger, and J. R. Jackson. 2011. Analysis of compensatory responses in land-locked Alewives to Walleye predation: a tale of two lakes. Transactions of the American Fisheries Society 140:1587-1603.

Ruzycki, J. R., and D. A. Beauchamp. 1997. A bioenergetics modeling assessment of the lake trout impact in Yellowstone Lake. Pages 127-133 *in* R. E. Gresswel, P. Dwyer, and R. H. Hamre, editors. Wild trout VI symposium. Federation of Flyfishers, Fort Collins, Colorado.

Ruzycki, J. R., W. A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah-Idaho. Transactions of the American Fisheries Society 130:1175-1189.

Ruzycki, J. R., D. A. Beauchamp, and D. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Ruzycki, J. 2004. Impact of lake trout introductions on cutthroat trout of selected western lakes of the continental United States. Doctoral dissertation, Utah State University, Logan.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society 141:1191-1206.

Schoener, T. W. 1968. The anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704-726.

Spencer, C. N., B. R. McClelland and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. BioScience 41(1):14-21.

Syslo, J. M., C. S. Guy, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and T. M. Koel. 2011. Response of non-native lake trout (Salvelinus namaycush) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park. Canadian Journal of Fisheries and Aquatic Sciences 68:2132-2145.

Teisberg, J. F., M. A. Haroldson, C. C. Schwartz, K. A. Gunther, J. F. Fortin, and C. T. Robbins. 2014. Contrasting past and current numbers of bears visiting Yellowstone cutthroat trout streams. Journal of Wildlife Management 78:369-378.

Theriot, E. C., S. C. Fritz, and R. E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park, Wyoming, U.S.A. Arctic and Alpine Research 29:304-314.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45:759-771.

Tronstad, L., R. Hall, T. Koel, and K. Gerow. 2010. Introduced lake trout produced a four-level trophic cascade in Yellowstone Lake. Transactions of the American Fisheries Society 139:1536-1550.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer δ15N and δ13C and the trophic position of aquatic consumers. Ecology 80:1395-1404.

Wallace, R. K. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110:72-76.

CHAPTER THREE

RESPONSE OF YELLOWSTONE CUTTHROAT TROUT TO SUPPRESSION OF NON-NATIVE LAKE TROUT IN THE YELLOWSTONE LAKE ECOSYSTEM

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: John M. Syslo

Contributions: Conceived the study, collected and analyzed data, and wrote the manuscript.

Co-Author: Christopher S. Guy

Contributions: Assisted with study design and development of study questions, discussed the results and implications, and edited the manuscript.

Co-Author: Todd M. Koel

Contributions: Assisted with developing study questions, assisted with sampling, obtained funding, and commented on the manuscript.

Co-Author: Patricia E. Bigelow

Contributions: Assisted with developing study questions, assisted with sampling, and commented on the manuscript.

Co-Author: Philip D. Doepke

Contributions: Conducted sampling, conducted fish aging, and commented on the manuscript.

Co-Author: Brian D. Ertel

Contributions: Conducted sampling, conducted fish aging, and commented on the manuscript.

Contribution of Authors and Co-Authors - Continued

Co-Author: Jeffrey L. Arnold

Contributions: Conducted sampling and commented on the manuscript.

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Abstract

The mechanical removal of non-native lake trout is considered necessary for the persistence of native Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park. Lake trout removal began in 1998; however, the reduction in lake trout abundance required for Yellowstone cutthroat trout persistence is undetermined. We used statistical catch-at-age (SCA) models to estimate abundance and fishing mortality for lake trout from 1998 through 2013 and Yellowstone cutthroat trout from 1986 through 2013. We then tested for compensatory density-dependence by evaluating individual growth, weight, maturity, and pre-recruit survival as a function of abundance. Finally, we developed a simulation model for the lake trout-Yellowstone cutthroat trout predator-prey system to determine the probability of Yellowstone cutthroat trout persisting at levels specified by performance metrics given reductions in lake trout abundance. Yellowstone cutthroat trout abundance declined from 1.96 million fish in 1986 to 463 000 fish in 2000 and increased to 1.31 million fish in 2012. Lake trout abundance increased from 125 700 fish in 1998 to 746 350 fish in 2012 and declined to 607 700 fish in 2013. Yellowstone cutthroat trout weight and pre-recruit survival decreased with increasing abundance; however, growth in length and maturity were not related to abundance. Lake trout growth in length, weight, maturity, and pre-recruit survival did not vary as a function of abundance. Simulation model results were highly variable because of uncertainty in lake trout pre-recruit survival. Conservative estimates for required lake trout reductions were > 97% of 2013 abundance for a > 70% probability of Yellowstone cutthroat trout persistence at the performance metrics outlined in the

Native Fish Conservation Plan. Lake trout removal will likely reduce lake trout abundance and result in Yellowstone cutthroat trout recovery if the amount of fishing effort exerted in 2013 is maintained for at least 15 years.

Introduction

Non-native fishes have been implicated in the decline of native fish populations worldwide (Dudgeon et al. 2006; Jelks et al. 2008), causing the frequency and scale of eradication or removal projects to increase in recent years (Britton et al. 2011). Eradication is an unlikely outcome for many programs relying on mechanical removal in large or open ecosystems (Britton et al. 2011); therefore, removal programs are often implemented for the purpose of reducing negative effects on native fish populations. Reports of mechanical removal reversing declines in native fish populations are sparse (Weidel et al. 2007) and ecological complexity can make efficacy difficult to demonstrate or predict (Coggins et al. 2011; Franssen et al. 2014).

Following the implementation of removal efforts, native and non-native populations are typically monitored to determine whether responses in abundance are evident (Franssen et al. 2014). Although monitoring is a critical component of non-native fish removal programs, population models are required to determine the reduction in non-native fishes required for the persistence of native fish populations at levels specified by management objectives (Peterson et al. 2008; Pate et al. 2014). Models also provide the ability to demonstrate or predict efficacy while accounting for multiple factors affecting abundance, including density-dependent population regulation (i.e., compensation), environmental variation, and the effects of bycatch on native fish populations.

Compensation resulting from density-dependent population regulation contributes to the ability of fish populations to recover from decreased abundance (Rose et al. 2001). The pre-recruit life stage can exhibit strong density-dependence (Myers et al. 1999). However, density-dependence in recruited life-stages can also regulate population growth through changes in growth, maturity schedules, and body condition, which are related to fecundity (Trippel 1995; Lorenzen and Enberg 2002; Vicenzi et al. 2008). Compensatory density-dependence is pervasive among fish populations (Rose et al. 2001), but can be difficult to evaluate because of the requirement for long-term demographic data from periods with contrasting abundance (Johnston and Post 2009; Catalano and Allen 2011). Non-native predator introductions resulting in collapse of native prey populations can provide opportunities to study population dynamics at varying abundances.

The lake trout (*Salvelinus namaycush*) is an apex predator native to northern North America that has been introduced to 15 countries and extensively within the United States (Crossman 1995). Lake trout have been introduced into large lakes and reservoirs in eight western US states (Martinez at al. 2009), where their presence has led to declines in native salmonid populations (Fredenberg 2002; Vander Zanden et al. 2003; Koel et al. 2005) and subsequently altered ecosystem structure and function (Tronstad et al. 2010; Ellis et al. 2011). The negative effects demonstrated by non-native lake trout led to the initiation of several mechanical removal efforts in the Western US (Martinez et al 2009).

Lake trout were discovered in Yellowstone Lake, Yellowstone National Park, in 1994 (Kaeding et al. 1996) following an introduction during the mid-to-late 1980s (Munro et al. 2005). Yellowstone Lake contains the largest population of non-hybridized Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in the world (Gresswell and Varley 1988) and represents 89% of historical lacustrine habitat currently occupied by Yellowstone cutthroat trout (Gresswell 2009). The Yellowstone Cutthroat Trout is considered a keystone species in the greater Yellowstone Ecosystem, with 4 mammal species and 16 bird species documented consuming Yellowstone cutthroat trout (Bergum et al. in review). Yellowstone cutthroat trout abundance declined dramatically following the establishment of a self-sustaining lake trout population in Yellowstone Lake. For example, the number of Yellowstone Cutthroat Trout ascending Clear Creek to spawn declined from 55,000 individuals in 1987 to 500 in 2007 (Koel et al. 2012). The decline in Yellowstone Cutthroat Trout abundance resulted in a four-level trophic cascade (Tronstad et al. 2010) and disruption of trophic linkages to non-piscine predators throughout the Yellowstone Lake basin (Crait and Ben-David 2006; Baril et al. 2013; Tiesberg et al. 2014).

A lake trout removal program was initiated in rapid response to lake trout discovery with the purpose of decreasing predation on Yellowstone cutthroat trout (McIntyre 1995). The National Park Service established objectives for Yellowstone cutthroat trout recovery based on the relative abundance observed in long-term monitoring (Koel et al. 2011). The levels of mortality and fishing effort required to suppress lake trout population growth have been evaluated (Syslo et al. 2011); however, the reduction in lake trout abundance that would allow for the persistence of Yellowstone cutthroat trout at levels specified by management objectives has not been assessed. Increases in fishing effort in recent years to achieve targets necessary for lake trout decline (Syslo et al. 2011) have co-occurred with increasing Yellowstone cutthroat trout catch in gill nets, and bycatch could impede Yellowstone cutthroat trout recovery.

The objective of this study was to develop a model of the lake trout – Yellowstone cutthroat trout predator – prey system to determine the response of Yellowstone cutthroat trout to potential reductions in lake trout abundance. First, we used long-term monitoring and catch data to develop statistical catch-at-age (SCA) models to estimate abundance and fishery characteristics (i.e., catchability and mortality) for Yellowstone cutthroat trout and lake trout. Second, we evaluated the effects of abundance and environmental variation on population metrics (i.e., individual growth, body condition, maturity schedule, and pre-recruit survival) for Yellowstone cutthroat trout and lake trout. Third, we used the results of SCA modeling and population metric analyses to develop a simulation model of the lake trout – Yellowstone cutthroat trout system to assess the decrease in lake trout abundance required for Yellowstone cutthroat trout to increase to levels specified by management objectives.

Materials and Methods

Study Area

Yellowstone Lake is at an elevation of 2,357 m, has a surface area of 34,020 ha, 239 km of shoreline, a mean depth of 48.5 m, and a maximum depth of 133 m (Morgan et al. 2003). The lake is typically ice covered from mid-December until late May or early

June. Thermal stratification typically occurs in late July and can last into September, with summer surface water temperature reaching 17°C and a thermocline at about 15 m (Koel et al. 2007). The lake is categorized as oligo-mesotrophic (Theriot et al. 1997), with diatoms dominating the phytoplankton assemblage throughout the year (Benson 1961; Tronstad et al. 2010). The zooplankton community consists primarily of the rotifer *Conochilus unicornis*, Copepoda *Diaptomus* spp. and *Cyclops* spp., and Cladocera *Daphnia* spp. (Benson 1961). The fish assemblage in the lake consists of two native species, Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*), and three introduced species in addition to lake trout, longnose sucker (*Catostomus catostomus*), redside shiner (*Richardsonius balteatus*), and lake chub (*Couesius plumbeus*; Gresswell and Varley 1988).

Data Collection

Yellowstone Cutthroat Trout Assessment Netting.

Gill nets were used to assess the Yellowstone cutthroat trout population at 11 sites throughout the lake in mid-September from 1978 through 2013 (Kaeding and Koel 2011). At each site, five sinking experimental gill nets were set overnight perpendicular to shore. Nets were set about 100 m apart with the near-shore end about 1.5 m deep. Nets were 1.5-m deep and 38-m long, consisting of 7.6-m panels of 19-, 25-, 32-, 38-, and 51-mm bar measure. All fish caught in Yellowstone cutthroat trout assessment netting were measured for total length (TL; nearest mm). Weight (nearest g), sex, and maturity were recorded for lake trout and incidental Yellowstone cutthroat trout mortalities. Scales were collected from ten Yellowstone cutthroat trout per 1-cm length group for aging.

Lake Trout Assessment Netting**.** A sampling program to assess the lake trout population was developed in 1997 (Ruzycki et al. 2003). Sixteen sites throughout the lake were sampled during early August with a total of six experimental gill nets per site. At each site, a small-mesh and large-mesh sinking gill net were set overnight at each of three depth strata (epilimnion [3 - 10 m], metalimnion [10 - 30 m], and hypolimnion [> 40 m]). Small-mesh gill nets were 2-m deep and 76-m long, consisting of 13.7-m panels of 19-, 25-, 32-, 38-, 44-, and 51-mm bar measure. Large-mesh gill nets were 3.3-m deep and 68.6-m long, consisting of 13.7-m panels of 57-, 64-, 70-, 76-, and 89-mm bar measure. Gill nets were set perpendicular to shore and nets within a stratum were set parallel about 100 m apart. Lake trout assessment netting sampled inconsistent sites from 1997 through 2009 and a new protocol was developed in 2010 and implemented through 2013. Lake trout assessment netting from 2010 through 2013 was similar to the program developed in 1997 (i.e., net specifications and depth strata) and included 24 sites per year. All fish caught in lake trout assessment netting were measured for TL. Weight (nearest g), sex, maturity, and gonad weight were recorded for lake trout and incidental Yellowstone cutthroat trout mortalities. Sagittal otoliths were collected from ten lake trout per 1-cm length group for aging.

Recreational Fishery**.** A voluntary angler report (VAR) system was used to assess angler effort and success by water body in Yellowstone National Park from 1979 through

2013 (Jones et al. 1980; Koel et al. 2012). The VAR system provided total angler effort (i.e., angler hours), size-ranges of fish caught, number of fish caught, and proportion of catch harvested by species for Yellowstone Lake.

Lake Trout Suppression Netting. Sinking gill nets were used to remove lake trout from 1998 through 2013 from late May through late October. Suppression netting consisted of 25-, 32-, 38-, 44-, 51-, 57-, 64-, 70-. and 76-mm bar-measure gill nets targeting lake trout at depths greater than 20 m to avoid Yellowstone cutthroat trout bycatch. Nets were set shallower than 20 m at known spawning locations during peak spawning activity. Gill net soak time varied from 1 to 7 nights. Annual effort (1 unit = 100 m of net set for 1 night) was 1 449 units in 1998 and increased to 62 210 units in 2013. Trap nets were used from 2010 through 2013 to target lake trout (i.e., > 450 mm TL) from late May through August. Eight to ten trap nets were deployed at fixed locations throughout Yellowstone Lake each year. Trap net leads were 180-305 m long and 9-15-m deep with a 6- x 6- x 12-m pot (Koel et al. 2012). Trap net soak times varied from 1 to 4 nights.

Age Data. Lake trout captured from 1998 through 2013 were aged using sagittal otoliths (see Syslo et al. 2011 for description of aging methods). Yellowstone cutthroat trout captured from 1978 through 2013 were aged using scales (Kaeding and Koel 2011). Nine analysts aged Yellowstone cutthroat trout during this period and substantial errors are apparent among analysts (Kaeding and Koel 2011). However, only two analysts aged scales from 1986 through 2013 and both analysts aged the same subset of 193 scales collected in 2003. A correction factor was developed from the subset and ages assigned by analyst 1 (i.e., 1986 -1996) were corrected relative to ages assigned by analyst 2 (i.e., 1997 – 2013). Total lengths for fish caught in assessment netting, gill netting, and recreational fisheries were converted to ages for SCA modeling using year-specific age-length keys (Isely and Grabowski 2007).

Modeling Overview

Modeling consisted of steps to estimate abundance, evaluate population metrics as a function of abundance, and use these results to develop a simulation model for the predator-prey system. Statistical catch-at-age analysis (SCA) models developed from catch data were used to estimate abundance and fishing mortality for Yellowstone cutthroat trout and lake trout. Population metrics (i.e., growth in length, weight, maturity, and pre-recruit survival) for Yellowstone cutthroat trout and lake trout were evaluated as functions of abundance estimated from SCA models. The results from SCA modeling and population metric analyses were used to develop population models for lake trout and Yellowstone cutthroat trout to assess the decrease in lake trout abundance required for Yellowstone cutthroat trout to increase to levels specified by management objectives.

Abundance (SCA Modeling)

Statistical catch-at-age analysis (SCA) was used to estimate abundance and fishing mortality for the Yellowstone cutthroat trout and lake trout populations through time. The SCA model for Yellowstone cutthroat trout was estimated for 1986 through 2013 because consistent age data (see above) existed for the period. The Yellowstone cutthroat trout SCA model included ages 1 – 7. Age 7 was included as an age-class containing fish age 7 and greater. The SCA model for lake trout was estimated for 1998 (i.e., the first year with substantial suppression netting effort) through 2013. The lake trout SCA model included ages 2-17. Recreational fishing was an important source of catch-at-age data for the Yellowstone cutthroat trout population. Recreational fishing was assumed to represent a negligible portion of mortality for lake trout.

The SCA model for Yellowstone cutthroat trout included data from three sources: Yellowstone cutthroat trout assessment netting (1986 – 2013), recreational fishing (1986 – 2013), and lake trout removal netting (1998 – 2013). We assumed a mortality rate of 100% for all Yellowstone cutthroat trout caught in gill nets (i.e., we assumed released fish did not survive). Lake trout assessment netting was inconsistent through time (see above); therefore, the lake trout SCA model only included data from lake trout removal netting. Lake trout catch from trap nets and gill nets were pooled. Total effort was obtained for each year as the pooled catch among gill nets and trap nets divided by gill net catch per unit effort (CPUE; Quinn and Deriso 1999).

Statistical catch-at-age analysis consists of the simultaneous estimation of a population model that projects abundances at age and a model that predicts age-specific harvest. Abundance at age was computed using an exponential equation (Table 3.1 equation 1). Annual recruitment ($N_{y,1}$) and abundance in the first year ($N_{1986,a}$ for Yellowstone cutthroat trout or $N_{1998,a}$ for lake trout) were estimated as parameters.

Total instantaneous mortality was partitioned into instantaneous natural and instantaneous fishing mortality (Table 3.1 equation 2). Instantaneous natural mortality

(*M*) was 0.99 for ages 1 and 2 Yellowstone cutthroat trout and 0.74 for Yellowstone cutthroat trout greater than age 2 (Stapp and Hayward 2002). For age-2 lake trout, *M* was assumed to equal the estimate for age-2 lake trout in Lake Superior (0.25; Sitar et al. 1999). For lake trout greater than age 2, *M* was estimated using Pauly's equation (Pauly 1980). The equation predicted $M = 0.16$ from von Bertalanffy growth parameters (see below) and a mean annual environmental water temperature of 5.1°C.

Instantaneous fishing mortality (*F*) for Yellowstone cutthroat trout was separated into gill net and recreational components. Recreational fishing was the only source of fishing mortality before 1998. Fishing mortality was the sum of gill net and recreational mortality from 1998 through 2013 (Table 3.1 equation 3). For lake trout, gill netting was the only mortality source. Fishing mortalities were a function of fishing effort, constant catchability, and age-specific fishery selectivity (Table 3.1 equations 4 and 5). Recreational fishing mortality for Yellowstone cutthroat trout included VAR estimates for the proportion of catch that was harvested (*h*). Estimates of *h* included 3.3% hooking mortality for Yellowstone cutthroat trout that were caught and released (Schill et al. 1986; Hunsaker et al. 1970). Age-specific selectivity for each fishery was modeled as a logistic function of age (Table 3.1 equation 6; Haddon 2011).

Predicted catch-at-age for gill net and recreational fisheries was estimated using the Baranov catch equation (Table 3.1 equation 7). Predicted CPUE for Yellowstone cutthroat trout in assessment netting was calculated from age-specific abundance, age-specific survey selectivity, and survey catchability (Table 3.1 equation 8). Predicted age proportions for each fishery were calculated from age-specific abundance, age-specific fishery selectivity, and fishery catchability (Table 3.1 equation 9).

Parameter estimates for SCA models were obtained by maximum likelihood estimation using AD Model Builder (Fournier et al. 2012). Parameters were estimated on the log scale by minimizing a negative log-likelihood function (Table 3.1 equation 10) where λ_f is an emphasis factor used to weight each likelihood component (L_f). Fishery harvest and assessment netting CPUE followed a lognormal distribution (Table 3.1 equation 11) and proportion by age followed a multinomial distribution (Table 3.1 equation 12; Linton et al. 2007). Two likelihood components were included for the lake trout model: a lognormal likelihood was used for gill-net catch and a multinomial likelihood was used for proportion by age in the gill net catch. The Yellowstone cutthroat trout model included six likelihood components: three lognormal likelihoods (i.e., one each for gill-net and recreational fishery catch and one for assessment netting catch per unit effort) and three multinomial likelihoods (i.e., one each for gill-net and recreational fishery proportion at age and one for assessment netting proportion at age). Effective sample sizes for multinomial distributions were the number of fish aged each year up to a maximum of 200 fish (Sitar et al. 1999). Emphasis factors (i.e., λ_f) were set to 1.0 (Linton et al. 2007) and variances for lognormal likelihood components were estimated during model fitting. Predicted lake trout catch poorly fit observed values with $\lambda = 1.0$; therefore, the emphasis factor was increased to 10 to improve model fit. Ninety-five percent confidence intervals for abundance and fishing mortality were approximated using asymptotic standard errors (i.e., estimate ± 1.96 SE).

Population Metrics

Growth. A von Bertalanffy growth model was used to evaluate changes in mean length-at-age as a function of abundance for Yellowstone cutthroat trout (Lorenzen and Enberg 2002). The model predicted mean length of age group *a* in year *y* ($L_{\mathrm{pred},a,y}$) from observed mean length of the cohort in the previous year ($L_{\mathrm{obs},a-1,y-1}$):

$$L_{\mathrm{pred},a,y} = L_{\infty A} - \left(L_{\infty A} - L_{\mathrm{obs},a-1,y-1}\right) \cdot \exp(-K),$$

where $L_{\infty \mathrm{A}}$ is the asymptotic length at the average observed abundance *A* during the year (see below) and *K* is the growth coefficient. Estimates of $L_{\infty \mathrm{A}}$ were a function of the limiting asymptotic length $L_{\infty \mathrm{L}}$ (i.e., maximum length as *A* approaches 0), the competition coefficient *g*, and average abundance during the year (*y*-1 to *y*):

$$L_{\infty A} = L_{\infty L} - g \cdot \left(\frac{A_{y-1}+A_y}{2}\right).$$

The model was fit to observed mean length at age by minimizing the sum of squares (SSQ):

$$SSQ = \sum_a \sum_y \left(L_{obs,a,y} - L_{pred,a,y}\right)^2.$$

The model above was compared to a model without the coefficient *g* (i.e., constant L_∞) using Akaikie’s Information Criterion (AIC; Burnham and Anderson 2002).

Lake trout growth was not evaluated using the above approach because of several years with missing data. Lake trout length-at-capture was evaluated as a function of abundance using a separate linear regression for each age (ages 2 – 13). Models with an intercept coefficient only were compared to models with a coefficient for abundance using AIC. A von Bertalanffy growth model (Isely and Grabowski 2007) was fit to lake trout length-at-age for all years pooled for use in simulation modeling (see below).

Weight. Weight was evaluated as a function of TL and abundance using linear regressions for log_{10}-transformed weight and length data. Models with coefficients for length only were compared to models that included coefficients for abundance using AIC. Interactions for TL by abundance were included to determine whether covariates changed the slope of the weight-length model.

Maturity. Maturity was evaluated as a function of TL and abundance using logistic regression for binary response data. Interactions for TL by abundance were included to determine whether covariates changed the shape of the length-maturity curve.

Pre-recruit Survival. Abundance estimates were used to estimate age-0 survival for Yellowstone cutthroat trout. Age-0 survival (S_0) was estimated as the abundance of age-1 fish in year y divided by egg abundance the previous year (y – 1). Egg abundance was estimated from the abundance of spawning fish and per-capita fecundity. Abundance of spawning females in each age class was estimated as the product of age-specific abundance, age-specific probability of maturity, proportion of mature fish spawning each year, and 0.5 (i.e., a 50:50 sex ratio was assumed). Thirty-four percent of mature fish were assumed to spawn every year with the remainder spawning in alternate years (Stapp and Hayward 2002). Thus, the probability of a mature fish spawning in any given year was $0.5 \cdot (1-0.34) + 0.34 = 0.67$. Age specific fecundity was estimated as the product of weight at age and weight-specific fecundity (2 633 eggs/kg; Jones et al. 1985).

Estimates of S_0 in year *y* were examined as a function of egg abundance in the previous year using linear regression for ln-transformed data. Yellowstone cutthroat trout recruitment was previously demonstrated to be a function of lake water level (Bulkley and Bensen 1962) and other climate variables related to lake water level (Kaeding 2010). Therefore, peak annual discharge (cubic meters per second; CMS) at the Yellowstone Lake outlet during the year of spawning (i.e., *y* -1) was included as a covariate in models evaluating pre-recruit survival as a function of egg abundance. A model with only an intercept coefficient (i.e., mean) was compared to a linear model with a coefficient for egg abundance, a linear model with a coefficient for peak discharge, and a linear model with coefficients for both egg abundance and peak discharge. A model with an interaction between egg abundance and peak discharge was also considered. Models were compared using Akaike's Information Criterion adjusted for small sample size (AIC_C; Burnham and Anderson 2002).

Lake trout pre-recruit survival was calculated as recruitment of age-2 fish in year *y* divided by egg abundance during year *y*-2. Egg abundance was estimated similarly to Yellowstone cutthroat trout, except lake trout were assumed to spawn every year. Pre-recruit survival in year *y* was examined as a function of egg abundance during the year of spawning (i.e., *y*-2) using linear regression. A model with only an intercept coefficient was compared to a linear model with a coefficient for egg abundance using AIC_C.

Simulation Model

Overview. A model of the lake trout – Yellowstone cutthroat trout system was developed to assess the response to continued suppression netting in Yellowstone Lake. The overall model included a lake trout population submodel and a Yellowstone cutthroat trout submodel that were linked through predation of Yellowstone cutthroat trout by lake trout. Leslie matrix models (Caswell 2001) were used to project lake trout and Yellowstone cutthroat trout populations with an annual time step. Models were constructed using information obtained from SCA models, analyses of population metrics, and literature values. Starting abundances (i.e., 2013 abundance estimates) and fishing mortality parameters (i.e., catchability and selectivity) were obtained from SCA models. Population metric submodels (i.e., growth in length, weight, maturity, and pre-recruit survival) were included in the simulation model and were a function of abundance and environmental variation (i.e., peak discharge) when results indicated the covariates influenced population metric values (see below).

Lake Trout Model. The lake trout Leslie matrix contained survival and fertility rates for ages 1 to 20 (Figure 3.1; Table 3.3 equation 1). Lake trout can live longer than 20 years; therefore, the age-20 was model as an age 20+ stage. The subdiagonal contained age-specific survival rates (*S*, Table 3.3 equation 2) and the top row contained age-specific fertility rates (*R*; Table 3.3 equation 3). Survival for fish recruited to the gear (i.e., ages 2 and greater) was a function of instantaneous natural and fishing mortality (Table 3.3 equation 2). Instantaneous natural mortality (*M*) was estimated for ages 2 – 20 using Pauly's equation (Pauly 1980) with von Bertalanffy growth parameters K and L_∞ with an annual water temperature of 5.1°C (Table 3.3 equation 4). Age-specific instantaneous fishing mortality (F) was a function of gill-net effort (E), catchability (q), and age-specific fishery selectivity (*sel*; Table 3.3 equation 5). Fishery selectivity was a logistic function of age (Table 3.3 equation 6). Estimates of pre-recruit (i.e., age 0 -1) survival were generated from a beta distribution using the estimated value (0.005 ± 0.003; SD). Length-at-age was predicted using a von Bertalanffy growth model (Table 3.3 equation 7) and age-specific fertility rate was a function of fecundity (Table 3.3 equation 8; Syslo et al. 2011) and maturity (Table 3.3 equation 9) at length. Parameters for the von Bertalanffy growth model and the model predicting fecundity-at-length were generated from multivariate normal distributions using observed variance-covariance matrices. The lake trout matrix was based on a pre-breeding census; therefore, fertility included pre-recruit survival (Table 3.3 equation 3). The matrix element for age-1 survival was set to 1.0 because S_R included survival for age-0 and age-1 fish. Fertility was multiplied by 0.5 to account for half of offspring being female (Table 3.3 equation 3).

Yellowstone Cutthroat Trout Model. A multi-state transition matrix (Caswell 2001) was used for Yellowstone cutthroat trout (Figure 3.1; Table 3.5 equation 1) to account for different mortality rates for nonspawning fish that remain in the lake and spawning fish that migrate to tributary streams (Stapp and Hayward 2002). The Yellowstone cutthroat trout transition matrix included a post-breeding census with age-0 fish as a distinct age class. The model was female based and included Yellowstone cutthroat trout age classes from 0 to 9. The ninth age class was modeled as an age 9+ stage. The top-left subdiagonal included the probability of survival of age-0 fish (S_0; Table 3.5 equation 2) and the probability of surviving and remaining in the nonspawning segment of the population (S_L; Table 3.5 equation 3) for ages 1 – 9+. The bottom-left subdiagonal included the probability of surviving and transitioning from the nonspawning to spawning segment of the population (G_L; Table 3.5 equation 4). The bottom-right subdiagonal included the probability of surviving and remaining in the spawning segment of the population (G_S; Table 3.5 equation 5) and the top-right subdiagonal included the probability of surviving and transitioning from the spawning to nonspawning segment of the population (S_S; Table 3.5 equation 6). The first row included the fertility rates (R; Table 3.5 equation 7) for fish in the spawning segment of the population.

Matrix elements including the probability of surviving and transitioning among nonspawning and spawning population segments were a function of age-specific survival and probability of spawning (Table 3.5 equations 3 - 6). The probability of spawning was the product of the proportion mature at age (m) and the proportion of mature fish spawning in a given year (V_S). Maturity at age was estimated using logistic regression coefficients from the model predicting maturity as a function of total length (TL)-at-age and abundance (Table 3.5 equation 8). Total length-at-age was estimated from the incremental von Bertalanffy growth model (Table 3.5 equation 9) with length at age 1 generated from a normal distribution given the mean and standard deviation from 1986 through 2013 (198 ± 16 mm). Parameters for models predicting m and TL were generated from multivariate normal distributions using the estimated variance-covariance matrices. The proportion of mature Yellowstone cutthroat trout spawning in consecutive years (V_{SS}) was assumed to be 0.34 (Stapp and Hayward 2002). The remainder of mature fish were assumed to spawn in alternate years (Stapp and Hayward 2002); therefore, the proportion of mature fish transitioning from the nonspawning to the spawning segment of the population in any given year (V_S) was 0.5. Values for V_S and V_{SS} were constant among simulations.

Age-specific survival rates were calculated from the sum of instantaneous natural (M) and fishing (F) mortality components (Table 3.5 equations 3 - 6). The estimate of M used for age-1 and age-2 fish in the SCA model (i.e., $M = 0.99$) caused simulated Yellowstone cutthroat trout abundance to decline when lake trout abundance was set to zero, indicating the estimate was excessive when combined with lake trout predation. Therefore, M for ages 1 and 2 was estimated using Pauly's equation (Pauly 1980) with von Bertalanffy growth parameters K and L_∞ and a mean annual water temperature of 7°C (Table 3.5 equation 10). The value of M used in SCA modeling for ages 3 and greater (i.e., 0.74) was used in the simulation model.

Calculation of age-specific survival required separate estimates of natural mortality for spawning fish that migrated to streams and nonspawning fish that remained in the lake throughout the year. Survival of Yellowstone cutthroat trout in spawning tributaries was previously estimated ($S_t = 0.87$; Gresswell 1995). For each simulation, S_t was generated from a beta distribution using the popbio package in R (Stubben and Milligan 2007) using a CV determined from previous catch curve analyses ($CV = 0.09$; J. M. Syslo, unpublished). Instantaneous natural mortality in spawning streams (M_S) was calculated as –ln(S_t). Instantaneous natural mortality in spawning streams was assumed to occur during 15 days (Stapp and Hayward 2002). Instantaneous natural mortality in the lake (M_L) was assumed to occur during the remaining 350 days of the year. A daily rate of M_L was calculated for each age class by partitioning M according to the proportion of spawning fish in each age class by solving equation 11 (Table 3.5; Stapp and Hayward 2002). For fish remaining in or transitioning to the nonspawning segment of the population, instantaneous natural mortality was $M_L \cdot 365$ (Table 3.5 equations 3 and 6). For fish remaining in or transitioning to the spawning segment of the population, instantaneous natural mortality was $M_L \cdot 350 + M_S$ (Table 3.5 equations 4 and 5).

Instantaneous fishing mortality from gill net (F_G) and recreational (F_R) fisheries was a function of effort (E), catchability (q), and age-specific selectivity (*sel*; Table 3.5 equation 12). Annual gill net effort (E_G) was assumed to be implemented without error. Annual recreational fishing effort (E_R) was generated from a normal distribution using the mean and SD (178 090 ± 33 782 angler hours) during 2001 – 2013, a period with catch and release regulations for Yellowstone cutthroat trout. Catchability values were generated on the ln scale using normal distributions with mean and SD obtained from SCA models. Age-specific selectivities (*sel*) were modeled as a logistic function of age (Table 3.5 equation 13) with parameters generated from a multivariate normal distribution using variance-covariance matrices from SCA models.

Fertility (R) was the product of age-specific abundance in the spawning segment of the population (n_S), age-specific weight (W), and weight-specific fecundity (*fec*; Table 3.5 equation 7). Weight-at-age was predicted from length-at-age using multiple linear regression coefficients for the model predicting weight as a function of TL and abundance (Table 3.5 equation 14). Parameters for the model predicting *W* were obtained from a multivariate normal distribution using the observed variance-covariance matrices. Weight-specific fecundity was 2 633 eggs/kg with SD = 144 eggs/kg (Jones et al. 1985). Fecundity was generated from a stretch beta distribution using the popbio package (Stubben and Milligan 2007). Fertilities were multiplied by 0.5 because half of offspring were assumed to be female (Table 3.5 equation 7).

Age-0 survival was generated as a linear function of ln–transformed egg abundance, annual peak discharge, and process error (ε; Table 3.5 equation 2). Process error for S_0 was generated at each time step from a normal distribution with a mean of 0 and *SD* equal to the residual standard deviation estimated during model fitting (*SD* = 0.28). Parameters for the model estimating S_0 were obtained from a multivariate normal distribution using the observed variance-covariance matrix. Values for peak discharge were generated by year within simulations using truncated normal distributions to restrict values between the observed minimum and maximum (peak discharge did not exhibit temporal patterns or autocorrelation). Mean peak discharge was 142 cubic meters per second (CMS; SD = 49) with a minimum of 51 and a maximum of 282. Egg abundance was calculated by summing the product of age-specific spawner abundance, weight at age, and weight-specific fecundity (Table 3.5 equation 15).

<u>Predation.</u> Per-capita consumption of Yellowstone cutthroat trout by lake trout was estimated during 1996-1999 (Ruzycki et al. 2003) and 2011-2013 (Chapter 2). Sparse consumption estimates prevented the estimation of a functional response.

Therefore, simulated per-capita predation varied between high and low rates depending on the ratio of Yellowstone cutthroat trout abundance to abundance of predatory lake trout (i.e., age 5 and greater). The threshold for high versus low consumption rates was determined by examining the ratio of Yellowstone cutthroat trout to lake trout abundance through time. A clear delineation indicated the ratio was below 17 Yellowstone cutthroat trout per lake trout during the 2000s. Therefore, consumption rates estimated from 1996-1999 were considered high and occurred when the abundance of Yellowstone cutthroat trout per lake trout was 17 or greater. Consumption rates estimated during 2011-2013 were considered low and occurred when the abundance of Yellowstone cutthroat trout per predatory lake trout was less than 17. Estimates of age-specific per-capita consumption (con_a) by lake trout were adjusted to account for mortality of lake trout occurring through the year (Table A.1; Hanson et al. 1997).

Age-specific per-capita consumption was multiplied by age-specific lake trout abundance and summed among ages to calculate total consumption of Yellowstone cutthroat trout. Total consumption was multiplied by the proportion of total consumption composed of each Yellowstone cutthroat trout age class (P_a) to estimate total consumption for each Yellowstone cutthroat trout age class (C_a; Table 3.3 equation 10). Age-0 Yellowstone cutthroat trout composed 0.36 of total consumption by lake trout, age-1 composed 0.35, age-2 composed 0.26 and age-3 composed 0.03. Age-specific consumption was subtracted from age-specific abundance (Table 3.5 equation 16) following multiplication of the abundance vectors (**n**) with the transition matrices (**A**) at each time step. Values for con_a and P_a were constant among simulations.

Starting Abundance. Starting abundances for Yellowstone cutthroat trout and lake trout were generated from normal distributions using means and SDs estimated for 2013 from the SCA models. Starting age structures were equal to the age structures for 2013 from the SCA models and were constant among simulations.

Simulations. The first objective was to determine the response of lake trout abundance to varying levels of fishing effort. Specifically, we were interested in the level of fishing effort required to maintain constant lake trout abundance (i.e., population growth rate equal to replacement) and whether lake trout abundance would decline with continued implementation of the maximum fishing effort observed in Yellowstone Lake (i.e., 63 000 units in 2013 [including trap nets]; see above). To determine the level of fishing effort required for constant lake trout abundance, levels of fishing effort varying from 1 000 to 63 000 units were simulated in increments of 500 units. Each level of effort was simulated 1 000 times and the median abundance among simulations was recorded at each time step through 30 years. Median abundances were averaged from year 21 through 30 and the average was compared to the starting abundance. The level of fishing effort resulting in the average abundance from year 21 through 30 being equal to the starting abundance was considered the amount of effort required for lake trout population growth rate to equal replacement (subsequently referred to as “maintenance level”). The second objective was to determine the response of the Yellowstone cutthroat trout population to continued suppression netting. The model was used to determine whether Yellowstone cutthroat trout abundance would increase with continued implementation of 63 000 units of effort per year.

Yellowstone National Park has defined performance metrics for Yellowstone cutthroat trout in Yellowstone Lake (Koel et al. 2011). The primary performance metric is to increase Yellowstone cutthroat trout to 42 fish per 100-m net night in assessment netting. The National Park Service also set a lesser performance metric of 25 Yellowstone cutthroat trout per 100-m net night if the primary metric is unrealistic given monetary and logistic constraints. The final objective for the simulation model was to determine the likelihood of achieving performance metrics for Yellowstone cutthroat trout given reductions in lake trout abundance achieved through the continued implementation of fishing effort. The level of fishing effort required to maintain constant lake trout abundance was less than 63 000 units (see Results). Therefore, we evaluated the probability of achieving performance metrics given scenarios where lake trout abundance was reduced through the implementation of 63 000 units of effort per year. Scenarios included the implementation of 63 000 units of effort per year for 0 to 20 years, with effort decreased to the maintenance level until year 30. For example, a scenario could consist of 63 000 units of effort for 10 years followed by the maintenance level for 20 years. Each scenario was simulated 1 000 times, and Yellowstone cutthroat trout CPUE (Table 3.5 equation 17) and abundance were recorded at each time step from year 0 to year 30. The probability of achieving performance metrics was calculated at each time step as the proportion of simulations with CPUE equal to or exceeding performance metric values. The proportion of simulations with Yellowstone cutthroat CPUE equal to or exceeding performance metrics and the median lake trout abundance were each averaged from year 21 through 30. The proportion of lake trout remaining was calculated for each scenario as the median abundance divided by 2013 abundance.

Results

Abundance (SCA Modeling)

SCA model parameters were successfully estimated for Yellowstone cutthroat trout (Table B.1) and lake trout (Table B.2). For Yellowstone cutthroat trout, predicted values for catch and age composition closely matched observed values for all fisheries (Figure 3.2). For lake trout, predicted and observed catch values closely matched for the gill-net fishery (Figure 3.3). Predicted and observed age composition matched closely for lake trout in the gill-net fishery (Figure 3.3) despite the emphasis factor being reduced relative to the emphasis factor for total catch.

Yellowstone cutthroat trout abundance was estimated at 1.96 million (1.64 – 2.28 million; 95% CI) in 1986 and declined to 461 000 (396 000 – 527 000) in 2003 (Figure 3.4). Abundance increased to 1.31 million in 2012 (1.01 million – 1.62 million; 95% CI), and declined to 932 000 in 2013 (680 000 – 1.18 million; Figure 3.4). Estimates of fully-selected recreational fishing mortality varied from 0.71 to 0.97 from 1986 through 1991 and declined to 0.22 – 0.38 during the 2000s (Figure 3.4). Fully-selected mortality from the gill-net fishery increased from 0.011 (0.009 – 0.014; 95% CI) in 1998 to 0.489 (0.375 – 0.604; 95% CI) in 2013 (Figure 3.4). Yellowstone cutthroat trout were not fully selected to the gill-net fishery, recreational fishery, or assessment netting until age 7 (Figure 3.5).

Lake trout abundance increased from 125 700 (108 326 – 143 074; 95% CI) in 1998 to 746 350 (595 016 – 897 684) in 2012 and declined to 607 700 (449 367 – 766 033) in 2013 (Figure 3.6). Fully selected instantaneous fishing mortality increased from 0.024 (0.021 -0.027; 95% CI) in 1998 to 1.11 (0.972 -1.248) in 2013 (Figure 3.6). Lake trout were fully selected to the fishery at age 4 (Figure 3.7).

Population Metrics

Growth. Yellowstone cutthroat trout mean length-at-age was not related to Yellowstone cutthroat trout abundance. The null model with a single L_∞ among annual abundance values had slightly greater AIC support than the model relating L_∞ to abundance with the growth coefficient g (Table 3.6), indicating abundance did not explain variation in mean length-at-age (Figure 3.8). For the null model, L_∞ was 647 (1.16; SE) and K was 0.18 (0.0007; SE).

Regressions of lake trout length at age as a function of lake trout abundance yielded mixed results. An abundance effect was supported for 6 of the 12 ages; however, a negative relationship between length-at-age and abundance only existed for age 2 (Table 3.7). Models for length-at-age as a function of abundance were characterized by low r^2 values (Table 3.7), indicating little variation was explained by abundance. A von Bertanlaffy growth model was fit to all observations from 1998 through 2013 for use in simulation modeling (see below), yielding $L_\infty = 864$ (12.61; SE), $K = 0.13$ (0.005), and $t_0 = -0.68$ (0.08).

Weight. Yellowstone cutthroat trout weight was best described by the model with main effects for TL and Yellowstone cutthroat trout abundance with an interaction effect (Table 3.6; $\beta_0 = -5.27$; $\beta_{\mathrm{TL}} = 3.11$; $\beta_{\mathrm{abundance}} = 1.94 \times 10^{-7}$; $\beta_{\mathrm{TL\ x\ abundance}} = -8.95 \times 10^{-8}$; df = 15 644). Total length explained the majority of variation in weight ($r^2 = 0.98$) and declines in weight-at-length given abundance increased with greater TL (Figure 3.9). For a 200-mm Yellowstone cutthroat trout, predicted weight declined from 74 g at the lowest abundance to 71 g at the greatest abundance, a decrease of 4% (Figure 3.9). For a 600-mm Yellowstone cutthroat trout, predicted weight declined from 2 153 g at the lowest abundance to 1 793 g at the greatest abundance, a decrease of 17% (Figure 3.9).

The best-supported model describing lake trout weight included main effects for TL and lake trout abundance with an interaction between abundance and TL (Table 3.8; $\beta_0 = -5.12$; $\beta_{\mathrm{TL}} = 3.04$; $\beta_{\mathrm{abundance}} = -3.06 \times 10^{-7}$; $\beta_{\mathrm{TL\ x\ abundance}} = 1.22 \times 10^{-7}$; df = 11 963). Total length explained the majority of variation in weight ($r^2 = 0.98$) and the effect of abundance on weight varied with lake trout TL (Figure 3.9). For a 200-mm lake trout, predicted weight was 75 g at the lowest abundance and 72 g at the greatest abundance, a decline of 4% (Figure 3.9). Weight was constant at varying abundance for 400-mm lake trout and increased with abundance for 600-mm lake trout (Figure 3.9). For 600-mm lake trout, weight was 2 160 g at the lowest abundance and 2 270 g at the greatest abundance, an increase of 5%. Given the counterintuitive effect of abundance on lake trout weight, the model with TL as the only covariate was used to predict weight in the simulation model (see below).

Maturity. The best supported model describing maturity for male Yellowstone cutthroat trout included main effects for TL and Yellowstone cutthroat trout abundance (Table 3.6; $\beta_0 = -11.15$; $\beta_{TL} = 0.032$; $\beta_{abundance} = -2.24 \times 10^{-7}$; df =6 180). Length at 0.5 maturity for male Yellowstone cutthroat was 370 mm TL at the maximum abundance and declined to 360 mm at the minimum abundance, a change of 3% (Figure 3.10). The best supported model describing maturity for female Yellowstone cutthroat trout included main effects for TL and abundance with an interaction effect (Table 3.6; $\beta_0 = -12.09$; $\beta_{TL} = 0.034$; $\beta_{abundance} = -4.37 \times 10^{-6}$; $\beta_{TLxabundance} = -4.37 \times 10^{-6}$;df =6 178). Female maturity at length was greater at low abundance for TL < 325 mm but greater at high abundance for TL ≥ 325 mm (Figure 3.10). However, length at 0.5 maturity for female Yellowstone cutthroat only changed 8 mm (i.e., 2%) between the lowest and greatest abundance (Figure 3.10). The logistic regression model including TL as the only covariate ($\beta_0 = -16.23$; $\beta_{TL} = 0.046$; df =6 180) was used to predict maturity for female Yellowstone cutthroat trout in the simulation model (see below) because abundance had a minimal effect on maturity.

For lake trout, logistic regression models including abundance were not supported over models including TL as the only covariate for males ($\beta_0 = -15.04$; $\beta_{TL} = 0.034$; df =1 462) and females ($\beta_0 = -13.71$; $\beta_{TL} = 0.025$; df =971; Table 3.8). Male lake trout matured at smaller TL than females, with 50% percent maturity occurring at 440 mm for males and 540 mm for females (Figure 3.11).

Pre-recruit Survival. Estimates of S_0 for Yellowstone cutthroat trout varied from 0.004 to 0.046 (Figure 3.12). Models including abundance had similar AIC support regardless of whether peak discharge was included; however, including peak discharge with an interaction for egg abundance and discharge improved the proportion of variation explained (Table 3.6; $\beta_0 = 86.67$; $\beta_{\text{eggs}} = -5.27$; $\beta_{\text{discharge}} = -13.30$; $\beta_{\text{eggs x discharge}} = 0.77$; df = 19; $r^2 = 0.83$). Age-0 survival declined with increasing egg abundance regardless of peak discharge (Figures 3.12 and 3.13). However, the effect of peak discharge varied with egg abundance. When egg abundance was less than 30 million, S_0 declined with increasing discharge (Figure 3.13). Age-0 survival increased with increasing discharge when egg abundance was greater than 30 million (Figure 3.13).

For lake trout pre-recruit survival, the intercept model had greater support ($\text{AIC}_\text{C} = -115.84$) than the model including egg abundance ($\text{AIC}_\text{C} = -113.95$). Pre-recruit survival was (0.005; 0.001 SE; $N = 14$).

Simulation Model

The level of effort required to maintain constant lake trout abundance (i.e., maintenance level) was 32 500 units (Figure 3.14). The implementation of 32 500 units of effort every year resulted in a decline in median Yellowstone cutthroat trout abundance through 30 years; however, the 95% confidence interval ranged from 0 to about 1 million after 30 years (Figure 3.14). Implementing 63 000 units of effort every year caused median lake trout abundance to decline to 75 (0 – 2 636; 95% CI) individuals and median Yellowstone cutthroat trout abundance to increase to 1.08 million (768 473 – 1.582 million) individuals after 30 years (Figure 3.14). The model predicted a decline in median Yellowstone cutthroat trout abundance until median lake trout abundance was reduced to 148 136 (47 000 – 312 000; 95% CI) fish greater than age 2 (Figure 3.14), a reduction of 76% from 2013 lake trout abundance.

The proportion of simulations with Yellowstone cutthroat trout CPUE equal to or exceeding performance metric values increased as the maximum fishing effort (i.e., 63 000 units) was implemented for longer time frames and larger reductions in lake trout abundance were obtained (Figure 3.15). The proportion of simulations with CPUE ≥ 25 (i.e., the secondary performance metric) was 0.10 with 0 years of 63 000 units of effort (i.e., maintenance level only) and increased to 0.97 with 20 years of 63 000 units of effort (Figure 3.15). The proportion of simulations with CPUE ≥ 42 (i.e., the primary performance metric) increased from 0.05 with 0 years of 63 000 units of effort to 0.95 with 20 years with 63 000 units of effort (Figure 3.15). Twelve years with 63 000 units of effort were required for CPUE ≥ 25 in at least 0.80 of simulations (Figure 3.15). The implementation of 63 000 units of effort for 12 years resulted in 14 045 lake trout remaining, or 0.02 of 2013 abundance (Figure 3.15). Thirteen years with 63 000 units of effort were required for CPUE ≥ 42 in at least 0.80 of simulations and for CPUE ≥ 25 in at least 0.90 of simulations (Figure 3.15). For CPUE ≥ 42 in at least 0.90 of simulations, 14 years with 63 000 units were required (Figure 3.15). Lake trout abundance was 10 070 fish (i.e., 0.02 remaining relative to 2013) after 13 years with 63 000 units of effort and 7 256 fish (i.e., 0.01 remaining relative to 2013) after 14 years with 63 000 units of effort (Figure 3.15).

Discussion

The simulation model indicated that large reductions in lake trout abundance were required for a high probability of Yellowstone cutthroat trout persisting at levels of abundance specified by performance metrics; however, the large number of parameters and associated variances resulted in considerable uncertainty. For example, the probability of Yellowstone cutthroat trout persistence given lake trout abundance was maintained at the 2013 estimate was 0.05 for the primary metric and 0.10 for the secondary metric. A probability of 0.10 is not trivial; however, a conservative approach to managing for Yellowstone cutthroat trout persistence in Yellowstone Lake would require the continuation of a large amount of fishing effort. We recommend implementing a large amount of fishing effort (i.e., at least 63 000 units) through the next several years and emphasize the importance of continued monitoring to assess the response of lake trout and Yellowstone cutthroat trout to continued lake trout removal.

The considerable uncertainty in simulation model results was largely driven by variation in the estimate of lake trout pre-recruit survival, which had a coefficient of variation (i.e., SD/mean) of 0.67. Given the high sensitivity of lake trout population growth rate to pre-recruit survival (Syslo et al. 2011; Cox et al. 2013), this uncertainty likely had a large influence on the variability observed in simulation model results. Additional variation was caused by the absence of density-dependence in the estimate for lake trout pre-recruit survival. An estimate of density dependence in pre-recruit survival would cause population trajectories to converge around carrying capacity, reducing variation among simulations. The continued estimation of pre-recruit survival is necessary to determine whether density-dependent patterns are expressed.

Despite the large amount of uncertainty in the simulation model results, the general requirement for a large reduction in lake trout abundance for Yellowstone cutthroat trout persistence in Yellowstone Lake appears to be reasonable. For example, Yellowstone cutthroat trout abundance declined in Yellowstone Lake before 1998, when lake trout abundance was 21% of the abundance estimated in 2013. Additionally, the only example (to our knowledge) of a prey population increasing following lake trout removal occurred in Lake Pend Oreille, Idaho, where an 82% decline in lake trout catch rate resulted in an 8.3-fold increase in the biomass of kokanee (*Oncorhynchus nerka*; A. M. Dux, Idaho Fish and Game; personal communication).

The level of mortality required to cause lake trout abundance to decline (i.e., lake trout population growth rate below replacement) is generally consistent among lake trout populations. Lake trout populations throughout the native range of the species declined when total annual mortality (A) exceeded 0.5 (Healy et al. 1978a) and numerous studies indicate a target of $A > 0.5$ is appropriate for suppressing non-native lake trout population growth. A population model indicated the lake trout population in Lake Pend Oreille was likely to decline when A was 0.45 – 0.50 (Hansen et al. 2010). Spawning potential ratio simulations for a non-native lake trout population in Lake McDonald, Glacier National Park, indicated recruitment overfishing was likely to occur when A was 0.44 – 0.49 (Dux 2005). Total annual mortality for lake trout exceeded 0.5 for the first time in 2012, and the decline in lake trout abundance in Yellowstone Lake from 2012 – 2013 occurred following an instantaneous fishing mortality (*F*) of 0.79 ($A = 0.61$) in 2012.

Following declines in abundance, exploited lake trout populations have exhibited compensatory responses through increased individual growth rates (Healey 1978a; Ferreri and Taylor 1996; Sitar and He 2006), increased body condition (Martin and Olver 1980), and increased maturity at length or age (Healy 1978a, 1978b; Ferreri and Taylor 1996). However, density-dependent compensation was not detected for lake trout population metrics in Yellowstone Lake despite 6-fold variation in abundance of lake trout. Although we observed large variation in abundance estimates, lake trout density in Yellowstone Lake may not have increased to sufficient levels for density-dependence to be fully expressed in population metrics. The density of lake trout age 4 and greater increased from 1.33 fish/ha in 1998 to 5.33 fish/ha in 2012. However, density in Yellowstone Lake in 2012 was about 1/3 the density of non-native lake trout in Flathead Lake, Montana (15.8 fish/ha), a population considered to be at carrying capacity (CSKT 2014). Similarly, density in Yellowstone Lake was lower than the density of non-native lake trout (15.5 fish/ha; age 3 and greater) in Fallen Leaf Lake, California (Al-Chokhachy et al. 2009).

Although we did not detect density-dependence in lake trout pre-recruit survival, our results have implications for the management of lake trout populations throughout the introduced range of the species. The estimate of pre-recruit survival for lake trout in Yellowstone Lake ($S_R = 0.005$) was 2.5 times higher than estimates from the native range used in previous simulation models for non-native lake trout populations (Syslo et al.

2011; Cox et al. 2013). Pre-recruit survival in Yellowstone Lake may have been higher than rates estimated for populations in the native range because the abundance of spawning lake trout in Yellowstone Lake has not approached equilibrium density. Additionally, Yellowstone Lake does not contain known interstitial egg predators, which are an important source of egg mortality in the native range of lake trout (Claramunt et al. 2005). Lake trout population growth rate is highly sensitive to pre-recruit survival (Ferreri et al. 1995; Syslo et al. 2011; Cox et al. 2013); therefore, studies evaluating strategies for lake trout suppression should consider the effects of pre-recruit survival rates that are higher than estimates from populations in the native range.

In contrast to lake trout, the evaluation of Yellowstone cutthroat trout population metrics given a 5-fold change in density elucidated important compensatory mechanisms regulating abundance. Weight-at-length varied by as much as 17% among densities observed from 1986 through 2013. Although fecundity data were not available for Yellowstone cutthroat trout at contrasting densities, it is likely that the observed variation in weight translated to variation in fecundity. Previous studies indicated relative fecundity (eggs/ kg body weight) was similar for Yellowstone cutthroat trout during a period of reduced density from overharvest in the 1950s through the early 1990s (Gresswell 2011). Therefore, observed variation in weight likely had an important effect on Yellowstone cutthroat trout population growth rate.

Age-0 survivial (S_0) was strongly density-dependent for Yellowstone cutthroat trout, varying 10-fold among egg abundances estimated for 1986 through 2013. Age-0 survival was a function of several metrics used to calculate egg abundance including abundance of Yellowstone cutthroat trout the preceding year, length-at-age, weight-at-length, and fecundity given weight. Therefore, estimates of S_0 were likely to be highly variable; however, S_0 estimates exhibited relatively low variation and the range of values observed in Yellowstone Lake encompassed estimates for salmonids exhibiting lacustrine-adfluvial life histories in other systems. For example, S_0 was 0.027 for Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in Trapper's Lake, CO (Stapp and Hayward 2002), and 0.02 for sockeye salmon (*Oncorhynchus nerka*) throughout the range of the species during the freshwater rearing phase (Bradford 1995).

Previous studies found contradictory results for the effect of hydrology on S_0 for Yellowstone cutthroat trout in Yellowstone Lake. Year-class strength in Pelican Creek and Chipmunk Creek from 1945-1956 was negatively related to lake water levels (Bulkley and Benson 1962). However, a model of the spawning run in Clear Creek from 1977 through 2007 indicated S_0 was positively related to mean annual discharge (Kaeding 2010). The above results can be explained using the relationship between S_0, egg abundance, and discharge estimated in this study. The negative effect of water level was estimated during a period with low Yellowstone cutthroat trout abundance, whereas the model indicating a positive effect of water level included several years of data from a period with high Yellowstone cutthroat trout abundance (Gresswell and Varley 1988; Koel et al. 2005). We surmise high water levels increase the availability of spawning habitat; however, the increase in spawning habitat only outweighs the negative effect of increased discharge (i.e., redd scouring) at sufficiently high densities of spawning fish.

The inclusion of compensatory responses to variations in density and environmental variation (i.e., water level) were critical to developing a realistic model of the lake trout – Yellowstone cutthroat trout system. However, we were not able to include all factors hypothesized to affect Yellowstone cutthroat trout population dynamics. The decline in Yellowstone cutthroat trout abundance that occurred through the 1990s and 2000s was hypothesized to be a function of several years of whirling disease and several years with low water levels in addition to lake trout (Koel et al. 2005; 2006). Lake trout and water level were included in the simulation model; however, the lack of sufficient information for the population-level effects of whirling disease prevented its inclusion. Within the lake, infection prevalence varied from 6 - 16% for Yellowstone cutthroat trout sampled in assessment netting (Murcia et al. 2014). In contrast, the simulation model indicated a lake trout population maintained at abundance observed in 2013 would consume an average of 47% of cutthroat trout abundance per year through the next 5 years. Thus, whirling disease does not appear to be a limiting factor for Yellowstone cutthroat trout population growth given lake trout estimated lake trout abundance.

The lake trout suppression program in Yellowstone Lake is the longest ongoing lake trout removal program in the Western USA (Martinez et al. 2009) and provides a rare example of a long-term mechanical-removal program for a non-native fish species in a large lentic ecosystem. The efficacy of mechanical removal programs for non-native fishes is often difficult to demonstrate (Coggins et al. 2011; Franssen et al. 2014); nevertheless, mechanical removal projects are being implemented or considered in several large, open water bodies throughout the world (Koehn 2004; Martinez et al. 2009; Tsayehe et al. 2013). Given the large amount of resources consumed by these programs, it is ideal to determine the extent of non-native fish reduction required for native fishes to persist at management targets prior to implementation. However, a substantial amount of data may be required to assess or predict efficacy for mechanical removal programs, as demonstrated by this study. Lake trout suppression in Yellowstone Lake highlights the importance of setting quantifiable objectives, establishing long-term monitoring programs, and sustaining a large amount of fishing pressure to reduce non-native fish populations in large water bodies.

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Tables and Figures

Table 3.1. Equations used in statistical catch-at-age modeling (see Table 3.2 for definition of symbols).

Equation	Number
$N_{y+1,a+1} = N_{y,a} \cdot e^{-Z_{y,a}}$	1
$Z_{y,a} = M_a + F_{y,a}$	2
$F_{y,a} = \begin{cases} F_{R,y,a}; & \text{for y} < 1998 \\ F_{G,y,a} + F_{R,y,a}; & \text{for y} \geq 1998 \end{cases}$	3
$F_{G,y,a} = q_G \cdot E_{G,y} \cdot s_{G,a}$	4
$F_{R,y,a} = q_R \cdot E_{R,y} \cdot s_{R,a} \cdot h_{y,a}$	5
$s_{f,a} = \dfrac{1}{1 + e^{-\log(19) \cdot \frac{(a-a_{50})}{(a_{95}-a_{50})}}}$	6
$\hat{C}_{f,y,a} = \dfrac{F_{f,y,a}}{Z_{y,a}} \cdot N_{y,a} \cdot (1 - e^{-Z_{y,a}})$	7
$\hat{U}_y = q_A \cdot \sum_a (s_{a_A} \cdot N_{y,a})$	8
$\hat{P}_{y,a} = \dfrac{q_A \cdot s_{a_A} \cdot N_{y,a}}{q_A \cdot \sum_a (s_{a_A} \cdot N_{y,a})}$	9
$L = \sum_f \lambda_f \cdot L_f$	10
$L_f = \dfrac{1}{2\sigma_f^2} \cdot \sum_y \left[\left(\ln \dfrac{C_{f,y}}{\hat{C}_{f,y}} \right)^2 \right] + n \cdot \ln(\sigma_f)$	11
$L_f = -\sum_y N_{E,f,y} \cdot \sum_a \left(P_{f,y,a} \cdot \ln[\hat{P}_{f,y,a}] \right)$	12

Table 3.2. Symbols used in statistical catch-at-age modeling.

Symbol	Description
y	Year index
a	Age index
f	Fishery index (A = Yellowstone cutthroat trout assessment netting; R = recreational; G = gill net)
N	Abundance
Z	Instantaneous total mortality
M	Instantaneous natural mortality
F	Instantaneous fishing mortality
q	Catchability
E	Observed fishing effort
s	Selectivity
h	Observed proportion of Yellowstone cutthroat trout catch that was harvested
a_{50}	Age of 50% fishery selectivity
a_{95}	Age of 95% fishery selectivity
$\hat{C}$	Predicted fishery catch
$\hat{U}$	Predicted assessment CPUE
C	Observed fishery catch
U	Observed assessment CPUE
$\hat{P}$	Predicted proportion of fish at age
P	Observed proportion of fish at age
L	Log-likelihood component
λ	Log-likelihood emphasis factor
n	Number of years
σ	Log-scale SD
N_E	Effective sample size of aged fish

Table 3.3. Equations used in simulation model for the lake trout population in Yellowstone Lake, Yellowstone National Park (see Table 3.4 for definition of symbols).

Equation	Number
Matrix projection	
$\mathbf{n}_y = \mathbf{n}_{y-1} \cdot \mathbf{A}_y$	1
Matrix elements	
$S_{a,y} = e^{(-M+-F_{a,y})}$	2
$R_{a,y} = fec_a \cdot m_{a,y} \cdot S_R \cdot 0.5$	3
Submodels	
$log_{10}(M) = -0.0066 + 0.643 \cdot \log_{10}(K) - 0.279 \cdot log_{10}(L_\infty) + 0.463 \cdot \log_{10}(temperature)$	4
$F_{a,y} = E_{G,y} \cdot q_G \cdot sel_{G,a}$	5
$sel_{G,a} = \dfrac{1}{1 + e^{-\log(19) \cdot \frac{(a-a_{50})}{(a_{95}-a_{50})}}}$	6
$TL_a = L_\infty \cdot \left(1 - e^{-K \cdot (a-t_0)}\right)$	7
$fec_a = \beta_0 + \beta_1 \cdot TL_a$	8
$m_{a,y} = \dfrac{e^{(\beta_0+\beta_1 \cdot TL_a)}}{1 + e^{(\beta_0+\beta_1 \cdot TL_a)}}$	9
Predation	
$C_{a,y} = P_a \cdot \sum_a n_{a,y} \cdot con_a$	10

Table 3.4. Symbols used in simulation model of lake trout and Yellowstone cutthroat trout populations in Yellowstone Lake, Yellowstone National Park.

Symbol	Definition
a	Age index
y	Year index
f	Fishery index (A = Yellowstone cutthroat trout assessment netting; R = recreational; G = gill net)
D	Peak discharge
$\mathbf{A}$	Projection matrix
$\mathbf{n}$	Abundance vector
n	Abundance
n_S	Abundance of spawning fish
S_L	Survival rate for non-spawning segment of population
S_S	Survival rate for spawning segment of population
S_t	Survival rate in spawning tributaries
S_R	Pre-recruit survival for lake trout
G_L	Probability of transitioning from non-spawning to spawning segment of population
G_S	Probability of remaining in spawning segment of population
R	Fertility
V_S	Probability of spawning
V_{SS}	Probability of spawning in consecutive years
m	Probability of maturity
M	Instantaneous natural mortality
M_L	Instantaneous natural mortality in lake
M_S	Instantaneous natural mortality in spawning tributaries
F	Instantaneous fishing mortality
W	Weight
fec	Fecundity
TL	Total length

Table 3.4. Continued.

Symbol	Definition
L_∞	Asymptotic length
K	Growth coefficient
t_0	Age at which TL = 0
β	Coefficient from length weight or length maturity models
sel	Fishery selectivity
a_{50}	Age at 50% fishery selectivity
a_{90}	Age at 90% fishery selectivity
E	Fishing effort
q	Catchability
C_a	Total consumption of Yellowstone cutthroat trout age class
P_a	Proportion of total consumption composed of each Yellowstone cutthroat trout age class
con_a	Per-capita consumption by each lake trout age class
CPUE	Catch per unit effort

Table 3.5. Equations used in simulation model for the Yellowstone cutthroat trout population in Yellowstone Lake, Yellowstone National Park (see Table 3.4 for definition of symbols).

Equation	Number
Matrix projection	
$\mathbf{n}_y = \mathbf{n}_{y-1} \cdot \mathbf{A}_y$	1
Matrix elements	
$\ln\left(S_{L,0,y}\right) = \beta_0 + \beta_1 \cdot ln\left(Eggs_{y-1}\right) + \beta_2 \cdot \ln(D_{y-1}) + \beta_3 \cdot \ln(Eggs_{y-1}) \cdot \ln(D_{y-1}) + \varepsilon_y$	2
$S_{L,a,y} = e^{(-M_{L,a,y} \cdot 365 + -F_{a,y})} \cdot (1 - V_S \cdot m_{a+1,y})$	3
$G_{L,a,y} = e^{(-M_{L,a,y} \cdot 350 + -M_S + -F_{a,y})} \cdot V_S \cdot m_{a+1,y}$	4
$G_{S,a,y} = e^{(-M_{L,a,y} \cdot 350 + -M_S + -F_{a,y})} \cdot V_{SS}$	5
$S_{S,a,y} = e^{(-M_{L,a,y} \cdot 365 + -F_{a,y})} \cdot (1 - V_{SS})$	6
$R_{a,y} = n_{S,y} \cdot W_{a,y} \cdot fec \cdot 0.5$	7
Submodels	
$m_{a,y} = \dfrac{e^{(\beta_0 + \beta_1 \cdot TL_a)}}{1 + e^{(\beta_0 + \beta_1 \cdot TL_a)}}$	8
$TL_a = L_\infty - (L_\infty - TL_{a-1}) \cdot e^{-K}$	9
$log_{10}(M) = -0.0066 + 0.643 \cdot \log_{10}(K) - 0.279 \cdot log_{10}(L_\infty) + 0.463 \cdot \log_{10}(temperature)$	10
$M = m_{a,y} \cdot V_S \cdot \left(M_S + 350 \cdot M_{L,a,y}\right) + \left(1 - m_{a,y} \cdot V_S\right) \cdot 365 \cdot M_{L,a,y}$	11
$F_{a,y} = E_{G,y} \cdot q_G \cdot sel_{G,a} + E_{R,y} \cdot q_R \cdot sel_{R,a}$	12
$sel_{f,a} = \dfrac{1}{1 + e^{-\log(19) \cdot \frac{(a - a_{50})}{(a_{95} - a_{50})}}}$	13
$W_{a,y} = \beta_0 + \beta_1 \cdot TL_a + \beta_2 \cdot n_{y-1} + \beta_3 \cdot TL_a \cdot n_{y-1}$	14

Table 3.5. Continued.

Equation	Number
$Eggs_y = \sum_a n_{S,a,y} \cdot W_{a,y} \cdot fec$	15
Predation	
$n_{a,y} - C_{a,y}$	16
Assessment	
$CPUE_y = \sum_a q_A \cdot sel_{A,a} \cdot n_{a,y}$	17

Table 3.6. Akaike information criterion (AIC), ΔAIC, and r^2 values for models of mean length-at-age (i.e., growth), weight, maturity, and pre-recruit survival as functions of abundance, total length (TL; mm), and peak discharge (i.e., cubic meters per second) for Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park.

Model	AIC	ΔAIC	r^2
Growth			
Abundance	1124.2	0.0	
Null	1126.5	2.3	
Weight			
TL + Abundance + TL x Abundance	-42528.2	0.0	0.98
TL + Abundance	-42440.1	88.1	0.98
TL	-42024.8	503.4	0.98
Maturity, males			
TL + Abundance	4180.9	0.0	0.56
TL + Abundance + TL x Abundance	4182.8	1.9	0.56
TL	4183.5	2.6	0.56
Maturity, females			
TL + Abundance + TL x Abundance	2986.8	0.0	0.66
TL + Abundance	2997.7	10.9	0.66
TL	3001.0	14.2	0.66
Pre-recruit survival			
Egg abundance + Peak discharge + Egg abundance x Peak discharge	16.7	0.0	0.83
Egg abundance + Peak discharge	17.9	1.2	0.79
Egg abundance	18.7	2.0	0.76
Null	49.5	32.8	
Peak discharge	50.4	33.7	0.00

Table 3.7. Best supported models for length-at-capture as a function of abundance by age for lake trout in Yellowstone Lake, Yellowstone National Park. Model support was determined by Akaike information criterion values (AIC; see Table C.1 for AIC rankings).

Age	Model	β_0	$\beta_{(Abundance)}$	r^2
2	Abundance	277.60	-0.000052	0.06
3	Null	320.90		
4	Abundance	340.80	0.000135	0.18
5	Abundance	417.21	0.000093	0.07
6	Abundance	499.68	0.000070	0.03
7	Abundance	552.32	0.000046	0.01
8	Null	602.86		
9	Abundance	422.50	0.000058	0.03
10	Null	645.48		
11	Null	669.50		
12	Null	692.30		
13	Null	737.10		

Table 3.8. Akaike information criterion (AIC), ΔAIC, and r^2 values for models of weight and maturity as a function of total length (TL; mm) and abundance for lake trout in Yellowstone Lake, Yellowstone National Park.

Model	AIC	ΔAIC	r^2
Weight			
TL + Abundance + TL x Abundance	-33689.1	0.0	0.98
TL	-33653.5	35.6	0.98
TL + Abundance	-33651.6	37.5	0.98
Maturity, males			
TL + Abundance + TL x Abundance	422.0	0.0	0.69
TL	423.2	1.2	0.68
TL + Abundance	424.0	2.0	0.68
Maturity, females			
TL + Abundance	321.9	0.0	0.49
TL	322.5	0.6	0.48
TL + Abundance + TL x Abundance	322.8	0.9	0.49

(a) Lake trout

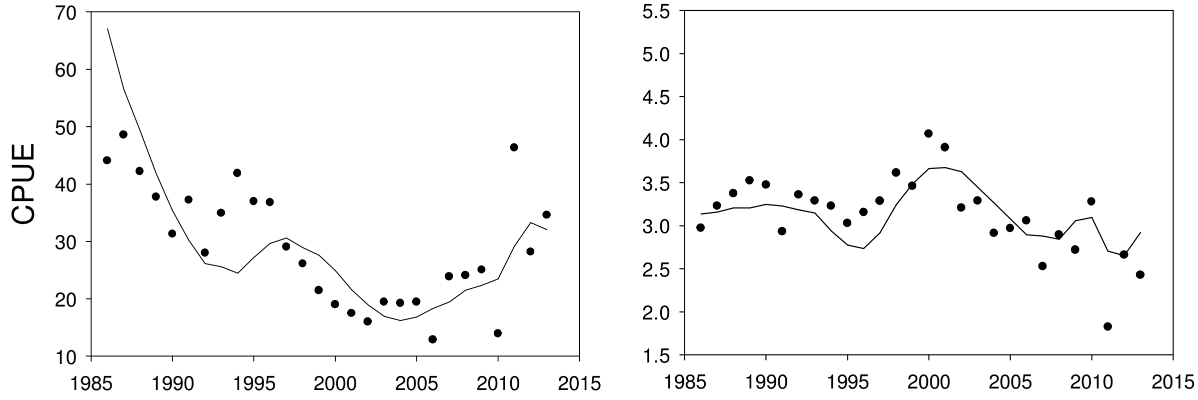
$$\begin{bmatrix} R_1 & \cdots & \cdots & R_{20+} \\ S_1 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & S_{19} & S_{20+} \end{bmatrix}$$

(b) Yellowstone cutthroat trout

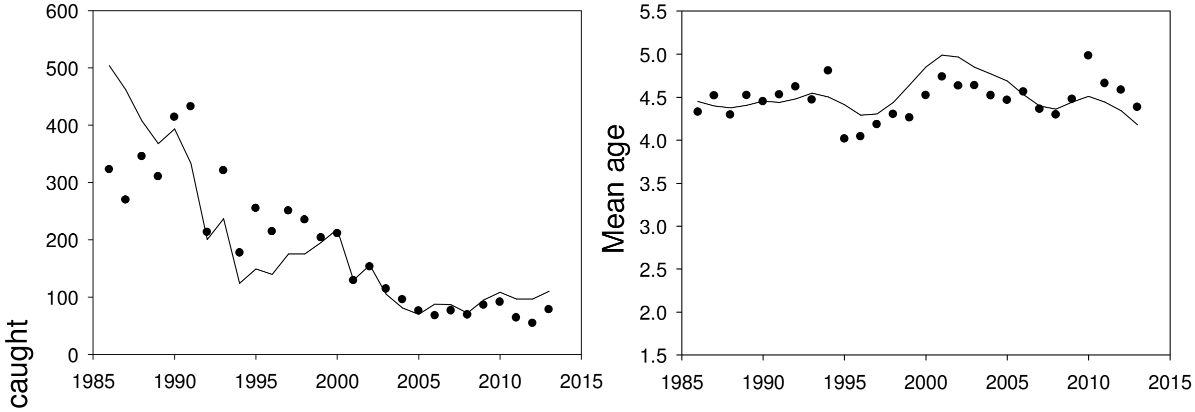
$$\begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & R_3 & R_4 & R_5 & R_6 & R_7 & R_8 & R_{9+} \\
S_{L0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & S_{L1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & S_{L2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & S_{L3} & 0 & 0 & 0 & 0 & 0 & 0 & S_{S3} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & S_{L4} & 0 & 0 & 0 & 0 & 0 & 0 & S_{S4} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & S_{L5} & 0 & 0 & 0 & 0 & 0 & 0 & S_{S5} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & S_{L6} & 0 & 0 & 0 & 0 & 0 & 0 & S_{S6} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{L7} & 0 & 0 & 0 & 0 & 0 & 0 & S_{S7} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{L8} & S_{L9+} & 0 & 0 & 0 & 0 & 0 & S_{S8} & S_{S9+} \\
0 & 0 & G_{L2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & G_{L3} & 0 & 0 & 0 & 0 & 0 & 0 & G_{S3} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & G_{L4} & 0 & 0 & 0 & 0 & 0 & 0 & G_{S4} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & G_{L5} & 0 & 0 & 0 & 0 & 0 & 0 & G_{S5} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & G_{L6} & 0 & 0 & 0 & 0 & 0 & 0 & G_{S6} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & G_{L7} & 0 & 0 & 0 & 0 & 0 & 0 & G_{S7} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_{L8+} & G_{L9+} & 0 & 0 & 0 & 0 & 0 & G_{S8} & G_{S9+}
\end{bmatrix}$$

Figure 3.1. Transition matrices used to model the lake trout (a) and Yellowstone cutthroat trout (b) populations in Yellowstone Lake. Matrix elements for lake trout are age–specific reproduction (R_a) and survival (S_a). Matrix elements for Yellowstone cutthroat trout are age-specific reproduction, survival in the lake (S_L), survival in the stream (S_S), probability of spawning (i.e., moving into the stream; G_L), probability of remaining in the spawning portion of the population in consecutive years (G_S).

(a) Assessment netting



(b) Recreational fishery



(c) Gill-net fishery

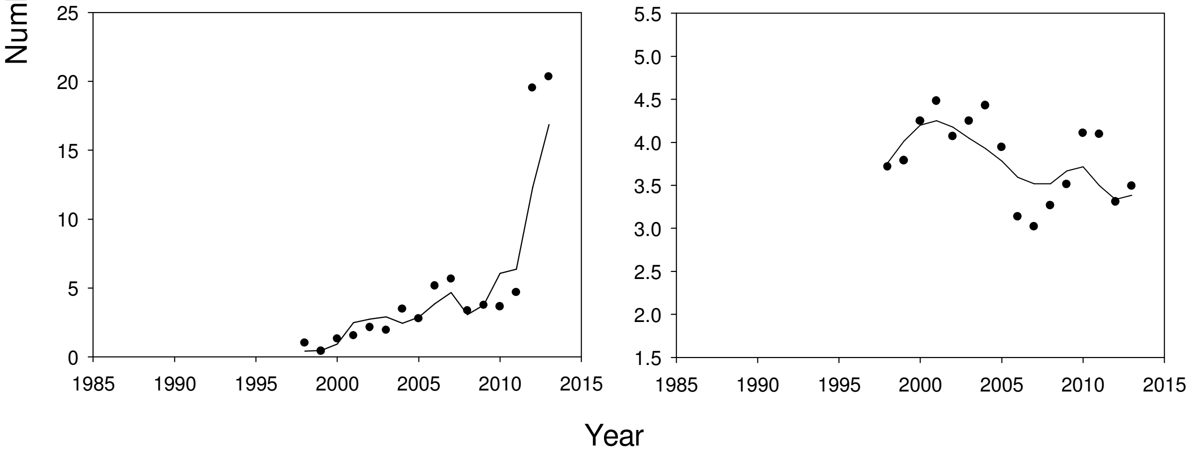


Figure 3.2. Observed (dots) and predicted (solid line) catch per unit effort (CPUE), catch, and mean age by fishery (i.e., assessment, recreational, and gill net) from a statistical catch-at-age model for Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park, from 1986 through 2013.

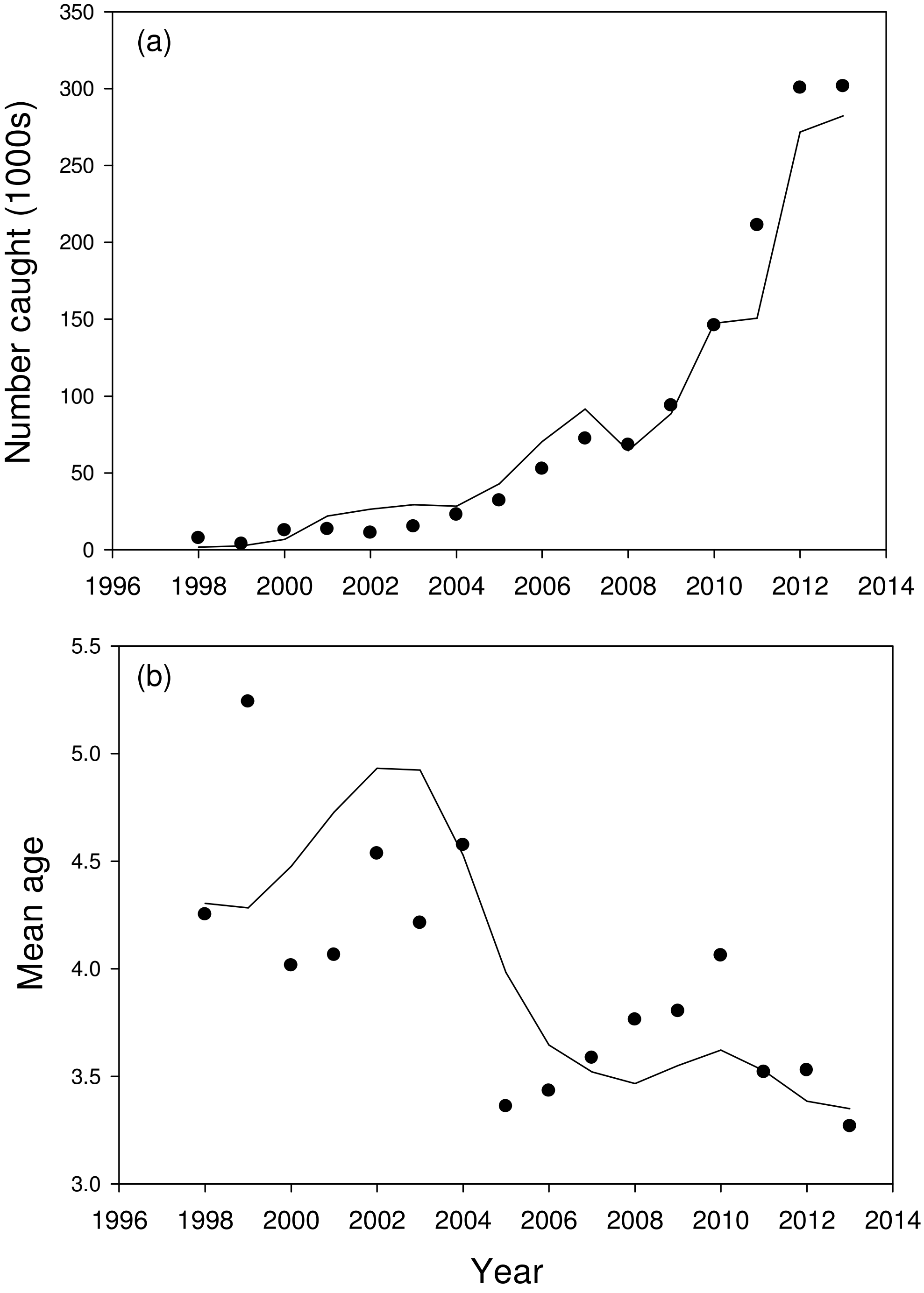


Figure 3.3. Observed (dots) and predicted (solid line) catch (a) and mean age (b) in the gill-net fishery from a statistical-catch-at age model for lake trout in Yellowstone Lake, Yellowstone National Park, from 1998 through 2013.

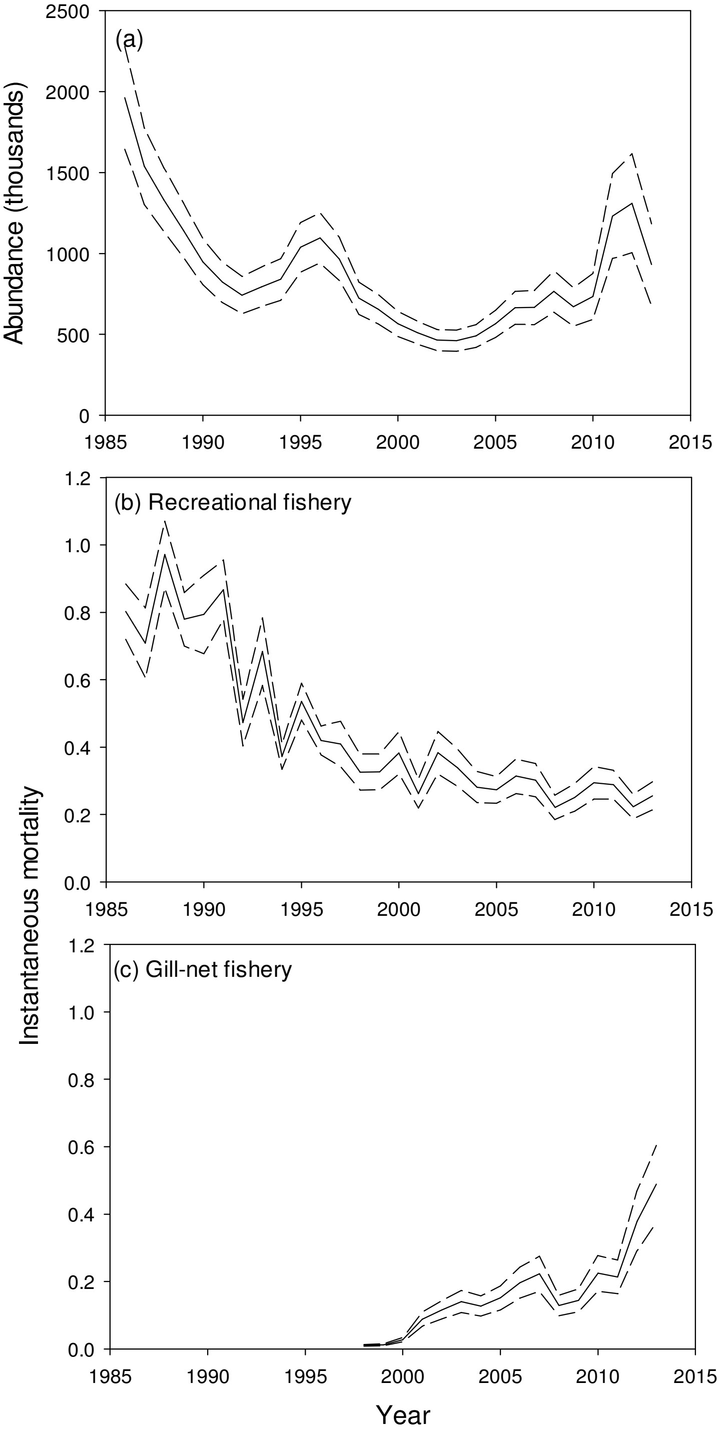


Figure 3.4. Predicted abundance (a) and fully-selected fishing mortality for the recreational (b) and gill-net (c) fisheries from a statistical catch-at-age model for Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park, from 1986 through 2013. Dashed lines delineate 95% confidence intervals.

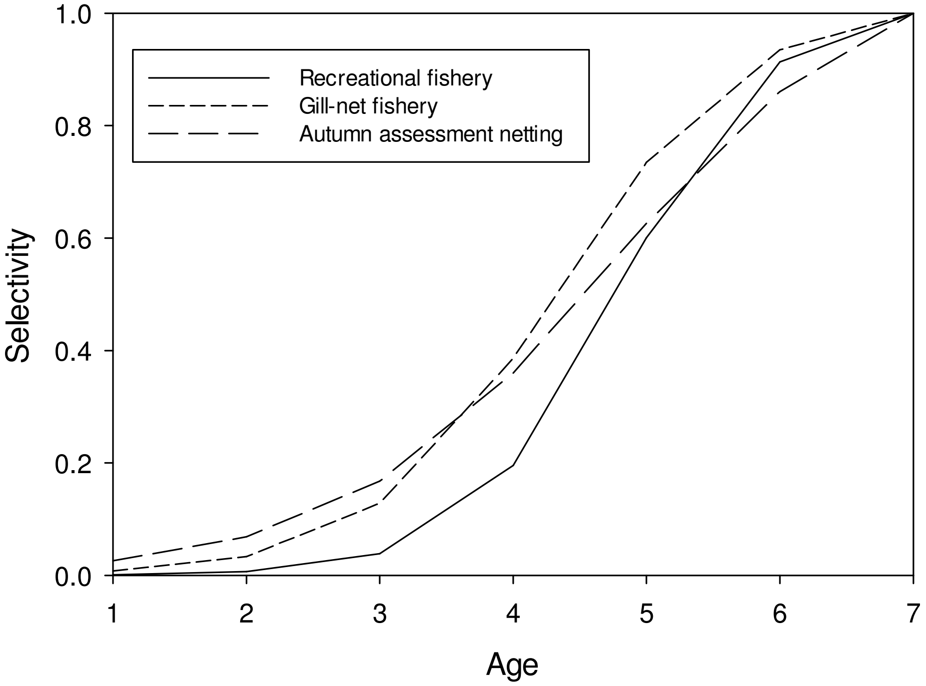


Figure 3.5. Age-specific selectivity by fishery from a statistical catch-at-age model for Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park, from 1986 through 2013.

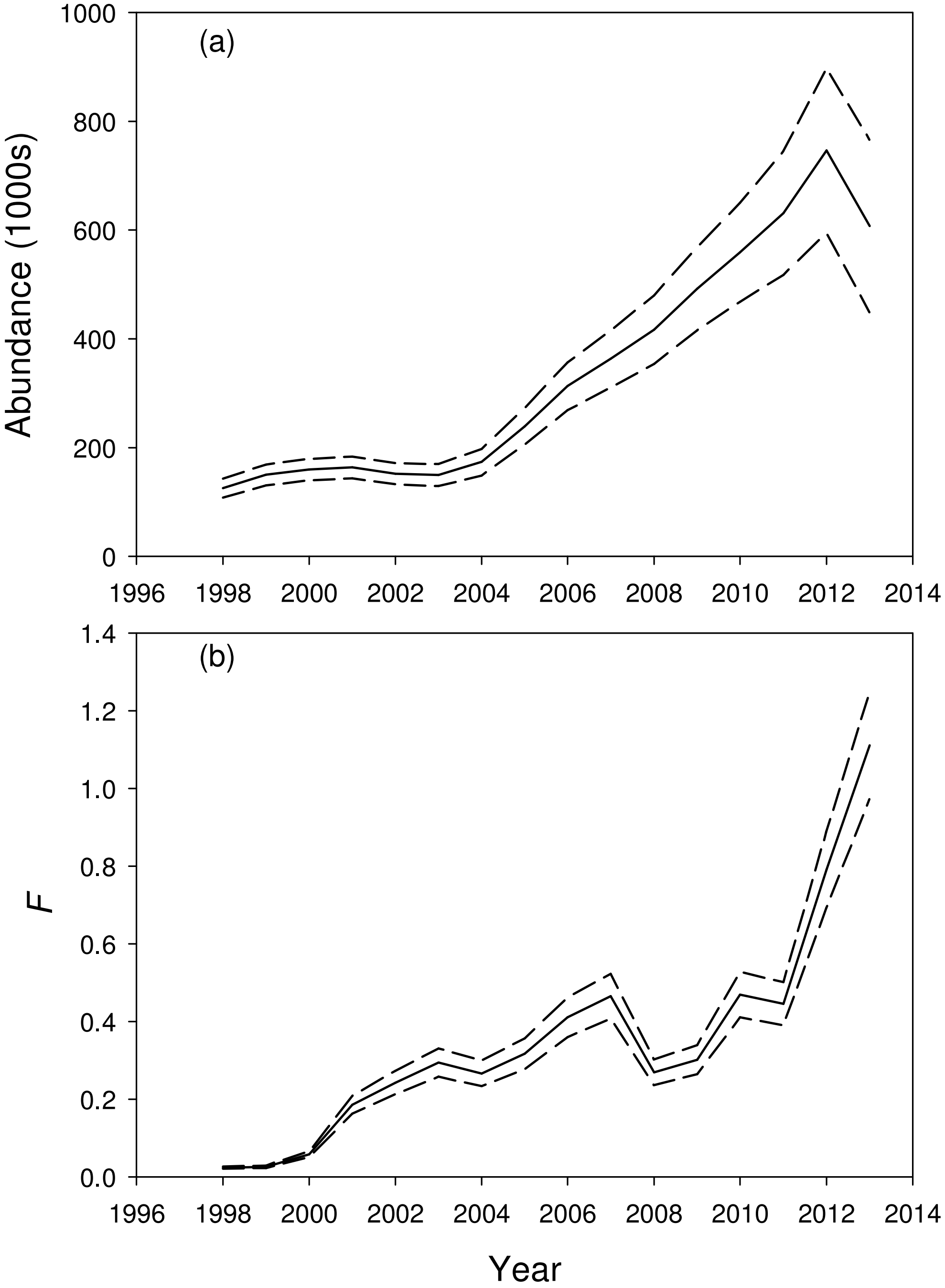


Figure 3.6. Predicted abundance (a) and fully-selected fishing mortality (b) for the gill-net fishery from a statistical catch-at-age model for lake trout in Yellowstone Lake, Yellowstone National Park, from 1998 through 2013. Dashed lines delineate 95% confidence intervals.

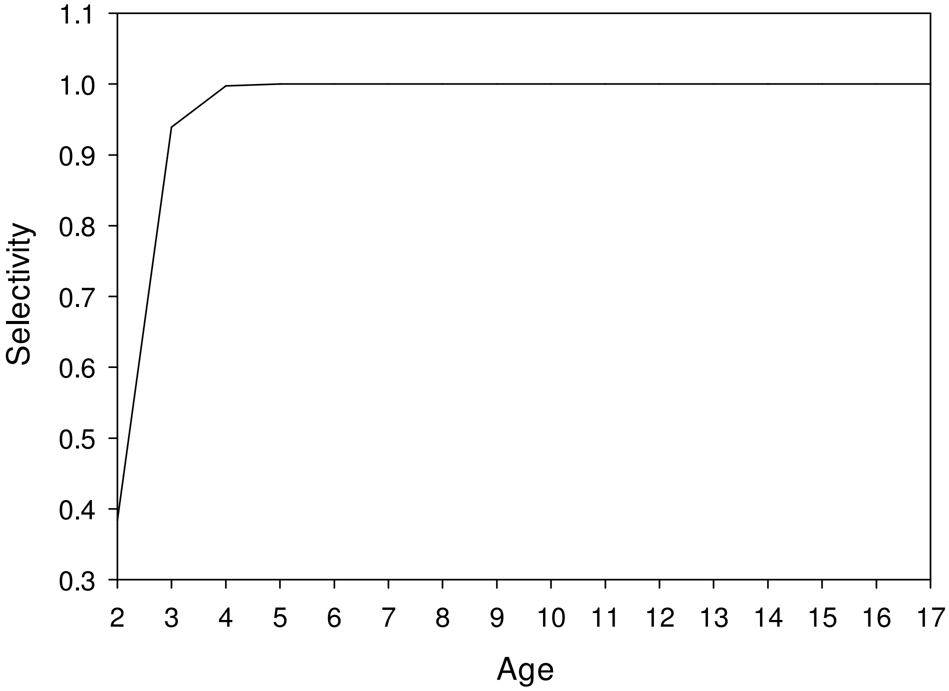


Figure 3.7. Age-specific selectivity for the gill-net fishery from a statistical catch-at-age model for lake trout in Yellowstone Lake, Yellowstone National Park, from 1998 through 2013.

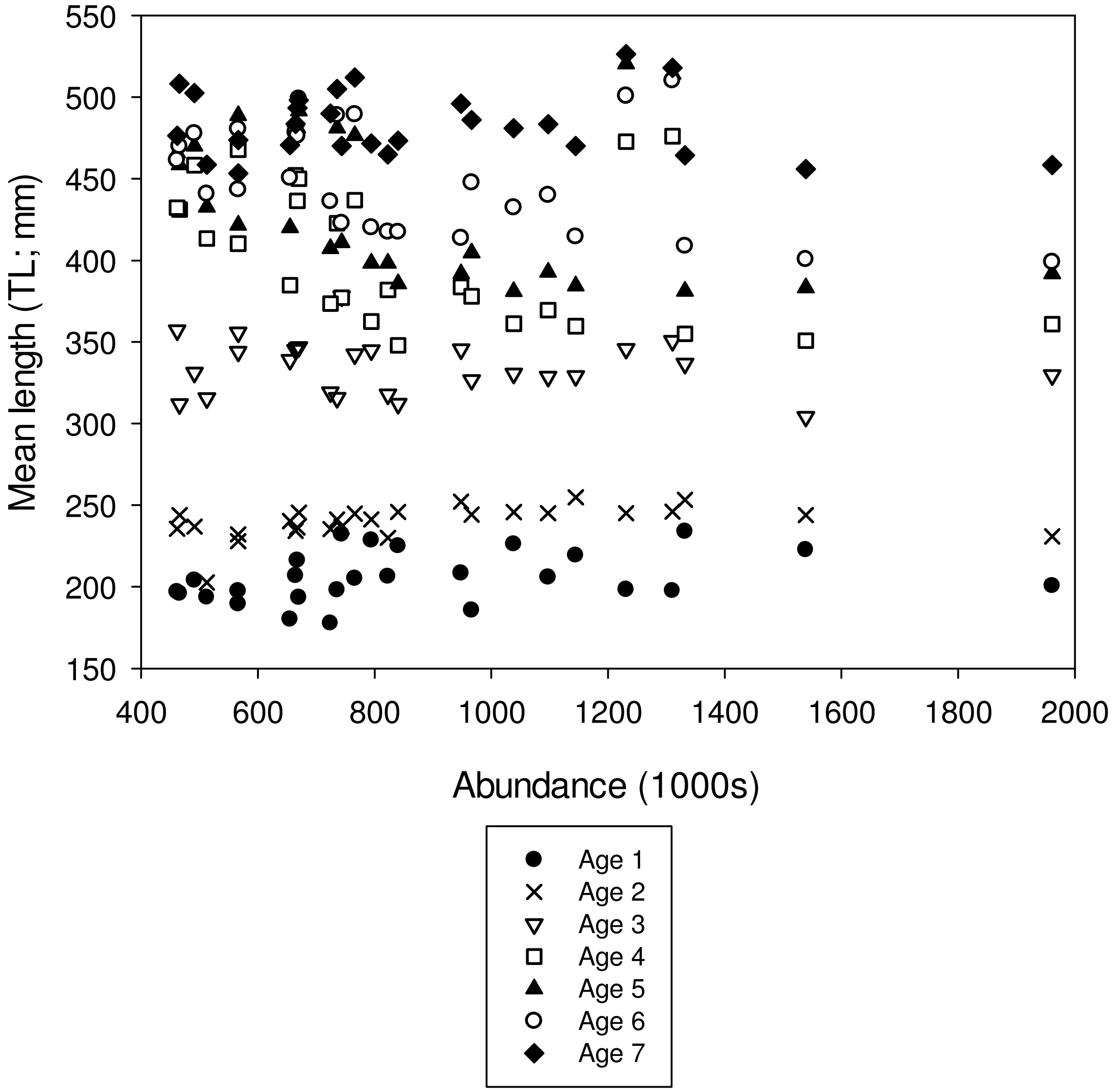


Figure 3.8. Yellowstone cutthroat trout mean length-at-age (mm) given Yellowstone cutthroat trout abundance estimates in Yellowstone Lake, Yellowstone National Park.

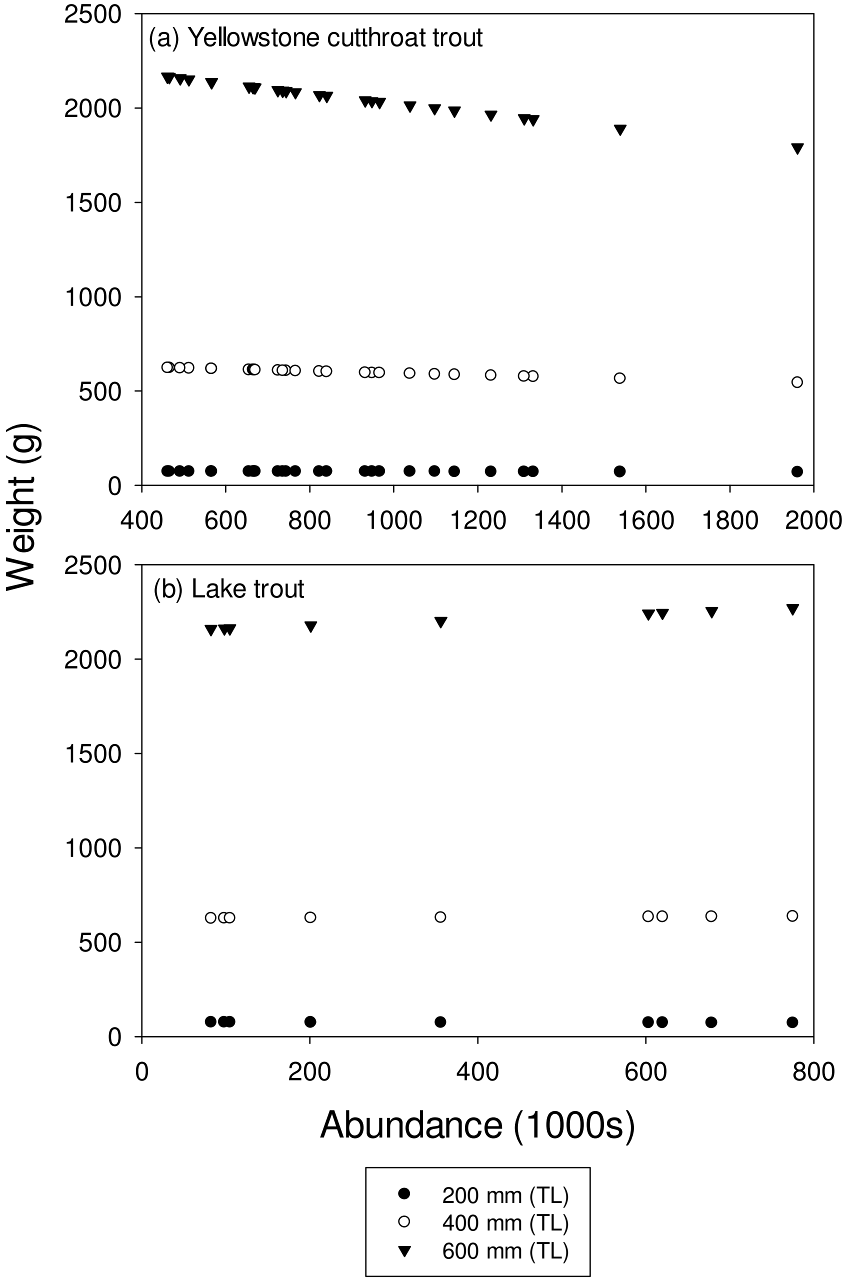


Figure 3.9. Predicted weight as a function of abundance for 200-mm, 400-mm, and 600-mm Yellowstone cutthroat trout (a) and lake trout (b) in Yellowstone Lake, Yellowstone National Park.

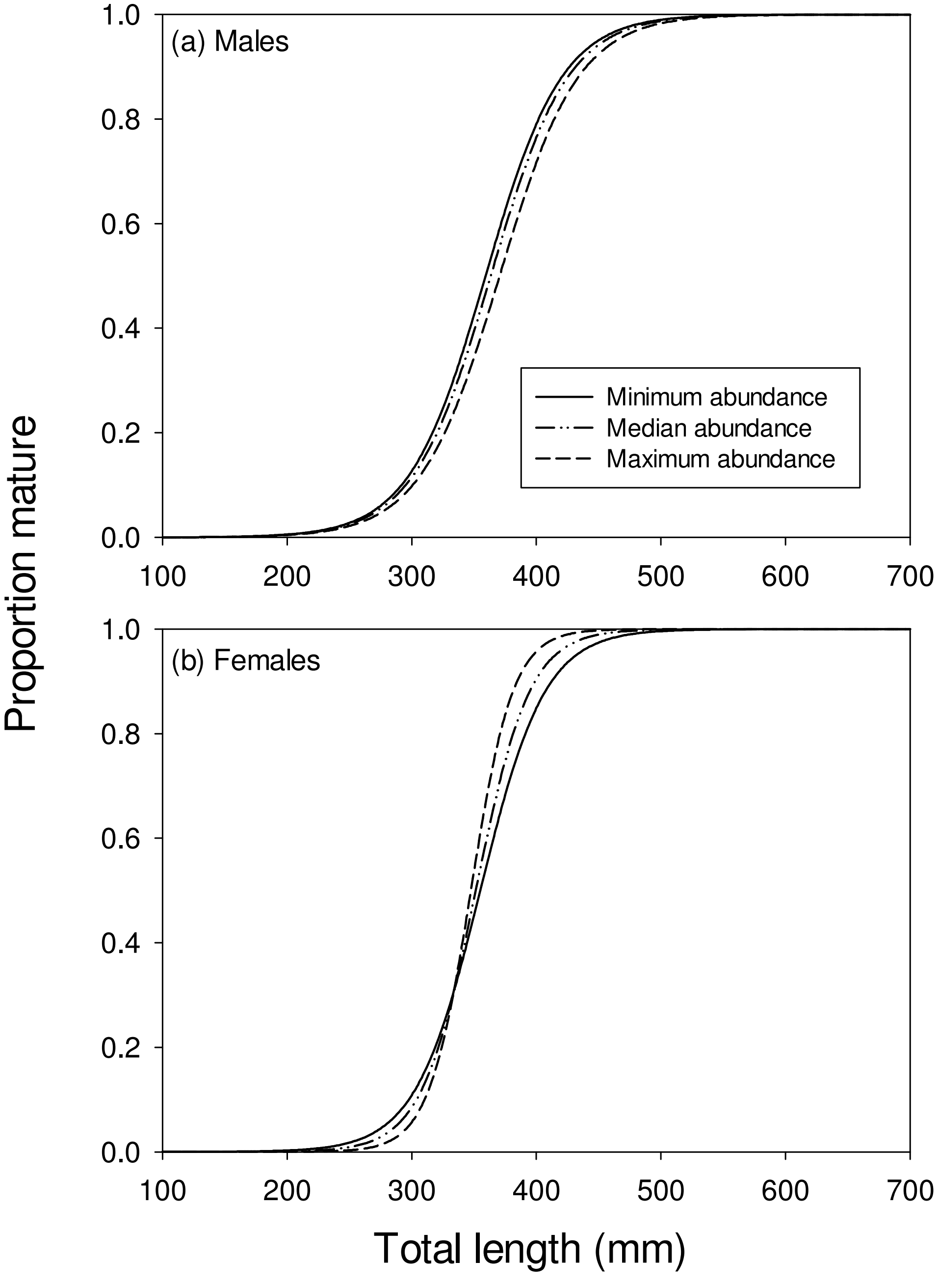


Figure 3.10. Maturity at length (TL; mm) for male (a) and female (b) Yellowstone cutthroat trout given minimum, median, and maximum abundance estimates in Yellowstone Lake, Yellowstone National Park.

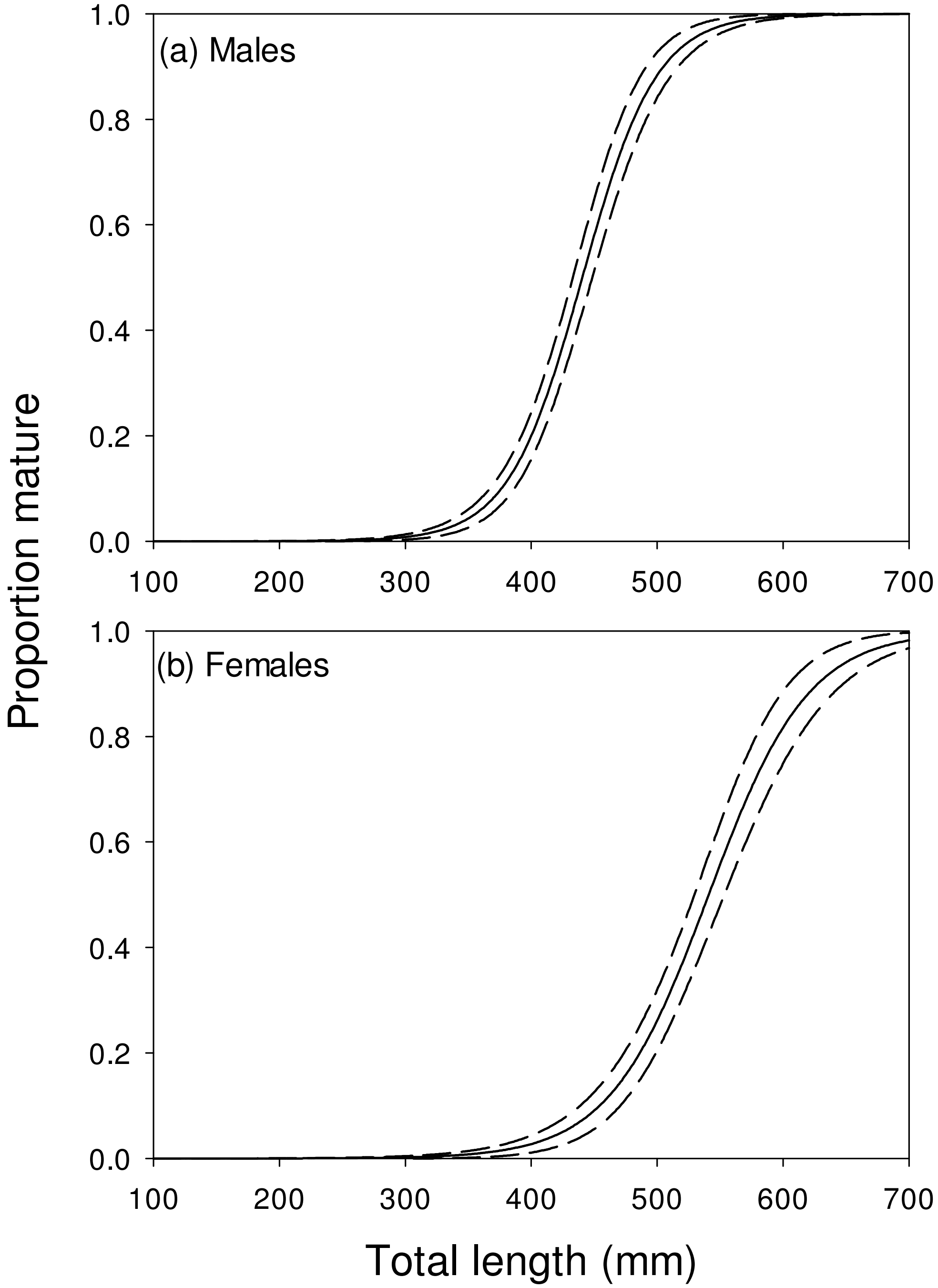


Figure 3.11. Maturity at length for male (a) and female (b) lake trout in Yellowstone Lake, Yellowstone National Park. Dashed lines delineate 95% confidence intervals.

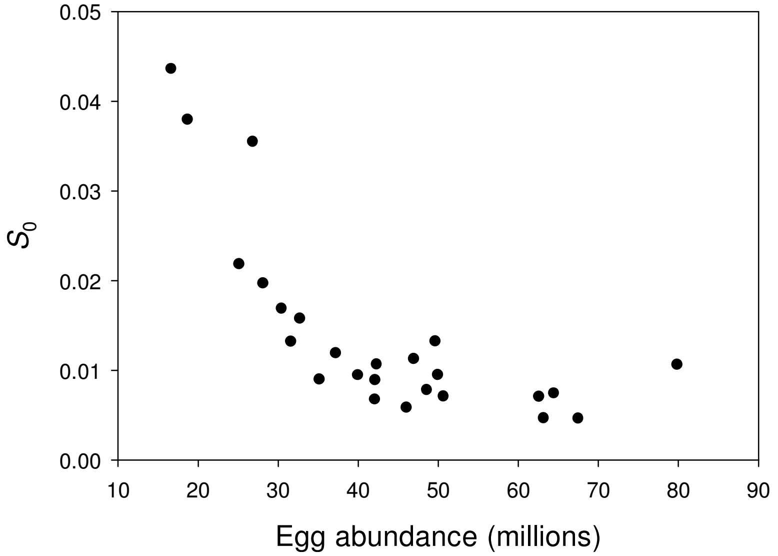


Figure 3.12. Estimates of age-0 survival (S_0) given egg abundance for Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park.

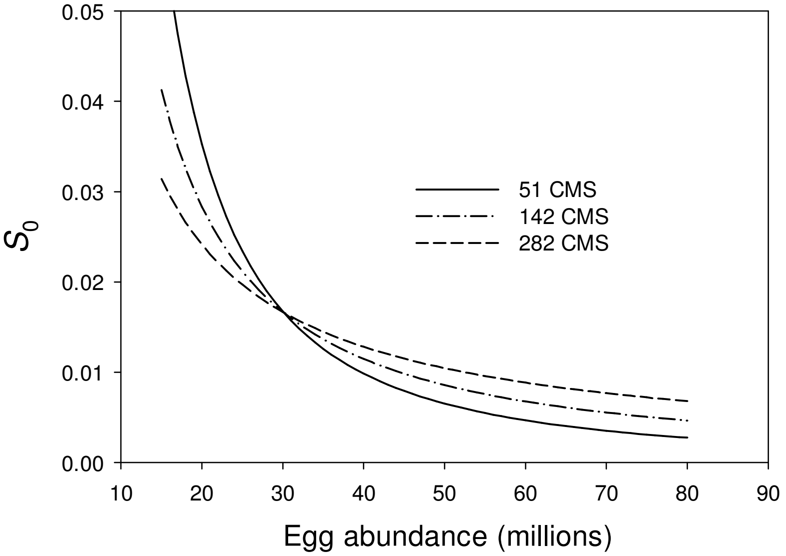
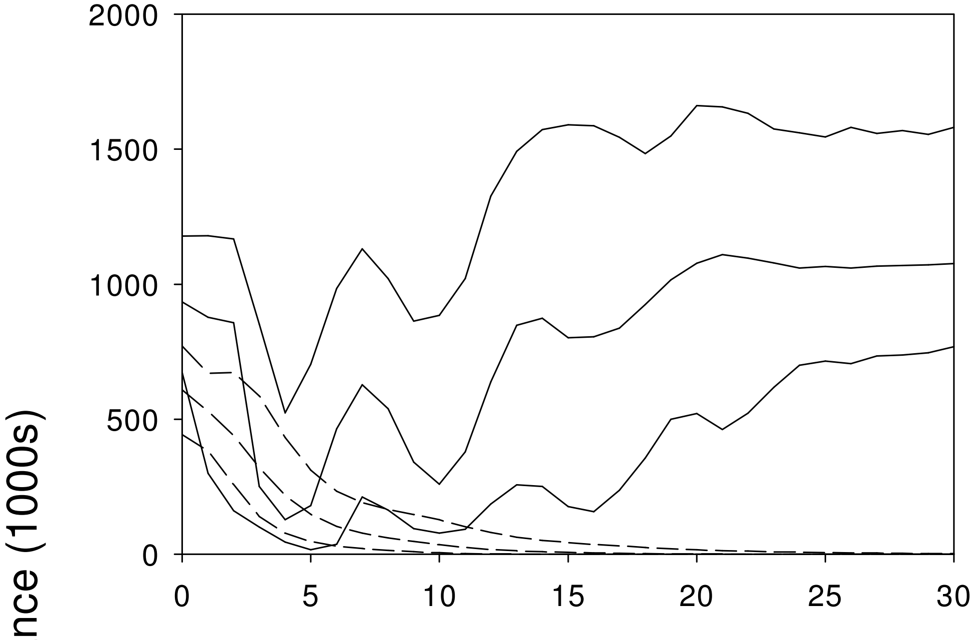


Figure 3.13. Predicted age-0 survival (S_0) given egg abundance and varying levels of peak discharge (cubic meters per second; CMS) for Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park. Peak discharge values are the minimum (i.e., 51 CMS) median (i.e., 142 CMS), and maximum (i.e., 282 CMS) observed from 1927 through 2013.

(a) 63 000 units every year



(b) 32 500 units every year

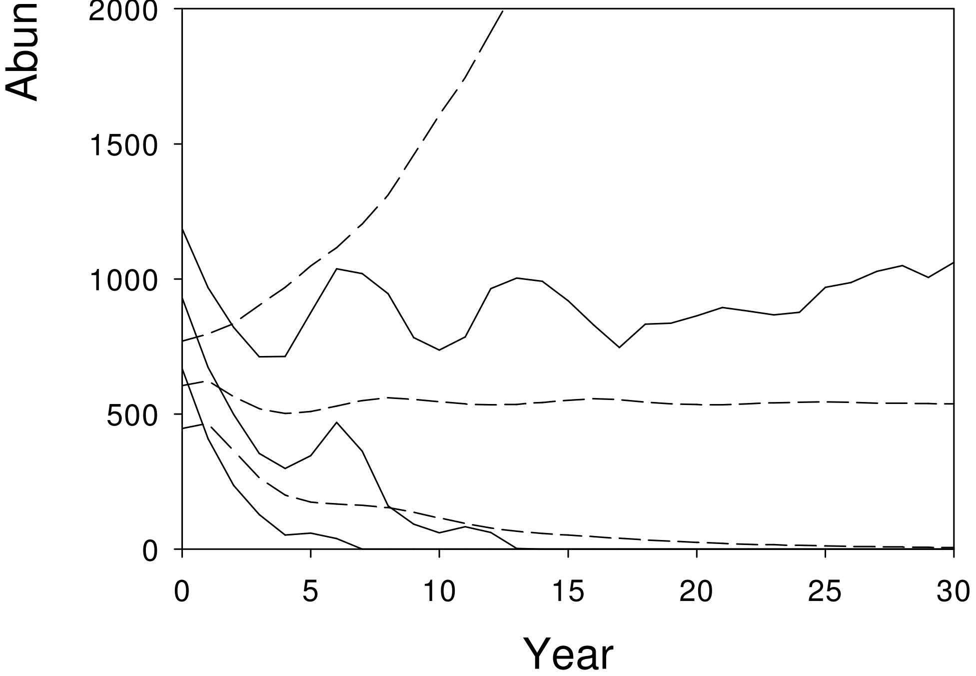


Figure 3.14. Abundance for age-1 and greater Yellowstone cutthroat trout (solid line) and age-2 and greater lake trout (dashed line) by simulation year for scenarios with 63 000 effort units implemented each year (a) and 32 500 units implemented each year (b). For each species, the center line delineates median abundance and the lower and upper lines delineate 95% confidence intervals.

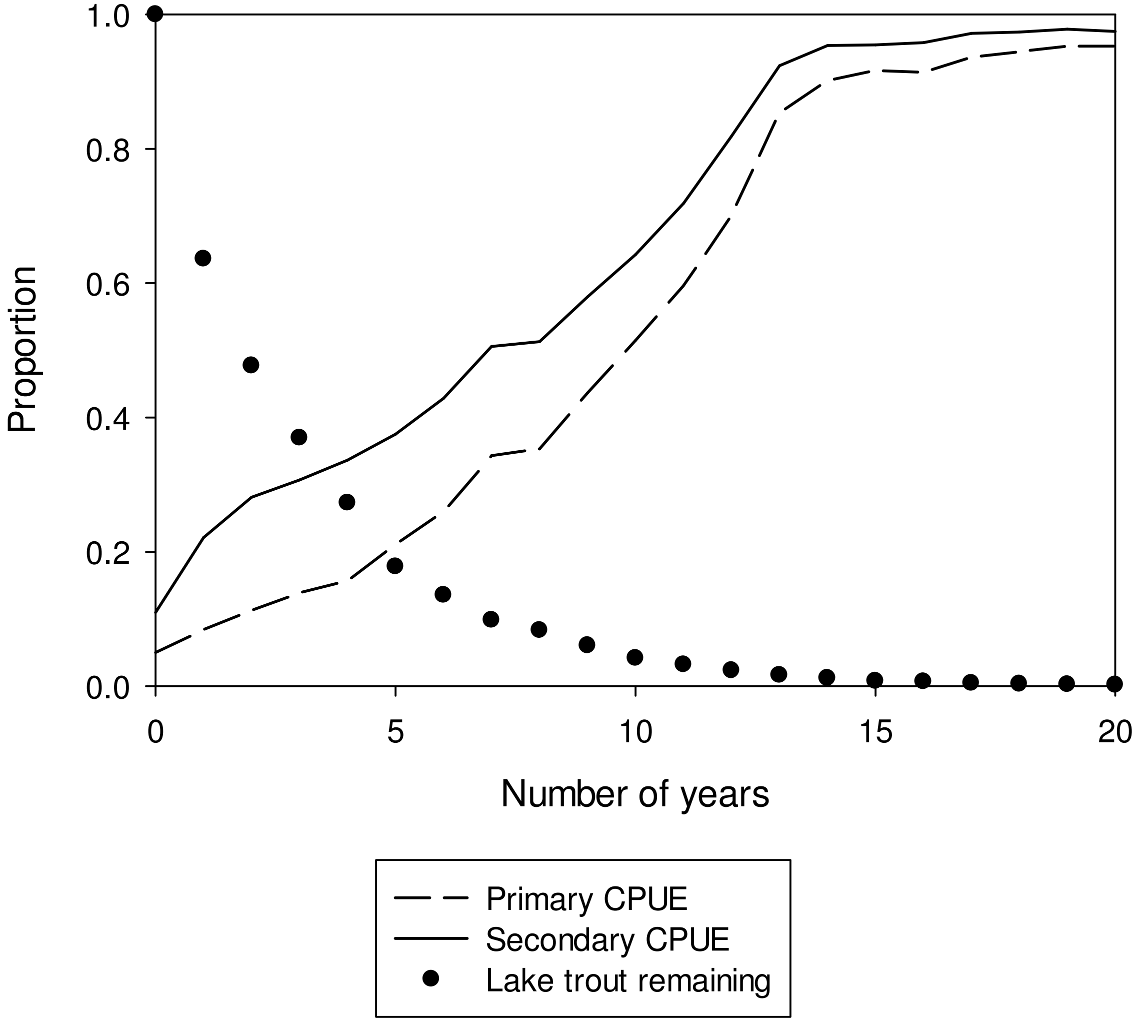


Figure 3.15. Proportion of lake trout abundance remaining (i.e., relative to 2013) and proportion of simulations with Yellowstone cutthroat trout catch per unit effort (CPUE) exceeding primary or secondary objectives as a function of the number of years with 63 000 units of fishing effort.

References

Al-Chokhachy, R., M. Peacock, L. Heki, and G. Thiede. 2009. Evaluating the reintroduction potential of Lahontan cutthroat trout in Fallen Leaf Lake, California. North American Journal of Fisheries Management 29:1296-1313.

Benson, N. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Service Fishery Research Report 56.

Bergum, D. J., K. A. Gunther, and L. M. Baril. In review. Impacts of Yellowstone cutthroat trout decline on mammals and birds in Yellowstone National Park.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1327-1338.

Britton, J. R., R. E. Gozlan, and G. H. Copp. 2011. Managing non-native fish in the environment. Fish and Fisheries 12:256-274.

Bulkley, R., and N. Benson. 1962. Predicting year-class abundance of Yellowstone Lake cutthroat trout. U.S. Fish and Wildlife Service Fishery Research Report 59.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Massachusetts.

Catalano, M. J., and M. S. Allen. 2011. A whole-lake density reduction to assess compensatory responses of gizzard shad *Dorosoma cepedianum*. Canadian Journal of Fisheries and Aquatic Sciences 68:955-968.

Claramunt, R. M., J. L. Jonas, J. D. Fitzsimmons, and J. E. Marsden. 2005. Influences of spawning habitat characteristics and interstitial predators on lake trout egg deposition and mortality. Transactions of the American Fisheries Society 134:1048-1057.

Coggins, L. G. Jr., M. D. Yard, and W. E. Pine III. 2011. Nonnative fish control in the Colorado River in Grand Canyon, Arizona: an effective program or serendipitous timing? Transactions of the American Fisheries Society 140:456-470.

Cox, B. S., C. S. Guy, and W. A. Fredenberg. 2013. Baseline demographics of a non-native lake trout population and inferences for suppression from sensitivity-elasticity analyses. Fisheries Management and Ecology 20:390-400.

Crossman, E. J. 1995. Introduction of the lake trout (*Salvelinus namaycush*) in areas outside its native distribution: a review. Journal of Great Lakes Research 21:17-29.

CSKT (Confederated Salish and Kootenai Tribes). 2014. Proposed strategies to benefit native species by reducing the abundance of lake trout in Flathead Lake, Montana. Final environmental impact statement. CSKT, Pablo, Montana.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C.A. Sulliven. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163-182.

Dux, A. M. 2005. Distribution and population characteristics of lake trout in Lake McDonald, Glacier National Park: implications for suppression. Master's thesis. Montana State University, Bozeman.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray, and B. S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences 108:1070 -1075.

Ferreri, C. P., W. W. Taylor, and D. B. Hayes. 1995. Evaluation of age-0 survival and its effects lake trout rehabilitation in the Michigan waters of Lake Superior. Journal of Great Lakes Research 21:218-224.

Ferreri, C. P., and W. W. Taylor. 1996. Compensation in individual growth rates and its influence on lake trout population dynamics in the Michigan waters of Lake Superior. Journal of Fish Biology 49:763-777.

Franssen, N. R., J. E. Davis, D. W. Ryden, and K. B. Gido. 2014. Fish community responses to mechanical removal of nonnative fishes in a large southwestern river. Fisheries 39:352-363.

Fredenberg, W. 2002. Further evidence that lake trout displace bull trout in Mountain lakes. Intermountain Journal of Sciences 8:143-152.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233-249.

Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pages 36-54 *in* M. K. Young, editor. Conservation assessment for inland cutthroat trout. USDA Forest Service, General Technical Report RM-GTR-256, Fort Collins, Colorado.

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.

Gresswell, R. E. 2009. Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region.

Gresswell, R.E. 2011. Biology, status, and management of the Yellowstone cutthroat trout. North American Journal of Fisheries Management 31:782-812.

Haddon, M. 2011. Modelling and quantitative methods in fisheries, 2nd edition. Chapman and Hall, New York.

Hansen, M.J., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid predator-prey dynamics in Lake Pend Orielle, Idaho, USA. Hydrobiologia 650: 85-100.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin System, Sea Grant Institute,WISCU-T-97-001, Madison.

Healy, M. C. 1978a. The dynamics of exploited lake trout populations and implications for management. Journal of Wildlife Management 42:307-328.

Healy, M. C. 1978b. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). Journal of the Fisheries Research Board of Canada 35:945-950.

Hunsaker II, D., L. F. Marnell, and F. P. Sharpe. 1970. Hooking mortality of Yellowstone cutthroat trout. The Progressive Fish-Culturist 231-235.

Isley, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187-228 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P.

Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 22:372-407.

Johnston, F. D., and J. R. Post. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecological Applications 19:449-467.

Jones, R. D., R. E. Gresswell, D. E. Jennings, S. M. Rubrecht, and J. D. Varley. 1980. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, technical report 1979, Yellowstone National Park, Wyoming.

Jones, R. D., D. G. Carty, R.E. Gresswell, K. A. Gunther, L. D. Lentsch, and J. Mohrman. 1985. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, technical report 1984, Yellowstone National Park, Wyoming.

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. 2010. Relative contributions of climate variation, lake trout predation, and other factors to the decline of Yellowstone Lake cutthroat trout during the three recent decades. Doctoral dissertation, Montana State University, Bozeman.

Kaeding, L. R., and T. M. Koel. 2011. Age, growth, maturity, and fecundity of Yellowstone cutthroat trout. Northwest Science 85:431-444.

Kaeding, L. R. 2012. Are Yellowstone Lake temperatures more suitable to nonnative lake trout than to native cutthroat trout? North American Journal of Fisheries Management 32:848-852.

Koehn, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. Freshwater Biology 49:882-894.

Koel, T., P. Bigelow, P. Doepke, B. Ertel, and D. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries 30:10-19.

Koel, T. M., J. L. Arnold, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2007. Yellowstone fisheries and aquatic sciences annual report, 2006. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2007-04.

Koel, T. M., P. E. Bigelow, J. L. Arnold, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2011. Native fish conservation plan environmental assessment. NPS, Yellowstone National Park, WY.

Koel, T. M., J. L. Arnold, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2012. Yellowstone fisheries and aquatic sciences annual report, 2011. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2012-03.

Linton, B. C., M. J. Hansen, S. T. Schram, and S. P. Sitar. 2007. Dynamics of a recovering lake trout population in eastern Wisconsin waters of Lake Superior, 1980-2001. North American Journal of Fisheries Management 27:940-954.

Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:49 -54.

Martin, N., and C. H. Olver. 1980. The lake Charr, *Salvelinus namaycush*. Pages 205-277 *in* E. Balon, editor. Charrs: salmonid fishes of the genus *Salvelinus*. Kluwer Boston, Inc., Hingham, Massachusetts.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western lake trout woes. Fisheries 34:424-442.

McIntyre, J. D. 1995. Review and assessment of possibilities for protecting the cutthroat trout of Yellowstone Lake from introduced lake trout. Pages 28-33 *in* J. D. Varley and Schullery, P., editors. The Yellowstone Lake crisis: confronting a lake trout invasion. Yellowstone Center for Resources, Yellowstone National Park Service, Yellowsone National Park, Wyoming.

Morgan, L., W. Shanks, D. Lovalvo, S. Johnson, W. Stephenson, K. Pierce, S. Harlan, C. Finn, G. Lee, M. Webring, B. Schulze, J. Duhn, R. Sweeney, and L. Balistrieri. 2003. Exploration and discovery in Yellowstone Lake: results from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. Journal of Volcanology and Geothermal Research 122:221-242.

Munro, A., T. McMahon, and J. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 62:79-87.

Murcia, S., B. L. Kerans, T. M. Koel, and E. MacConnell. 2014. *Myxobolus cerebralis* (Hofer) infection risk in native cutthroat trout *Oncorhynchus clarkii* (Richardson) and its relationships to tributary environments in the Yellowstone Lake Basin. Journal of Fish Diseases 37:1-16.

Myers, R. M., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404-2419.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil, Conseil International pour l'Exploration de la Mer 39:175 -192.

Pate, W. M., B. M. Johnson, J. M. Lepak, and D. Brauch. 2014. Managing for coexistence of kokanee and trophy lake trout in a montane reservoir. North American Journal of Fisheries Management 34:908-922.

Pazzia, I., M. Trudel, M. Ridgway, and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59:1593-1605.

Peterson, D. P., K. D. Fausch, J. Watmough, and R. A. Cunjak. 2008. When eradication is not an option: modeling strategies for electrofishing suppression of nonnative brook trout to foster persistence of sympatric native cutthroat trout in small streams. North American Journal of Fisheries Management 28:1847-1867.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Rose, K. A., J. H. Cowan, Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293-327.

Ruzycki, J., D. Beauchamp, and D. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Schill, D. J., J. S. Griffit, and R. E. Gresswell. 1986. Hooking mortality of cutthroat trout in a catch-and-release segment of the Yellowstone River, Yellowstone National Park. North American Journal of Fisheries Management 6:226-232.

Sitar, S. P., J. R. Bence, J. E. Johnson, M. P. Ebener, and W. W. Taylor. 1999. Lake trout mortality and abundance in southern Lake Huron. North American Journal of Fisheries Management 19:881.

Sitar, S. P., and J. X. He. 2006. Growth and maturity of hatchery and wild lean lake trout during population recovery in Michigan waters of Lake Superior. Transactions of the American Fisheries Society 135:915-923.

Stapp, P., and G. Hayward. 2002. Effects of an introduced piscivore on native trout: insights from a demographic model. Biological Invasions 4:299-316.

Stubben, C. J. and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:1-23.

Syslo, J. M., C. S. Guy, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and T. M. Koel. 2011. Response of non-native lake trout (*Salvelinus namaycush*) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park. Canadian Journal of Fisheries and Aquatic Sciences 68:2132-2145.

Theriot, E. C., S. C. Fritz, and R. E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park, Wyoming, U.S.A. Arctic and Alpine Research 29:304-314.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45:759-771.

Tronstad, L., R. Hall, T. Koel, and K. Gerow. 2010. Introduced lake trout produced a four-level trophic cascade in Yellowstone Lake. Transactions of the American Fisheries Society 139:1536-1550.

Tsayehe, I., M. Catalano, G. Sass, D. Glover, and B. Roth. 2013. Prospects for fishery-induced collapse of invasive Asian carp in the Illinois River. Fisheries 38:445-454.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6:274-288.

Vincenzi, S., A. J. Crivelli, D. Jesensek, and G A. De Leo. 2008. The role of density-dependent individual growth in the persistence of freshwater salmonid populations. Oecologia 156:523-534.

Weidel, B., D. Josephson, and C. Kraft. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack Lake. Transactions of the American Fisheries Society 136:778-789.

CHAPTER FOUR

CONCLUSIONS

The Yellowstone Lake ecosystem underwent a massive change following the introduction of lake trout (Koel et al. 2005; Tronstad et al. 2010). As a well-studied system with a simple fish assemblage, Yellowstone Lake provided a unique opportunity to study the ecology of a native and non-native salmonid in a large natural lake. The combination of long-term data, a large increase in a non-native piscivore population, and the collapse of a native prey population, provided a unique opportunity to evaluate ecological processes (including prey limitation and density-dependent compensatory responses in population dynamics) that are considered to have pervasive effects of populations, but are difficult to observe.

Examining the feeding habits of nonnative fishes is critical for determining the ecological effects of species introductions. Diet studies are commonly conducted for non-native fishes to evaluate trophic overlap or the effects of piscivory on native fishes (Ruzycki et al. 2001; Clarke et al. 2005; Schoen et al. 2012); however, studies documenting long-term changes in feeding habits are rare. Chapter 2 examined trophic overlap between non-native lake trout and native Yellowstone cutthroat trout from 2011 – 2013, 18 years after the discovery of lake trout. Lake trout and Yellowstone cutthroat trout diets were then compared to results from diet studies conducted during previous periods with contrasting Yellowstone cutthroat trout and lake trout catch per unit effort (CPUE) to determine whether diet changes occurred with changes in density.

Lake trout were trophically similar to Yellowstone cutthroat trout from 2011 – 2013 as a result of large (i.e., piscivorous) lake trout shifting from a diet dominated by Yellowstone cutthroat trout during the early stages of invasion to a diet dominated by benthic amphipods. Additionally, Yellowstone cutthroat trout diets shifted from domination by zooplankton to amphipods following a decline in abundance. Not only do Yellowstone cutthroat trout face the threat posed by predation from lake trout, but they also face the potential threat of competition if lake trout abundance remains high and amphipods are limiting.

Diet studies for lake trout in Yellowstone Lake have only been conducted during the ice-free season (i.e., May through October). Fish were common in winter diets of lake trout in Lake Opeongo, Ontario (Martin 1954), and for non-native lake trout in Lake Chelan, Washington (Schoen 2012). If predation on Yellowstone cutthroat trout increases during the winter, we would have underestimated the effect of lake trout predation on Yellowstone cutthroat trout abundance. Future research should address lake trout diets in Yellowstone Lake during the winter.

Temporal diet shifts for both species indicated bioenergetically preferable prey (i.e., Yellowstone cutthroat trout in lake trout diets and amphipods in Yellowstone cutthroat trout diets) composed a larger proportion of the diet when consumer CPUE was low. Therefore, results from Chapter 2 indicated temporal diet shifts provided potential mechanisms for compensatory responses in weight, growth, or maturity schedule, which were evaluated in Chapter 3. Additionally, the estimation of consumption at contrasting predator-prey ratios was important for developing a simulation model to predict the response of Yellowstone cutthroat trout to ongoing lake trout suppression (Chapter 3).

In Chapter 3, long-term monitoring and catch data were used to develop statistical catch-at-age (SCA) models to estimate abundance and fishery characteristics (i.e., catchability and mortality) for Yellowstone cutthroat trout and lake trout. I then evaluated the effects of abundance and environmental variation on population metrics (i.e., individual growth, weight, maturity schedule, and pre-recruit survival) for Yellowstone cutthroat trout and lake trout. The 5-fold variation in Yellowstone cutthroat trout abundance and 6-fold variation in lake trout abundance provided an opportunity to evaluate population metrics for compensatory responses to variation in density. Following the observation of diet shifts in Chapter 2, I hypothesized that compensatory responses would be evident in population metrics for both species. Yellowstone cutthroat trout weight and pre-recruit survival decreased with increasing abundance; however, growth in length and maturity were not related to abundance. Lake trout growth in length, weight, maturity, and pre-recruit survival did not vary as a function of abundance. This result was surprising considering drastic shift from piscivory to consumption of benthic amphipods observed in Chapter 2. The results from bioenergetics modeling indicated lake trout were able to obtain adequate caloric inputs through consumption rates that were elevated relative to lake trout in systems where they are primarily piscivorous (Chapter 2).

Finally, I used the results of SCA modeling and population metric analyses to develop a simulation model of the lake trout – Yellowstone cutthroat trout system to assess the decrease in lake trout abundance required for Yellowstone cutthroat trout to increase to levels specified by management objectives. The simulation model indicated substantial decreases in lake trout abundance relative to 2013 levels was required for a reasonably high probability of Yellowstone cutthroat trout persisting at or above levels specified by performance metrics. However, the large number of variables influencing lake trout and Yellowstone cutthroat trout abundances resulted in considerable uncertainty, underscoring the difficulty in predicting the response of native fish populations to the mechanical removal of non-native fishes.

Although Yellowstone cutthroat trout composed a smaller proportion of lake trout diet from 2011 through 2013 and per-capita consumption of Yellowstone cutthroat trout was reduced relative to the late 1990s, the scaling of per-capita consumption by lake trout abundance indicated several hundred thousand Yellowstone cutthroat trout individuals would continue to be consumed each year if lake trout abundance was maintained at the 2013 estimate. Therefore, the continuation of lake trout suppression is necessary for Yellowstone cutthroat trout to persist at the desired abundance. Fortunately, the amount of fishing effort exerted in 2013 appears to be sufficient to cause the lake trout population decline to levels necessary for Yellowstone cutthroat trout persistence. My results indicate that a large amount of suppression effort should be continued for the next several years. Given the large amount of resources consumed by lake trout suppression, the evaluation of alternative strategies for increasing lake trout mortality is important. The identification of spawning locations is important for inflicting high rates of mortality on adult lake trout while they are aggregated in Autumn. Additionally, methods for inflicting mortality on developing embryos should continue to be researched and implemented (Cox et al. 2012).

Abundance and population characteristics should continue to be estimated through the future to improve the understanding of key vital rates. Lake trout pre-recruit survival contributed substantial variation to the simulation model (Chapter 3), and continued estimation of this vital rate may reduce the variation and allow for the detection of density-dependence. If density-dependence is expressed in pre-recruit survival, an upper limit for lake trout abundance may be determined and more realism included in simulation models. The continued estimation of abundance and population characteristics relies on the continued monitoring of lake trout and Yellowstone cutthroat trout populations.

The lake trout suppression program in Yellowstone Lake is the longest ongoing lake trout removal program in the Western USA (Martinez et al. 2009) and provides a rare example of a long-term mechanical-removal program for a non-native fish species in a large lentic ecosystem. The efficacy of mechanical removal programs for non-native fishes is often difficult to demonstrate (Coggins et al. 2011; Franssen et al. 2014); nevertheless, mechanical removal projects are being implemented or considered in several large, open water bodies throughout the world (Koehn 2004; Martinez et al. 2009; Tsayehe et al. 2013). The combination of long-term data and contrasting abundances observed in Yellowstone Lake allowed for the development of a realistic model of the predator-prey system, which provided guidance for the lake trout suppression program. Lake trout suppression in Yellowstone Lake highlights the importance of setting quantifiable objectives, establishing long-term monitoring programs, and sustaining a large amount of fishing pressure to reduce non-native fish populations in large water bodies.

REFERENCES

Al-Chokhachy, R., M. Peacock, L. Heki, and G. Thiede. 2009. Evaluating the reintroduction potential of Lahontan cutthroat trout in Fallen Leaf Lake, California. North American Journal of Fisheries Management 29:1296-1313.

Baril, L. M., D. W. Smith, T. Drummer, and T. M. Koel. 2013. Implications of cutthroat trout declines for breeding ospreys and bald eagles at Yellowstone Lake. Journal of Raptor Research 17:234-235.

Beauchamp, D. A., M. W. Kershner, N. C. Overman, J. Rhydderch, J. Lin, and L. Hauser. 2006. Trophic interactions on nonnative lake trout and lake whitefish in the Flathead Lake foodweb. Report to the Confederated Salish-Kootenai Tribes.

Beauchamp, D. A., D. H. Wahl, and B. M. Johnson. 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Benson, N. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Service Fishery Research Report 56.

Bergum, D. J., K. A. Gunther, and L. M. Baril. In review. Impacts of Yellowstone cutthroat trout decline on mammals and birds in Yellowstone National Park.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1327-1338.

Britton, J. R., R. E. Gozlan, and G. H. Copp. 2011. Managing non-native fish in the environment. Fish and Fisheries 12:256-274.

Bronte, C. R., S. T. Schram, J. H. Slegeby, and B. L. Swanson. 1995. Density-independent survival of wild lake trout in the Apostle Islands area of Lake Superior. Journal of Great Lakes Research 21:246-252.

Bryan, S. D., C. A. Soupir, W. G. Duffy, and C. E. Freiburger. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. Journal of Freshwater Ecology 11:153-161.

Bulkley, R., and N. Benson. 1962. Predicting year-class abundance of Yellowstone Lake cutthroat trout. U.S. Fish and Wildlife Service Fishery Research Report 59.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalization of alien recreational freshwater fisheries. Hydrobiologia 500:217-230.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Massachusetts.

Catalano, M. J., and M. S. Allen. 2011. A whole-lake density reduction to assess compensatory responses of gizzard shad *Dorosoma cepedianum*. Canadian Journal of Fisheries and Aquatic Sciences 68:955-968.

Chipps, S. R., and J. E. Garvey. 2007. Assessment of diets and feeding patterns. Pages 473-514 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Cianco, J. E., M. A. Pascual, and D. A. Beauchamp. 2007. Energy density of Patagonian aquatic organisms and empirical predictions based on water content. Transactions of the American Fisheries Society 136:1415-1422.

Claramunt, R. M., J. L. Jonas, J. D. Fitzsimmons, and J. E. Marsden. 2005. Influences of spawning habitat characteristics and interstitial predators on lake trout egg deposition and mortality. Transactions of the American Fisheries Society 134:1048-1057.

Clarke, L. R., D. T. Vidergar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:267-277.

Coggins, L. G. Jr., M. D. Yard, and W. E. Pine III. 2011. Nonnative fish control in the Colorado River in Grand Canyon, Arizona: an effective program or serendipitous timing? Transactions of the American Fisheries Society 140:456-470.

Cox, B. S., A. M. Dux, M. C. Quist, and C. S. Guy. 2012. Use of a seismic air gun to reduce survival of nonnative lake trout embryos: a tool for conservation? North American Journal of Fisheries Management 32:292-298.

Cox, B. S., C. S. Guy, and W. A. Fredenberg. 2013. Baseline demographics of a non-native lake trout population and inferences for suppression from sensitivity-elasticity analyses. Fisheries Management and Ecology 20:390-400.

Crait, J. R., and M. Ben-David. 2006. River otters in Yellowstone Lake depend on a declining cutthroat trout population. Journal of Mammalogy 87:485-494.

Crossman, E. J. 1995. Introduction of the lake trout (*Salvelinus namaycush*) in areas outside its native distribution: a review. Journal of Great Lakes Research 21:17-29.

CSKT (Confederated Salish and Kootenai Tribes). 2014. Proposed strategies to benefit native species by reducing the abundance of lake trout in Flathead Lake, Montana. Final environmental impact statement. CSKT, Pablo, Montana.

Cucherousset, J., and J. Olden. 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36:215-230.

Cummins, K. W., and J.C. Wuycheck. 1971. Caloric equivalents and investigations in ecological energetics. Mitteilungen international Vereinigung fur theorische und angewandte Limnologie 18:1-151.

Dextrase, A. J., and N. E. Mandrak. 2006. Impacts of alien invasive species species on fauna at risk in Canada. Biological Invasions 8:13-24.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C.A. Sulliven. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163-182.

Dux, A. M. 2005. Distribution and population characteristics of lake trout in Lake McDonald, Glacier National Park: implications for suppression. Master's thesis. Montana State University, Bozeman.

Dux, A. M., C. S. Guy, and W. A. Fredenberg. 2011. Spatiotemporal distribution and population characteristics of a nonnative lake trout population, with implications for suppression. North American Journal of Fisheries Management 31:187-196.

Eby, L. A., L. G. Rudstam, and J. F. Kitchell. 1995. Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1564-1571.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. Trends in Ecology and Evolution 21:576-584.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray, and B. S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences 108:1070 -1075.

Elrod, J. H., and R. O'Gorman. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979-1987. Transactions of the American Fisheries Society 120:290-302.

Evans, D. O., and C. C. Willox. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycush*, by stocking of non-native stocks. Canadian Journal of Fisheries and Aquatic Sciences 48:134-147.

Feiner, Z. S., J. A. Rice, A. J. Bunch, and D. D. Aday. 2013. Trophic niche and diet overlap between invasive white perch and resident white bass in a southeastern reservoir. Transactions of the American Fisheries Society 142:912-919.

Ferreri, C. P., W. W. Taylor, and D. B. Hayes. 1995. Evaluation of age-0 survival and its effects lake trout rehabilitation in the Michigan waters of Lake Superior. Journal of Great Lakes Research 21:218-224.

Ferreri, C. P., and W. W. Taylor. 1996. Compensation in individual growth rates and its influence on lake trout population dynamics in the Michigan waters of Lake Superior. Journal of Fish Biology 49:763-777.

Franssen, N. R., J. E. Davis, D. W. Ryden, and K. B. Gido. 2014. Fish community responses to mechanical removal of nonnative fishes in a large southwestern river. Fisheries 39:352-363.

Fredenberg, W. 2002. Further evidence that lake trout displace bull trout in Mountain lakes. Intermountain Journal of Sciences 8:143-152.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233-249.

Gardner, W. S., T. F. Nalepa, W. A. Frez, E. A. Cichoki, and P. F. Landrum. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. Canadian Journalof Fisheries and Aquatic Sciences 42:1827-1832.

Garvey, J. E., and S. R. Chipps. 2012. Diets and energy flow. Pages 733 – 779 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries Techniques, 3rd edition. American Fisheries Society, Bethesda, MD.

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.

Gresswell, R. E., W. J. Liss, and G. L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 51:298-309.

Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pages 36-54 *in* M. K. Young, editor. Conservation assessment for inland cutthroat trout. USDA Forest Service, General Technical Report RM-GTR-256, Fort Collins, Colorado.

Gresswell, R. E. 2009. Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region.

Gresswell, R.E. 2011. Biology, status, and management of the Yellowstone cutthroat trout. North American Journal of Fisheries Management 31:782-812.

Haddon, M. 2011. Modelling and quantitative methods in fisheries, 2nd edition. Chapman and Hall, New York.

Hansen, M.J., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid predator-prey dynamics in Lake Pend Orielle, Idaho, USA. Hydrobiologia 650: 85-100.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin System, Sea Grant Institute,WISCU-T-97-001, Madison.

Healy, M. C. 1978a. The dynamics of exploited lake trout populations and implications for management. Journal of Wildlife Management 42:307-328.

Healy, M. C. 1978b. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). Journal of the Fisheries Research Board of Canada 35:945-950.

Hondorp, D. W., S. A. Pothoven, and S. B. Brandt. 2005. Influence of Diporeia density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. Transactions of the American Fisheries Society 134:588-601.

Hunsaker II, D., L. F. Marnell, and F. P. Sharpe. 1970. Hooking mortality of Yellowstone cutthroat trout. The Progressive Fish-Culturist 231-235.

Isley, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187-228 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 22:372-407.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:127-143.

Johnston, F. D., and J. R. Post. 2009. Density-dependent life-history compensation of an iteroparous salmonid. Ecological Applications 19:449-467.

Jones, R. D., R. E. Gresswell, D. E. Jennings, S. M. Rubrecht, and J. D. Varley. 1980. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, technical report 1979, Yellowstone National Park, Wyoming.

Jones, R. D., D. G. Carty, R.E. Gresswell, K. A. Gunther, L. D. Lentsch, and J. Mohrman. 1985. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, technical report 1984, Yellowstone National Park, Wyoming.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:127-143.

Jones, R.D., R. Andrascik, D.G. Carty, E.M. Colvard, R. Ewing, W.R.Gould, R.E. Gresswell, D.L. Mahoney, T. Olliff, and S.E. Relyea. 1990. Fishery and aquatic management program. U.S. Fish and Wildlife Service, Technical Report for 1989, Yellowstone National Park, Wyoming.

Juanes, F., J. Buckel, and F. S. Scharf. 2002. Feeding ecology of piscivorous fishes. Pages 267-283 *in* P. J. Hart and J. D. Reynolds, editors. Handbook of fish biology and fisheries. Blackwell, Hoboken, New Jersey.

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. 2010. Relative contributions of climate variation, lake trout predation, and other factors to the decline of Yellowstone Lake cutthroat trout during the three recent decades. Doctoral dissertation, Montana State University, Bozeman.

Kaeding, L. R., and T. M. Koel. 2011. Age, growth, maturity, and fecundity of Yellowstone cutthroat trout. Northwest Science 85:431-444.

Kaeding, L. R. 2012. Are Yellowstone Lake temperatures more suitable to nonnative lake trout than to native cutthroat trout? North American Journal of Fisheries Management 32:848-852.

Kaplinski, M. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wyoming. Master's thesis, Northern Arizona University, Flagstaff.

Koehn, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. Freshwater Biology 49:882-894.

Koel, T., P. Bigelow, P. Doepke, B. Ertel, and D. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries 30:10-19.

Koel, T. M., D. L. Mahony, K. L. Kinnan, C. Rasmussen, C. J. Hudson, S. Murcia, and B. L. Kerans. 2006. *Myxobolus cerebralis* in native cutthroat trout of the Yellowstone Lake Ecosystem. Journal of Aquatic Animal Health 18:157-175.

Koel, T. M., J. L. Arnold, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2007. Yellowstone fisheries and aquatic sciences annual report, 2006. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2007-04.

Koel, T. M., P. E. Bigelow, J. L. Arnold, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2011. Native fish conservation plan environmental assessment. NPS, Yellowstone National Park, WY.

Koel, T. M., J. L. Arnold, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2012. Yellowstone fisheries and aquatic sciences annual report, 2011. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2012-03.

Linton, B. C., M. J. Hansen, S. T. Schram, and S. P. Sitar. 2007. Dynamics of a recovering lake trout population in eastern Wisconsin waters of Lake Superior, 1980-2001. North American Journal of Fisheries Management 27:940-954.

Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:49 -54.

Luecke, C., and D. Brandt. 1993. Estimating the energy density of Daphnid prey for use with rainbow trout bioenergetics models. Transactions of the American Fisheries Society 122:386-389.

Martin, N. V. 1954. Catch and winter food of lake trout in certain Algonquin Park Lakes. Journal of the Fisheries Research Board of Canada 11:5-10.

Martin, N., and C. H. Olver. 1980. The lake Charr, *Salvelinus namaycush*. Pages 205-277 *in* E. Balon, editor. Charrs: salmonid fishes of the genus *Salvelinus*. Kluwer Boston, Inc., Hingham, Massachusetts.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western lake trout woes. Fisheries 34:424-442.

Martinussen, P. A., G. Robertsen, and S. Einum. 2011. Density-dependent diet composition of juvenile Atlantic salmon (*Salmo salar*). Ecology of Freshwater Fish 20:384-392.

Matuszek, J. E., B. J. Shuter and J. M. Casselman. 1990. Changes in lake trout growth and abundance after introduction of cisco into Lake Opeongo, Ontario. Transactions of the American Fisheries Society 119:718-729.

McHugh, P., P. Budy, G. Thiede, and E. VanDyke. 2008. Trophic relationships on nonnative brown trout, *Salmo trutta*, and native Bonneville cutthroat trout, *Onchorhynchus clarkii utah*, in a northern Utah, USA river. Environmental Biology of Fishes 81:63-75.

McIntyre, J. D. 1995. Review and assessment of possibilities for protecting the cutthroat trout of Yellowstone Lake from introduced lake trout. Pages 28-33 *in* J. D. Varley and Schullery, P., editors. The Yellowstone Lake crisis: confronting a lake trout invasion. Yellowstone Center for Resources, Yellowstone National Park Service, Yellowsone National Park, Wyoming.

McMahon, T. E., and D. H. Bennett. 1996. Walleye and northern pike: boost or bane to Northwest fisheries? Fisheries 21:6-13.

Minigawa, M., and E. Wada. 1984. Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. Geochimica et Cosmochimica Acta 48:1135-1140.

Morgan, L., W. Shanks, D. Lovalvo, S. Johnson, W. Stephenson, K. Pierce, S. Harlan, C. Finn, G. Lee, M. Webring, B. Schulze, J. Duhn, R. Sweeney, and L. Balistrieri. 2003. Exploration and discovery in Yellowstone Lake: results from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. Journal of Volcanology and Geothermal Research 122:221-242.

Munro, A., T. McMahon, and J. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 62:79-87.

Murcia, S., B. L. Kerans, T. M. Koel, and E. MacConnell. 2014. *Myxobolus cerebralis* (Hofer) infection risk in native cutthroat trout *Oncorhynchus clarkii* (Richardson) and its relationships to tributary environments in the Yellowstone Lake Basin. Journal of Fish Diseases 37:1-16.

Myers, R. M., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404-2419.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil, Conseil International pour l'Exploration de la Mer 39:175 -192.

Pate, W. M., B. M. Johnson, J. M. Lepak, and D. Brauch. 2014. Managing for coexistence of kokanee and trophy lake trout in a montane reservoir. North American Journal of Fisheries Management 34:908-922.

Pazzia, I., M. Trudel, M. Ridgway, and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59:1593-1605.

Peterson, D. P., K. D. Fausch, J. Watmough, and R. A. Cunjak. 2008. When eradication is not an option: modeling strategies for electrofishing suppression of nonnative brook trout to foster persistence of sympatric native cutthroat trout in small streams. North American Journal of Fisheries Management 28:1847-1867.

Plosila, D. S. 1977. Relationship of strain and size of stocking to survival of lake trout in Adirondack lakes. New York Fish and Game Journal 24:1-24. Post., D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Pothoven, S. A., T. F. Nalepa, P. J. Schneeberger, and S. B. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21:876-883.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Quist, M. C., C. S. Guy, R. J. Bernot, and J. L. Stephen. 2002. Efficiency of removing food items from walleyes using acrylic tubes. Journal of Freshwater Ecology 17:179-184.

Rand, P. S., and D. J. Stewart. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983-1993: a test of bioenergetics model prediction. Canadian Journal of Fisheries and Aquatic Sciences 55:307-317.

Richards, J. M., M. J. Hansen, C. R. Bronte, and S. P. Sitar. 2004. Recruitment dynamics of the 1971-1991 year-classes of lake trout in Michigan waters of Lake Superior. North American Journal of Fisheries Management 24:475-489.

Rose, K. A., J. H. Cowan, Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293-327.

Roseman, E. F., J. S. Schaeffer, E. Bright, and D. G. Fielder. 2014. Angler-caught piscivore diets reflect fish community changes in Lake Huron. Transactions of the American Fisheries Society 143:1419-1433.

Rudstam, L. G., T. E. Brooking, S. D. Krueger, and J. R. Jackson. 2011. Analysis of compensatory responses in land-locked Alewives to Walleye predation: a tale of two lakes. Transactions of the American Fisheries Society 140:1587-1603.

Ruzycki, J. R., and D. A. Beauchamp. 1997. A bioenergetics modeling assessment of the lake trout impact in Yellowstone Lake. Pages 127-133 *in* R. E. Gresswel, P. Dwyer, and R. H. Hamre, editors. Wild trout VI symposium. Federation of Flyfishers, Fort Collins, Colorado.

Ruzycki, J. R., W. A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah-Idaho. Transactions of the American Fisheries Society 130:1175-1189.

Ruzycki, J., D. Beauchamp, and D. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Ruzycki, J. 2004. Impact of lake trout introductions on cutthroat trout of selected western lakes of the continental United States. Doctoral dissertation, Utah State University, Logan.

Schill, D. J., J. S. Griffit, and R. E. Gresswell. 1986. Hooking mortality of cutthroat trout in a catch-and-release segment of the Yellowstone River, Yellowstone National Park. North American Journal of Fisheries Management 6:226-232.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: pulsed predatory inertia of lake trout and decline of kokanee. Transactions of the American Fisheries Society 141:1191-1206.

Schoener, T. W. 1968. The anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704-726.

Simberloff, D. 2001. Biological invasions – how are they affecting us, and what can we do about them? Western North American Naturalist 61:308-315.

Sitar, S. P., J. R. Bence, J. E. Johnson, M. P. Ebener, and W. W. Taylor. 1999. Lake trout mortality and abundance in southern Lake Huron. North American Journal of Fisheries Management 19:881.

Sitar, S. P., and J. X. He. 2006. Growth and maturity of hatchery and wild lean lake trout during population recovery in Michigan waters of Lake Superior. Transactions of the American Fisheries Society 135:915-923.

Spencer, C. N., B. R. McClelland and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. BioScience 41(1):14-21.

Stapp, P., and G. Hayward. 2002. Effects of an introduced piscivore on native trout: insights from a demographic model. Biological Invasions 4:299-316.

Stubben, C. J. and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:1-23.

Syslo, J. M., C. S. Guy, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and T. M. Koel. 2011. Response of non-native lake trout (*Salvelinus namaycush*) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park. Canadian Journal of Fisheries and Aquatic Sciences 68:2132-2145.

Teisberg, J. F., M. A. Haroldson, C. C. Schwartz, K. A. Gunther, J. F. Fortin, and C. T. Robbins. 2014. Contrasting past and current numbers of bears visiting Yellowstone cutthroat trout streams. Journal of Wildlife Management 78:369-378.

Theriot, E. C., S. C. Fritz, and R. E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park, Wyoming, U.S.A. Arctic and Alpine Research 29:304-314.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45:759-771.

Tronstad, L., R. Hall, T. Koel, and K. Gerow. 2010. Introduced lake trout produced a four-level trophic cascade in Yellowstone Lake. Transactions of the American Fisheries Society 139:1536-1550.

Tsayehe, I., M. Catalano, G. Sass, D. Glover, and B. Roth. 2013. Prospects for fishery-induced collapse of invasive Asian carp in the Illinois River. Fisheries 38:445-454.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer δ15N and δ13C and the trophic position of aquatic consumers. Ecology 80:1395-1404.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6:274-288.

Vincenzi, S., A. J. Crivelli, D. Jesensek, and G A. De Leo. 2008. The role of density-dependent individual growth in the persistence of freshwater salmonid populations. Oecologia 156:523-534.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused biological change. New Zealand Journal of Ecology 21:1-16.

Wallace, R. K. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110:72-76.

Weidel, B., D. Josephson, and C. Kraft. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack Lake. Transactions of the American Fisheries Society 136:778-789.

APPENDICES

APPENDIX A

CONSUMPTION RATES USED IN SIMULATION MODEL

Table A.1. Per-capita consumption rates by lake trout age class accounting for age-specific mortality through the year.

	Age														
Effort	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17+
							Prey:predator ≥ 17								
32500	10.5	10.3	28.1	27.7	27.3	26.9	26.2	26.2	25.8	25.8	25.8	25.8	25.8	25.8	25.8
63000	8.2	7.8	15.5	15.1	14.3	13.4	13.1	12.7	12.7	12.7	12.3	12.3	12.3	12.3	12.3
							Prey:predator < 17								
32500	0.0	0.0	4.7	5.3	6.5	14.0	16.0	17.3	18.3	18.9	20.2	20.8	21.4	22.0	22.7
63000	0.0	0.0	2.6	2.9	3.4	7.0	8.0	8.4	9.0	9.3	9.6	9.9	10.2	10.5	10.8

APPENDIX B

PARAMETER ESTIMATES FROM STATISTICAL CATCH-AT-AGE MODELS

Table B.1. Log-scale parameter estimates (asymptotic SD) for a statistical catch-at-age model for Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park. Model parameters are described in Table 2.

Parameter	Estimate (SD)
$N_{y,1}$	13.95 (0.09), 13.62 (0.09), 13.55 (0.09), 13.40 (0.09), 13.18 (0.09), 13.07 (0.09), 13.00 (0.09), 13.16 (0.09), 13.22 (0.09), 13.49 (0.08), 13.47 (0.08), 13.22 (0.08), 12.79 (0.08), 12.84 (0.08), 12.66 (0.08), 12.60 (0.08), 12.50 (0.08), 12.56 (0.08), 12.66 (0.08), 12.85 (0.08), 13.02 (0.09), 12.94 (0.09), 13.15 (0.09), 12.85 (0.10), 13.08 (0.11), 13.77 (0.16), 13.65 (0.13), 13.00 (0.19)
$N_{1986,a}$	13.14 (0.09), 12.04 (0.10), 11.32 (0.12), 10.64 (0.13), 9.05 (0.19), 8.15 (0.28)
a_{50_G}	1.47 (0.03)
a_{95_G}	1.85 (0.04)
a_{50_R}	1.57 (0.02)
a_{95_R}	1.86 (0.02)
a_{50_A}	1.55 (0.05)
a_{95_A}	2.04 (0.06)
q_G	-11.75 (0.12)
q_R	-9.98 (0.08)
q_A	-7.78 (0.11)
σ_G	-0.98 (0.18)
σ_R	-1.24 (0.16)
σ_A	-1.37 (0.14)

Table B.2. Log-scale parameter estimates (asymptotic SD) for a statistical catch-at-age model for lake trout in Yellowstone Lake, Yellowstone National Park. Model parameters are described in Table 2.

Parameter	Estimate (SD)
$N_{y,2}$	10.86 (0.09), 10.81 (0.09), 10.57 (0.10), 10.54 (0.11), 10.49 (0.11), 10.75 (0.10), 11.23 (0.10), 11.71 (0.09), 11.95 (0.09), 12.04 (0.09), 12.21 (0.10), 12.25 (0.10), 12.36 (0.11), 12.62 (0.12), 12.81 (0.13), 12.42 (0.19)
$N_{1998,a}$	10.86 (0.09), 10.22 (0.10), 10.18 (0.10), 8.25 (0.23), 8.12 (0.25), 7.94 (0.27), 6.92 (0.45), 6.31 (0.61), 6.29 (0.63), 7.00 (0.46), 7.00 (0.48), 7.02 (0.50), 7.34 (0.49), 7.11 (0.62), 6.41 (1.22), 5.20 (1.08)
a_{50_G}	0.74 (0.05)
a_{95_G}	1.11 (0.02)
q_G	-11.10 (0.06)
σ_G	-0.69 (0.06)

APPENDIX C

LAKE TROUT GROWTH MODEL COMPARISONS

Table C.1. Akaike information criterion (AIC) and ΔAIC values for linear regression models of length at capture as a function of abundance for lake trout in Yellowstone Lake, Yellowstone National Park.

Model	**AIC**	**ΔAIC**
Age 2		
Abundance	3792.3	0.0
Null	3812.3	20.0
Age 3		
Null	4759.1	0.0
Abundance	4760.9	1.8
Age 4		
Abundance	4954.6	0.0
Null	5039.2	84.6
Age 5		
Abundance	4669.0	0.0
Null	4695.0	26.0
Age 6		
Abundance	5028.1	0.0
Null	5039.4	11.3
Age 7		
Abundance	4690.7	0.0
Null	4693.8	3.1
Age 8		
Null	3577.0	0.0
Abundance	3578.6	1.6
Age 9		
Abundance	2875.6	0.0
Null	2879.8	4.2

Table C.1. Continued.

Model	**AIC**	**ΔAIC**
Age 10		
Null	2435.8	0.0
Abundance	2436.6	0.8
Age 11		
Null	1560.9	0.0
Abundance	1561.2	0.3
Age 12		
Null	1131.1	0.0
Abundance	1132.9	1.8
Age 13		
Null	770.3	0.0
Abundance	772.3	2.0