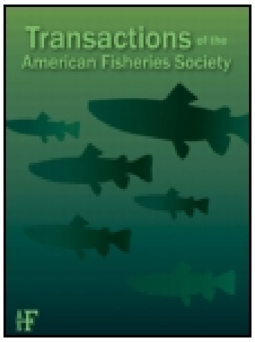

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ARTICLE

Feeding Ecology of Native and Nonnative Salmonids during the Expansion of a Nonnative Apex Predator in Yellowstone Lake, Yellowstone National Park

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Abstract

The illegal introduction of Lake Trout *Salvelinus namaycush* into Yellowstone Lake, Yellowstone National Park, preceded the collapse of the native population of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, producing a four-level trophic cascade. The Yellowstone Cutthroat Trout population's collapse and the coinciding increase in Lake Trout abundance provided a rare opportunity to evaluate the feeding ecology of a native prey species and a nonnative piscivore species after the restructuring of a large lentic ecosystem. We assessed diets, stable isotope signatures, and depth-related CPUE patterns for Yellowstone Cutthroat Trout and Lake Trout during 2011–2013 to evaluate trophic overlap. To evaluate diet shifts related to density, we also compared 2011–2013 diets to those from studies conducted during previous periods with contrasting Yellowstone Cutthroat Trout and Lake Trout CPUEs. We illustrate the complex interactions between predator and prey in a simple assemblage and demonstrate how a nonnative apex predator can alter competitive interactions. The diets of Yellowstone Cutthroat Trout were dominated by zooplankton during a period when the Yellowstone Cutthroat Trout CPUE was high and were dominated by amphipods when the CPUE was reduced. Lake Trout shifted from a diet that was dominated by Yellowstone Cutthroat Trout during the early stages of the invasion to a diet that was dominated by amphipods after Lake Trout abundance had increased and after Yellowstone Cutthroat Trout prey had declined. The shifts in Yellowstone Cutthroat Trout and Lake Trout diets resulted in increased trophic similarity of these species through time due to their shared reliance on benthic amphipods. Yellowstone Cutthroat Trout not only face the threat posed by Lake Trout predation but also face the potential threat of competition with Lake Trout if amphipods are limiting. Our results demonstrate the importance of studying the long-term feeding ecology of fishes in invaded ecosystems.

Nonnative piscivorous fishes have altered freshwater ecosystems throughout the world (Eby et al. 2006; 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). The imposition of top-down

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regulation on native fish populations via predation can ultimately result in trophic cascades within water bodies (Tronstad et al. 2010; Ellis et al. 2011). In addition to lengthening the food chains, nonnative piscivores can compete with native prey species, as most piscivorous fishes exhibit ontogenetic diet shifts (Juanes et al. 2002). Additionally, prey switching by nonnative piscivores is necessary to sustain predator biomass in systems where prey abundance is reduced (McMahon and Bennett 1996; Roseman et al. 2014). Thus, the trophic niche of nonnative predators can change through time, indicating that competition with native species can become an important interaction in addition to predation.

The Lake Trout *Salvelinus namaycush* is a large-bodied apex piscivore that has been introduced into 15 countries around the world and extensively throughout the United States (Crossman 1995), including large lakes and reservoirs in eight western states (Martinez et al. 2009). In water bodies where Lake Trout have been introduced, the predatory demand of the nonnative Lake Trout population can exceed the available prey supply even before the Lake Trout increase to high densities (Johnson and Martinez 2000), thereby generating declines in native fish populations (Donald and Alger 1993; Fredenberg et al. 2002) and altering ecosystem structure and function (Tronstad et al. 2010; 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 increase their energy intake through cannibalism (Martin and Olver 1980). Cannibalism is considered an important factor regulating juvenile survival and the population growth rate in Lake Trout (Evans and Willox 1991; Richards et al. 2004). In addition to cannibalism, the Lake Trout's diet can regulate the population growth rate. For example, invertivorous populations of Lake Trout have lower individual growth rates than piscivorous populations (Matuszek et al. 1990; Pazzia et al. 2002).

Diet shifts can also affect the population dynamics of native fish species in systems where Lake Trout have been introduced. Declines in density can lead to an increase in per capita prey availability as well as 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 an increased population growth rate at reduced abundance (Rose et al. 2001).

The Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, a subspecies of the Cutthroat Trout *O. clarkii*, is native to western Wyoming, eastern Idaho, and southern Montana (Behnke 2002). Yellowstone Lake, located within Yellowstone National Park, contains the largest population of nonhybridized Yellowstone Cutthroat Trout (Gresswell and Varley 1988) and represents nearly 80% of the remaining lacustrine habitat for the subspecies (Gresswell et al. 1994). The Yellowstone Cutthroat Trout is considered a keystone species in the Greater Yellowstone Ecosystem, as 4 mammal species and 16 bird species have been documented to consume Yellowstone Cutthroat Trout (Schullery and Varley 1995).

Nonnative Lake Trout were discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996), and the effect of this introduction on Yellowstone Cutthroat Trout has been substantial (Koel et al. 2005, 2012). For example, the number of Yellowstone Cutthroat Trout ascending Clear Creek to spawn declined from 55,000 individuals in 1987 to 500 individuals in 2007 (Koel et al. 2012). During the same period, Lake Trout expanded from a small introductory population that was mostly confined to a single basin of the lake (Koel et al. 2007) to a population numbering about 300,000 that was distributed lakewide (Syslo et al. 2011; Koel et al. 2012). The increase in Lake Trout and the decline in Yellowstone Cutthroat Trout 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; Teisberg et al. 2014). The large change in Yellowstone Cutthroat Trout abundance and the subsequent effects that spread throughout the Yellowstone Lake basin provide a classic example of how a nonnative apex piscivore can alter a freshwater ecosystem.

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 by the National Park Service during 1995 with the purpose of reducing Lake Trout abundance so as to decrease predation on Yellowstone Cutthroat Trout. However, despite the removal of 830,000 Lake Trout from the lake during 1995–2011, Lake Trout abundance continued to increase (Syslo et al. 2011; Koel et al. 2012). If Lake Trout occupy a trophic position similar to that of 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.

Examining the diets of nonnative fishes is critical for determining the ecological effects of species introductions. Diet studies focused on nonnative fishes are commonly conducted 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. The collapse of the Yellowstone Cutthroat Trout population and the coinciding increase in Lake Trout abundance in Yellowstone Lake provided a rare opportunity to evaluate the feeding ecology of a native prey species and a nonnative piscivore species after the restructuring of a large lentic ecosystem.

We were interested in the role played by a nonnative apex piscivore in structuring food web dynamics and competition. An understanding of the ecological roles of Lake Trout and Yellowstone Cutthroat Trout under varying levels of predator and prey densities is important for predicting the success of Lake Trout suppression efforts that are meant to enhance Yellowstone Cutthroat Trout, which is the ultimate goal of the removal program. Our objectives were to assess trophic overlap between and temporal diet shifts exhibited by Yellowstone Cutthroat Trout and Lake Trout after the Lake Trout population increase and the Yellowstone Cutthroat Trout population collapse. We predicted that given ontogenetic diet shifts, Yellowstone Cutthroat Trout would exhibit the greatest degree of trophic overlap with small (nonpiscivorous) Lake Trout but would exhibit no trophic overlap with large (piscivorous) Lake Trout. We predicted that the Yellowstone Cutthroat Trout diet would include more bioenergetically favorable prey items after Yellowstone Cutthroat Trout abundance was reduced. We also predicted that after the Yellowstone Cutthroat Trout population collapse, (1) the proportion of Yellowstone Cutthroat Trout in Lake Trout diets would decline and (2) the proportions of invertebrates and other fishes (including conspecifics) in Lake Trout diets would increase.

METHODS

Overview

We used a variety of methods to better understand the feeding ecology of Yellowstone Cutthroat Trout and Lake Trout in Yellowstone Lake. To evaluate trophic overlap, we examined diet contents, carbon and nitrogen stable isotope signatures (δ^{13}C and δ^{15}N), and depth-related CPUE patterns in Yellowstone Cutthroat Trout and Lake Trout during 2011–2013. We used CPUE to characterize relative abundances of the two species through time. We also compared diet data from 2011–2013 with data from previous diet studies focused on Yellowstone Cutthroat Trout (1989; Jones et al. 1990) and Lake Trout (1996–1999; Ruzycki et al. 2003). Finally, a bioenergetics model was used to estimate consumption by Lake Trout in 2011–2013 for comparison with the results from 1996–1999 (Ruzycki et al. 2003).

Study Area

Yellowstone Lake (elevation = 2,357 m; Figure 1) has a surface area of 34,020 ha, 239 km of shoreline, a mean depth

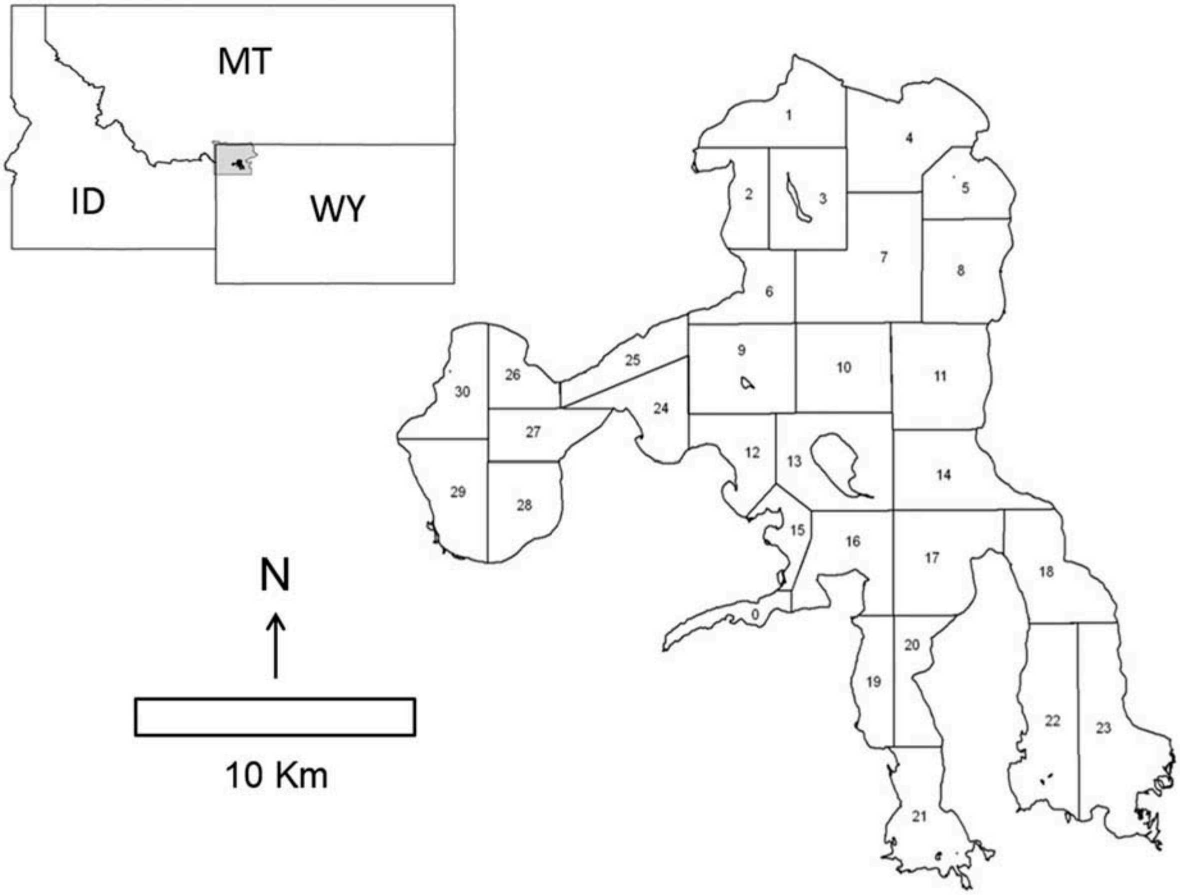

FIGURE 1. Location of Yellowstone Lake within Yellowstone National Park (inset: gray area); and a map of Yellowstone Lake, depicting the gillnetting areas that were used to assess the populations of native Yellowstone Cutthroat Trout and nonnative Lake Trout.

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 through late May or early June. Thermal stratification generally takes place in late July and can last into September, with summer surface water temperature reaching 17°C and the thermocline occurring at about 15 m (Koel et al. 2007).

The lake is categorized as oligomesotrophic (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 rotifers *Conochilus unicornis*, copepods *Diaptomus* and *Cyclops*, and cladocerans *Daphnia* spp. (Benson 1961). The benthic macroinvertebrate assemblage is dominated by the amphipods *Hyalella azteca* and *Gammarus lacustris* (Benson 1961). *Gammarus lacustris* occurs at a wider range of depths than *H. azteca* and contributed a larger proportion of the diet historically consumed by Yellowstone Cutthroat Trout (Benson 1961). The fish assemblage in the lake consists of two native species: the Yellowstone Cutthroat Trout and Longnose Dace *Rhinichthys cataractae*. There are three nonnative species in addition to Lake Trout: the Longnose Sucker *Catostomus catostomus*, Redside Shiner *Richardsonius balteatus*, and Lake Chub *Couesius plumbeus* (Gresswell and Varley 1988).

Sampling

Yellowstone Cutthroat Trout assessment netting program.—Gill nets were used to assess the Yellowstone Cutthroat Trout population at 11 sites throughout the lake in mid-September during 1978–2013 (Kaeding and Koel 2011). At each site, five sinking experimental gill nets were set perpendicular to shore and were fished overnight. Nets were set about 100 m apart, with the nearshore end about 1.5 m deep. Nets were 1.5 m deep × 38 m long and consisted of five 7.6-m panels (19-, 25-, 32-, 38-, and 51-mm bar measure mesh). All fish that were caught during the Yellowstone Cutthroat Trout assessment netting efforts were measured for TL (nearest mm). Weight (nearest g), sex, and maturity were recorded for incidental mortalities of Yellowstone Cutthroat Trout.

Lake Trout assessment netting program.—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, the program also sampled the Yellowstone Cutthroat Trout population. Sixteen sites throughout the lake were sampled during early August, with six experimental gill nets deployed per site. At each site, a small-mesh sinking gill net and a large-mesh sinking gill net were set overnight at each of three depth strata: the epilimnion (3–10 m), metalimnion (10–30 m), and hypolimnion (>40 m). Small-mesh gill nets were 2 m deep × 82.2 m long and consisted of six 13.7-m panels (19-, 25-, 32-, 38-, 44-, and 51-mm bar measure mesh). Large-mesh gill nets were 3.3 m deep × 68.6 m long, consisting of five 13.7-m panels (57-, 64-, 70-, 76-, and 89-mm bar measure mesh). Gill nets were set perpendicular to shore, and nets within a stratum were set parallel and about 100 m apart. To avoid incidental mortality of Yellowstone Cutthroat Trout (Ruzycki 2004), the shallow stratum (3–10 m) was not sampled in 1998. Lake Trout assessment netting was inconsistent during 1999–2009; therefore, a new protocol was developed in 2010 and was implemented through 2013. The assessment netting protocol used during 2010–2013 was similar to the program developed in 1997 (i.e., in terms of net specifications and depth strata) but included 24 sites/year, and the shallow stratum was not sampled during 2011. All of the fish that were sampled during the Lake Trout assessment netting program were measured for TL. Weight (nearest g), sex, maturity, and gonad weight were recorded for Lake Trout and for incidental mortalities of Yellowstone Cutthroat Trout. In 2013, sagittal otoliths for use in age estimation were sampled from 10 Lake Trout per 1-cm length group (see Syslo et al. 2011 for a description of aging methods).

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

Diet analysis.—Yellowstone Cutthroat Trout and Lake Trout diets were sampled from all netting types in 2011. To account for potential temporal variation in prey availability, diet sampling for both species was stratified by season: prestratification (before August 1), stratification (August 1–September 20), and poststratification (after September 20). Due to logistical constraints, diets were not sampled during the ice cover season. To account for ontogenetic diet shifts, an attempt was made to sample at least 15 individuals from each 50-mm length-class (starting at 150 mm) for each species during each season. In 2011, about 50% of the stomachs from Lake Trout larger than 400 mm were empty; therefore, Lake Trout larger than 400 mm were sampled for diets again in 2013. Stomach content samples were primarily obtained during Lake Trout assessment netting in the stratification season; however, stomach contents from large Lake Trout (>450 mm TL) were also sampled from trap nets to augment the assessment netting sample sizes. During the prestratification and poststratification seasons, stomachs were obtained by subsampling fish that were captured during suppression netting efforts (gill nets and trap nets). An attempt was made to only sample fish from gill nets that were set for one night. Stomach contents were sampled from as many gillnetting areas (Figure 1) as possible during each season. Each time a gill net was lifted in a gillnetting area that had not been previously sampled during 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 the fish for stomach contents. When trap nets were lifted, the first three fish within each 50-mm length-class were sampled from each net.

In the laboratory, stomachs and stomach contents were removed from dead Lake Trout and Yellowstone Cutthroat Trout. Stomach contents from live Yellowstone Cutthroat Trout were obtained via gastric lavage by using acrylic tubes (Quist et al. 2002). Tubes were about 375 mm long, with 1-mm-thick walls and an inner diameter of 8, 11, 14, 18, or 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 the stomach contents were dislodged into a tray. Lavage was repeated until prey items were no longer produced. Stomach contents were fixed in a 10% solution of buffered formalin and were then preserved in a 70% solution of ethanol.

Prey items were identified to the family or order level for invertebrates and to the species level for fish. Prey items were separated by taxon, and the blotted wet weight (nearest 0.01 g) was recorded for each prey category. Prey fish were measured for TL when possible. We found no identifiable Lake Trout prey in the stomachs of Lake Trout (see Results); therefore, when estimating weight at ingestion, we assumed that all unidentified digested salmonids were Yellowstone Cutthroat Trout. For digested Yellowstone Cutthroat Trout and unidentified salmonids, the vertebral column length or SL was converted to TL at ingestion by using existing regression equations for Yellowstone Cutthroat Trout (Ruzycki and Beauchamp 1997). The TL at ingestion was converted to wet weight (W; g) by using a weight–length regression for Yellowstone Cutthroat Trout that were sampled during Yellowstone Cutthroat Trout assessment netting in 2011 ($r^2 = 0.98$, $N = 968$, $P < 0.01$),

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

Recovery of stomach contents via gastric lavage can vary from 60% to 90% by weight (Quist et al. 2002). Therefore, recovery of prey items was assessed by performing lavage on a subset ($N = 16$) of incidental mortalities rather than sacrificing additional Yellowstone Cutthroat Trout. For each prey type, the mean proportional diet contribution by weight (MPW) was estimated based on (1) samples that were obtained by using gastric lavage and (2) samples of total stomach contents (contents from gastric lavage combined with the remaining stomach contents). Mean MPWs for the prey types only differed by 0.00–0.04 between gastric lavage and total stomach contents, indicating that gastric lavage produced a representative sampling of the Yellowstone Cutthroat Trout diet.

Stable isotope analysis.—The analysis of diets provides high taxonomic resolution during evaluations of trophic position; however, diets can be temporally variable (Garvey and Chipps 2012). Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) can be used to provide a measure of feeding habits, reflecting the foraging behavior that occurred over the preceding several weeks to months (Satterfield and Finney 2002; Vander Zanden et al. 2015). The $\delta^{15}N$ of consumers increases relative to that of the food source, providing a measure of trophic position (Minigawa and Wada 1984). In contrast, the $\delta^{13}C$ of consumers is similar to the ratios in their prey, providing an indication of food origin. Specifically, $\delta^{13}C$ values tend to be greatest (less negative) in littoral zones, to decrease in pelagic zones, and to be highly negative in profundal zones (Vander Zanden and Rasmussen 1999). The combination of diet analysis and stable isotope analysis provides a powerful approach for assessing trophic position (Clarke et al. 2005; Feiner et al. 2013).

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

Fish tissue samples and amphipods were placed in a portable cryogenic freezer (Model CX100; Taylor Wharton, Theodore, Alabama) during collection. Samples were freeze-dried for 18 h by using a Labconco Freezone 1 (Labconco Corporation, Kansas City, Missouri) and were 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 Stable Isotope Facility, University of California–Davis, 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

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \cdot 1{,}000,$$

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 standards were Vienna Pee Dee Belemnite for carbon and atmospheric nitrogen for 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 of Yellowstone Lake from late May through October by using a vertical temperature logger array. Temperature loggers were placed along a steel cable every 1 m at 1–20-m depths and every 10 m at depths greater than 20 m.

Trophic Overlap

Diet overlap.—The MPW for each prey type detected in Lake Trout and Yellowstone Cutthroat Trout diets was estimated for each season during 2011–2013 (Chipps and Garvey 2007). The MPW was calculated for three Yellowstone Cutthroat Trout length-classes (160–300, 301–475, and 476–575 mm) and four Lake Trout length-classes (160–300, 301–475, 476–575, and 576–920 mm) to account for ontogenetic variation in the diet (to permit temporal comparisons, length-classes were later condensed to match the length-classes used in previous studies). Schoener's index of diet overlap (D) was used to estimate overlap between the Yellowstone Cutthroat Trout diet and the Lake Trout diet (Schoener 1968),

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

where p_{ij} is the proportional contribution of prey type i to the diet for species j; and p_{ik} is the proportional contribution of prey type i to the diet for species k. We estimated D in comparisons between each Yellowstone Cutthroat Trout length-class and Lake Trout length-class sampled within each season. Values of D that were at least 0.60 were considered significant (Wallace 1981).

Isotopic niche overlap.—Amphipod δ^{15}N was regressed as a linear function of δ^{13}C, and the regression equation was used as a baseline for correcting δ^{15}N values for Yellowstone Cutthroat Trout and Lake Trout (Vander Zanden and Rasmussen 1999; Post 2002). Corrected δ^{15}N and δ^{13}C were plotted in bivariate space, and the isotopic niche size for each species × length-class combination was estimated with standard ellipses (Jackson et al. 2011). We used the Stable Isotope Analysis in R (SIAR) package to estimate the ellipse areas corrected for small sample size (SEA$_C$; Jackson et al. 2011; R Development Core Team 2014). Briefly, the SIAR package uses Bayesian inference and multivariate ellipse-based methods to estimate standard ellipses that contain about 40% of the data, representing the core niche area (Jackson et al. 2011, 2012). Niche overlap for Lake Trout and Yellowstone Cutthroat Trout of a given length-class was estimated as the proportion of the Yellowstone Cutthroat Trout ellipse area that overlapped with Lake Trout ellipses (Feiner et al. 2013).

Relative abundance.—The Yellowstone Cutthroat Trout and Lake Trout CPUEs (number of fish per 100 m of net) in the Lake Trout assessment netting program were used to determine the vertical distribution of each species. The proportion of total CPUE contributed by each length-class at each depth stratum in 2010–2013 was estimated for each species. The CPUE data from Lake Trout assessment netting in 2011 were omitted because the epilimnion was not sampled (see above).

Temporal Shifts

Relative abundance.—The Yellowstone Cutthroat Trout CPUE calculated from Yellowstone Cutthroat Trout assessment netting efforts (1978–2013) and the Lake Trout CPUE calculated from Lake Trout assessment netting efforts (1997, 2010, 2012, and 2013) were used to assess relative abundances through time. Lake Trout CPUEs for 2010, 2012, and 2013 were considered to represent the relative abundances during the period of diet sampling (2011–2013). Mean CPUE (±95% confidence interval) was estimated among sites for each length-class (see above) and each year.

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

Bioenergetics.—For Lake Trout ages 2–17, consumption was estimated by 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 May 20, corresponding to the average date of ice-off.

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

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

where TL_t is total length of Lake Trout at age t (years). The TL at age was converted to weight at age by using an equation for Lake Trout sampled during Lake Trout assessment netting efforts ($N = 422$),

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

Spawning losses were simulated on September 1 by reducing the body weight by the average age-specific gonadosomatic index (GSI) among mature males and females (Table 1). Age at first maturity was 4 years for males and 6 years for females (Syslo et al. 2011). For mature Lake Trout, the male GSI was assumed to equal 3.3% (Ruzycki et al. 2003), and the female GSI varied from 8.8% at age 6 to 15.8% at age 17. Male and female Lake Trout were assumed to spawn every year because examination of gonads in the field did not indicate skipped spawning.

Diet data for 160–300-mm and 301–475-mm Lake Trout were pooled because fish constituted a negligible proportion of the diet for those length-classes. Estimates of Lake Trout diet proportions by weight were available for the pre-stratification, stratification, and poststratification seasons. Diets consumed during the ice cover season were simulated by linear interpolation between the poststratification season diet and the pre-stratification season diet (Ruzycki et al. 2003). Literature values were used for prey energy densities (see Table 2); we assumed indigestible percentages of 15% for invertebrate prey and 3% for fish prey (Beauchamp et al. 2007).

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

Thermal history for each Lake Trout length-class was calculated by using daily temperature profiles and Lake Trout depth distributions. Temperature profiles measured from late May through October were available (see above). The temperature observed immediately after ice-off (3.5°C) was used as the environmental temperature for Lake Trout throughout the ice cover season. The Lake Trout depth distribution for the stratification season was estimated from the Lake Trout assessment netting data. Depth distributions during the pre-stratification and poststratification seasons were estimated based on the depths of Lake Trout sampled during suppression netting efforts (gill nets and trap nets).

RESULTS

Trophic Overlap

Yellowstone Cutthroat Trout diet.—Amphipods composed greater than 0.60 of the diet by weight for Yellowstone Cutthroat Trout in all length-classes during all seasons in 2011 (Table 3). During the pre-stratification season, chironomids composed the second-greatest proportion of the diet for all Yellowstone Cutthroat Trout length-classes. During the stratification season, the second-highest diet proportion was contributed by cladocerans for 160–300-mm Yellowstone Cutthroat Trout; cladocerans and insects constituted the second-greatest diet proportion for the 301–475-mm length-class. During stratification, Yellowstone Cutthroat Trout in the 476–575-mm length-class consumed amphipods almost exclusively (Table 3). During the poststratification season, cladocerans made up the second-highest proportion of the diet for the 301–475-mm and 476–575-mm length-classes.

Lake Trout diet.—In 2011–2013, amphipods constituted a greater proportion of the diet by weight than any other prey type for all Lake Trout length-classes in all seasons, with the exception of the 160–300-mm length-class during the pre-stratification season (Table 4). Copepods contributed 0.28–0.57 of the diet for 160–300-mm Lake Trout; cladocerans composed up to 0.32 of the diet for the 301–475-mm length-class. The proportion of fish in Lake Trout diets increased through the year. Yellowstone Cutthroat Trout made up 0.03–0.21 of the diet for 476-mm and larger Lake Trout, and unidentified salmonids composed up to 0.12 of the Lake Trout diet (Table 4). Cyprinids constituted less than 0.01 of the Lake Trout diet, and no Longnose Suckers were observed in the stomach contents. During the poststratification season, Lake Trout eggs composed 0.07–0.16 of the diet for 301–475-mm, 476–575-mm, and 576–920-mm Lake Trout (Table 4). Overall, 67 salmonid individuals were found in Lake Trout diets. Fifty-five of the salmonids were identified as Yellowstone Cutthroat Trout, whereas no Lake Trout were identified in Lake Trout diets.

TABLE 2. Energy density of prey organisms used in bioenergetics simulations for Lake Trout in Yellowstone Lake.

Prey group	Surrogate	Energy densit (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 (leeches)		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	Rainbow Trout *Oncorhynchus mykiss*	5,764	Hanson et al. 1997
Unidentified salmonids	Rainbow Trout	5,764	Hanson et al. 1997
Cyprinids	Emerald Shiner *Notropis atherinoides*	5,108	Bryan et al. 1996
Unidentified fish	Rainbow Trout	5,764	Hanson et al. 1997

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

Diet overlap.—Values of *D* were greater than 0.60 for half of the comparisons between Yellowstone Cutthroat Trout and Lake Trout belonging to the various length-classes (Table 5). The *D*-values were less than 0.60 for comparisons between 160–300-mm Lake Trout and all Yellowstone Cutthroat Trout length-classes in all seasons; values exceeded 0.60 for comparisons between 476–575-mm Lake Trout and all Yellowstone Cutthroat Trout length-classes in all seasons (Table 5). Diet overlap between the two species was greatest during the pre-stratification season.

TABLE 3. Diet composition (proportion by weight) for each Yellowstone Cutthroat Trout length-class within Yellowstone Lake during three seasons in 2011 (Cla = cladocerans; Cop = copepods; Amp = amphipods; Chi = chironomids; Ins = insects; the following prey groups were not observed: leeches, mollusks, Lake Trout eggs, Yellowstone Cutthroat Trout, unidentified salmonids, cyprinids, and unidentified fish).

Length-class (mm TL)	*N*	Prey group				
		Cla	Cop	Amp	Chi	Ins[a]
Pre-stratification						
160–300	12	0.00	0.06	0.84	0.09	0.00
301–475	26	0.02	0.08	0.76	0.12	0.03
476–575	33	0.00	0.00	0.81	0.16	0.00
Stratification						
160–300	41	0.27	0.00	0.60	0.01	0.12
301–475	36	0.10	0.00	0.74	0.06	0.10
476–575	60	0.01	0.00	0.96	0.00	0.03
Poststratification						
160–300	7	0.00	0.00	0.99	0.00	0.00
301–475	27	0.26	0.02	0.72	0.00	0.00
476–575	25	0.22	0.00	0.72	0.00	0.06

[a] Includes Ephemeroptera, Trichoptera, Plecoptera, and non-chironomid dipterans.

Isotopic niche overlap.—A significant negative relationship between amphipod δ^{13}C and δ^{15}N values provided a baseline for standardizing δ^{15}N (Figure 2). Predicted δ^{15}N increased from 1.3‰ in the littoral zone to 7.1‰ in the profundal zone. Values of δ^{13}C varied from –27.0‰ to –13.6‰ for Yellowstone Cutthroat Trout and from –28.9‰ to –18.2‰ for Lake Trout (Figure 3). Corrected δ^{15}N varied from –1.3‰ to 3.4‰ for Yellowstone Cutthroat Trout and from 0.6‰ to 4.6‰ for Lake Trout (Figure 3). Corrected δ^{15}N was similar between 476–575-mm Yellowstone Cutthroat Trout and all Lake Trout length-classes (Figure 3; Table 6). Lake Trout in all length-classes were enriched in δ^{15}N relative to 160–300-mm and 301–475-mm Yellowstone Cutthroat Trout (Figure 3; Table 6). The SEA_C values for Yellowstone Cutthroat Trout were 1.6–7.0 times greater than those for Lake Trout (Table 6). The largest SEA_C was observed for 160–300-mm Yellowstone Cutthroat Trout and was 2.5 times greater than the SEA_C for 301–575-mm Yellowstone Cutthroat Trout. For Lake Trout, SEA_C was largest for the 160–300-mm length-class and generally declined with increasing length-class. Despite substantial overlap in the range of δ^{13}C and corrected δ^{15}N among Yellowstone Cutthroat Trout and Lake Trout length-classes, ellipse overlap only occurred between 476–575-mm Yellowstone Cutthroat Trout and 301–475-mm (3% of ellipse area) or 476–575-mm (6% of ellipse area) Lake Trout (Figure 3).

Relative abundance.—Catches declined with depth for all length-classes of Yellowstone Cutthroat Trout (Figure 4). For 160–300-mm Yellowstone Cutthroat Trout, 0.90 of the fish were caught at depths less than 10 m. The proportion of Yellowstone Cutthroat Trout caught at a depth less than 10 m was 0.75 for the 301–475-mm length-class and 0.68 for the 476–575-mm length-class. The greatest catch rates for all length-classes of Lake Trout occurred in the 11–30-m stratum, with the 160–475-mm length-class spanning the broadest depth range (Figure 4). The proportion of Lake Trout sampled from

TABLE 4. Diet composition (proportion by weight) for each Lake Trout length-class within Yellowstone Lake during three seasons in 2011–2013 (Cla = cladocerans; Cop = copepods; Amp = amphipods; Lee = leeches; Chi = chironomids; Ins = insects; Mol = mollusks; Egg = Lake Trout eggs; Yel = Yellowstone Cutthroat Trout; Sal = unidentified salmonids; Cyp = cyprinids; Fis = unidentified fish).

		Prey group											
Length-class (mm TL)	*N*	Cla	Cop	Amp	Lee	Chi	Ins[a]	Mol	Egg	Yel	Sal	Cyp	Fis
Pre-stratification													
160–300	46	0.00	0.57	0.35	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
301–475	81	0.00	0.12	0.70	0.04	0.12	0.00	0.00	0.00	0.00	0.01	0.00	0.01
476–575	54	0.00	0.06	0.71	0.11	0.08	0.00	0.00	0.00	0.03	0.00	0.00	0.02
576–920	66	0.00	0.00	0.81	0.06	0.07	0.00	0.00	0.00	0.06	0.01	0.00	0.00
Stratification													
160–300	64	0.04	0.28	0.43	0.14	0.08	0.02	0.00	0.00	0.02	0.00	0.00	0.00
301–475	53	0.29	0.05	0.32	0.21	0.13	0.01	0.00	0.00	0.00	0.00	<0.01	0.00
476–575	46	0.04	0.00	0.59	0.13	0.00	0.00	0.01	0.00	0.20	0.00	0.00	0.02
576–920	49	0.00	0.00	0.55	0.04	0.00	0.00	0.00	0.00	0.21	0.10	<0.01	0.09
Poststratification													
160–300	18	0.06	0.35	0.45	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
301–475	87	0.32	0.12	0.46	0.02	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
476–575	50	0.06	0.02	0.60	0.02	0.00	0.00	0.00	0.16	0.06	0.02	0.00	0.06
576–920	50	0.00	0.00	0.57	0.00	0.00	0.02	0.00	0.08	0.20	0.12	<0.01	0.00

[a] Includes Ephemeroptera, Trichoptera, Plecoptera, and non-chironomid dipterans.

the 11–30-m stratum was 0.84 for the 476–575-mm length-class and 0.77 for the 576–920-mm length-class. The proportion of Lake Trout sampled at depths greater than 40 m was 0.00 for the 576–920-mm length-class and 0.02 for the 476–575-mm length-class, increasing to 0.21 for 301–475-mm fish and to 0.34 for 160–300-mm fish.

Temporal Shifts

Yellowstone Cutthroat Trout.—In Yellowstone Cutthroat Trout assessment netting conducted during 1978–2013, the Yellowstone Cutthroat Trout CPUE was variable for the 160–300-mm length-class, declined for 301–475-mm fish, and increased for 476–575-mm fish (Figure 5). The CPUE

TABLE 5. Schoener's index of diet overlap (*D*) for Lake Trout and Yellowstone Cutthroat Trout length-classes that were sampled within Yellowstone Lake during three seasons in 2011–2013. Bold italics indicate significant *D*-values (≥0.60).

Yellowstone Cutthroat Trout length-class (mm TL)	Lake Trout length-class (mm TL)			
	160–300	301–475	476–575	576–920
Pre-stratification				
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***
Stratification				
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
Poststratification				
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

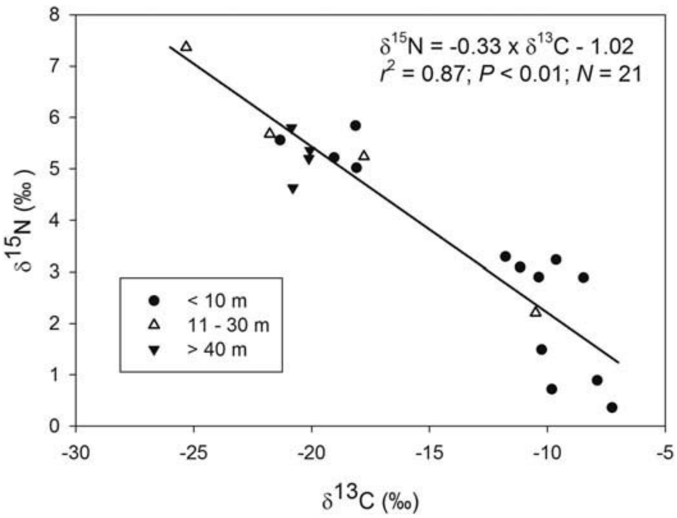

FIGURE 2. Regression of the nitrogen stable isotope signature ($\delta^{15}N$) as a function of the carbon stable isotope signature ($\delta^{13}C$) for amphipods sampled in Yellowstone Lake, Yellowstone National Park (symbols represent depth intervals).

for 160–300-mm Yellowstone Cutthroat Trout was greater in 2011 than in any other year and was 2.8 times greater than the CPUE observed in 1989. For 301–475-mm Yellowstone Cutthroat Trout, the CPUE declined by 90% from 1989 to 2011. The CPUE for 476–575-mm Yellowstone Cutthroat Trout was 10 times greater in 2011 than in 1989 (Figure 5); however, fish in that length-class represented a small proportion of the overall relative abundance.

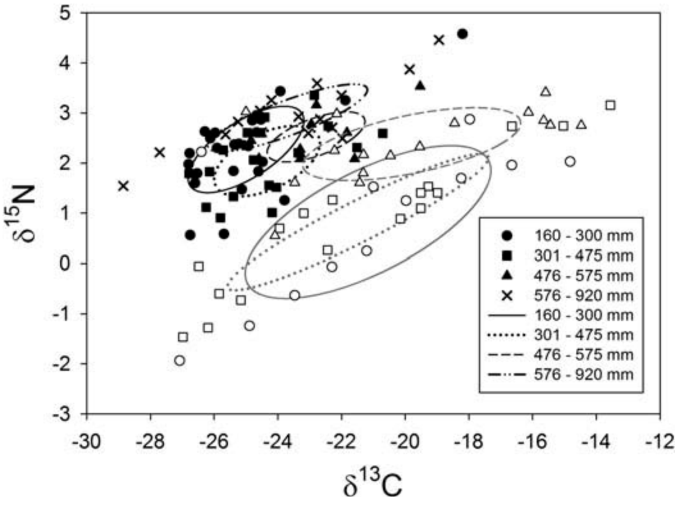

FIGURE 3. Individual stable isotope values ($\delta^{15}N$, $\delta^{13}C$) and standard ellipse areas (SEA_C) for Yellowstone Cutthroat Trout length-classes (open symbols; gray lines) and Lake Trout length-classes (solid symbols; black lines) in Yellowstone Lake, 2011–2013.

TABLE 6. Sample sizes (N), mean (SD in parentheses) carbon and nitrogen stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$), and mean standard ellipse areas (SEA_C) for Lake Trout and Yellowstone Cutthroat Trout length-classes within Yellowstone Lake, 2011–2013.

Length-class (mm TL)	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	SEA_C
Lake Trout				
160–300	25	–25.00 (1.82)	2.27 (0.86)	3.85
301–475	18	–24.34 (1.66)	2.04 (0.70)	3.34
476–575	10	–22.80 (1.54)	2.52 (0.50)	2.13
576–920	17	–23.70 (2.50)	2.90 (0.68)	2.69
Yellowstone Cutthroat Trout				
160–300	12	–21.17 (3.86)	0.83 (1.52)	14.96
301–475	17	–21.48 (4.10)	0.83 (1.35)	6.08
476–575	16	–19.80 (3.42)	2.38 (0.73)	6.82

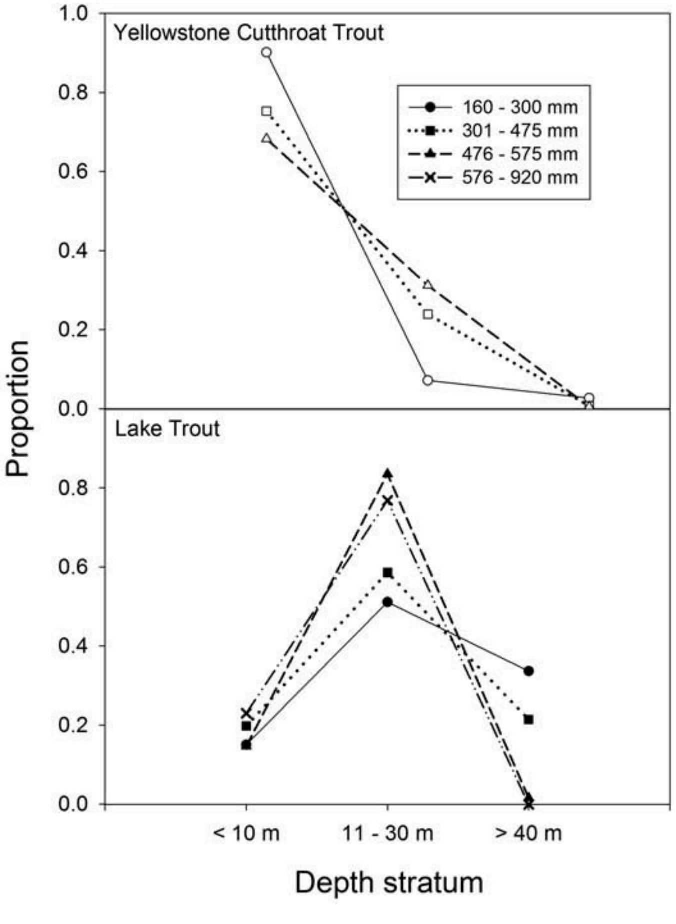

FIGURE 4. Proportion of Yellowstone Cutthroat Trout CPUE (upper panel) and Lake Trout CPUE (lower panel) for each length-class at each depth stratum, as determined during Lake Trout assessment netting in Yellowstone Lake (pooled data for 2010–2013).

Yellowstone Cutthroat Trout shifted from a diet dominated by cladocerans in 1989 to a diet dominated by amphipods in 2011. Amphipods increased from representing 0.08 of the Yellowstone Cutthroat Trout's diet during the stratification season in 1989 to making up 0.79 of the diet in 2011 (Figure 6). The diet proportion contributed by cladocerans declined from 0.80 during the stratification season in 1989 to 0.11 in 2011 (Figure 6).

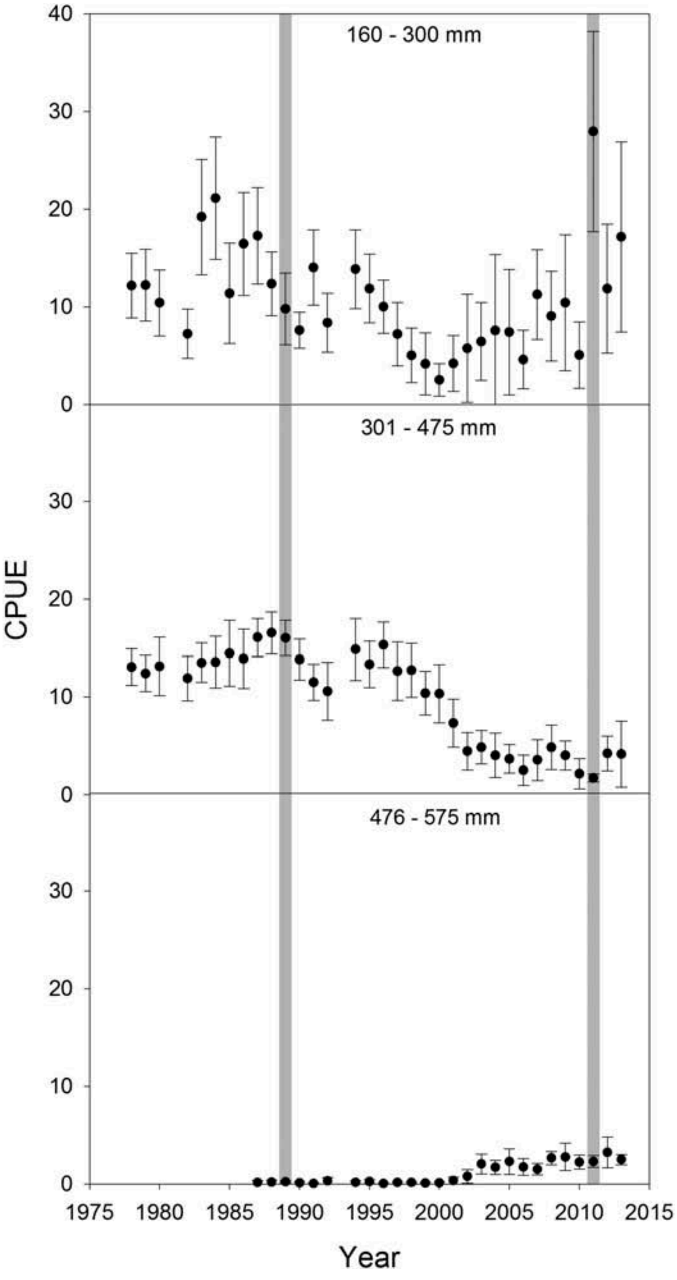

FIGURE 5. Mean CPUE (fish·100 m of gill net; ±95% confidence interval) for each length-class of Yellowstone Cutthroat Trout, as determined during Yellowstone Cutthroat Trout assessment netting efforts in Yellowstone Lake, 1978–2013. Gray vertical bars delineate years in which diet data were collected.

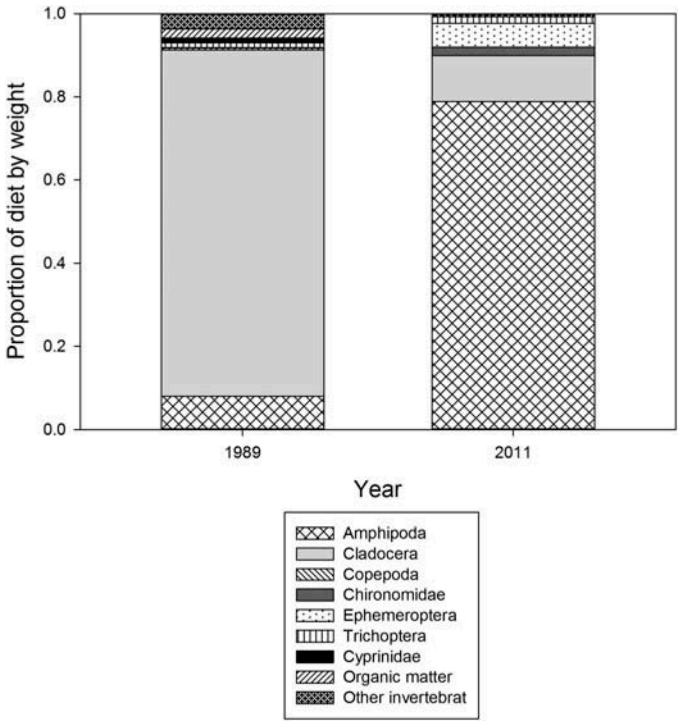

FIGURE 6. Diet composition (proportion by weight) for Yellowstone Cutthroat Trout (all length-classes pooled) sampled from Yellowstone Lake during the stratification season in 1989 (*N* = 132; Jones et al. 1990) and 2011 (*N* = 267; present study; other invertebrat = other invertebrates).

Lake Trout.—Compared with 1997 data, the mean Lake Trout CPUE during 2010–2013 was six times greater for the 160–300-mm length-class, three times greater for 301–475-mm fish, four times greater for 476–575-mm fish, and similar for 576–920-mm fish (Figure 7).

Lake Trout age-classes that predominately consumed Yellowstone Cutthroat Trout in 1996–1999 (Ruzycki et al. 2003) consumed mostly amphipods during 2011–2013 (Figure 8). In 1996–1999, the per capita consumption of Yellowstone Cutthroat Trout biomass by Lake Trout varied from 1.5 to 2.5 kg/year for Lake Trout ages 5–8 and from 4 to 8 kg/year for age-8 and older Lake Trout (Figure 9). During 2011–2013, per capita consumption of salmonid biomass (i.e., Yellowstone Cutthroat Trout biomass and unidentified salmonid biomass combined) varied from 0.4–0.6 kg/year for age-5–7 Lake Trout and 1.4–2.2 kg/year for age-8 and older Lake Trout. Per capita consumption of Yellowstone Cutthroat Trout individuals during 1996–1999 was 13 fish/year for Lake Trout ages 3–4; 42 fish/year for Lake Trout ages 5–8; and 41 fish/year for age-9 and older Lake Trout (Figure 9). During 2011–2013, per capita consumption of individual salmonids (Yellowstone Cutthroat Trout and unidentified salmonids combined) was 0.1 fish/year for Lake Trout ages 3–4; 9 fish/year for Lake Trout ages 5–7; and 20–32 fish/year for age-8 and older Lake Trout.

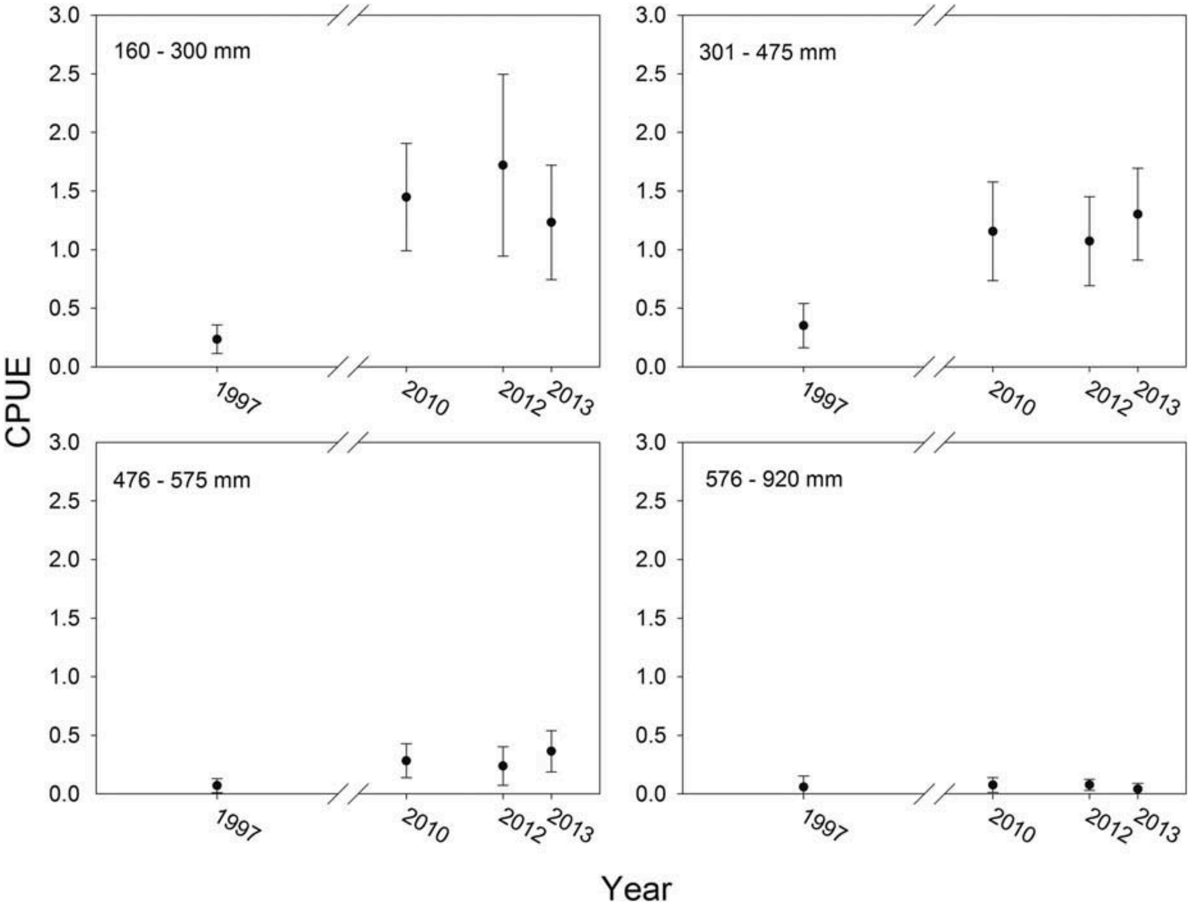

FIGURE 7. Mean CPUE (fish·100 m of gill net; ±95% confidence interval) for each length-class of Lake Trout, as determined during Lake Trout assessment netting efforts in Yellowstone Lake, 1997–2013.

DISCUSSION

Our results indicate that the alterations to food web structure in Yellowstone Lake were ultimately more complex than the addition of a fourth trophic level. Previous studies indicated that the Lake Trout's introduction resulted in the addition of a trophic level to the Yellowstone Lake ecosystem, producing a four-level trophic cascade (Tronstad et al. 2010). Specifically, Lake Trout occupied the position of apex predator (Ruzycki et al. 2003), causing a decline in the abundance of predominately planktivorous Yellowstone Cutthroat Trout, which in turn led to increased zooplankton biomass and decreased phytoplankton biomass (Tronstad et al. 2010). Our results indicate that Yellowstone Cutthroat Trout and Lake Trout exhibited diet shifts that resulted in increased trophic similarity through time as a result of their shared reliance on benthic amphipods after the Yellowstone Cutthroat Trout population's collapse. Therefore, Yellowstone Cutthroat Trout not only face the threat posed by Lake Trout predation but also face the potential threat of competition if Lake Trout abundance remains high and 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. Benson (1961) observed greater amphipod densities in areas where Yellowstone Cutthroat Trout abundance was reduced through exploitation. We surmise that the Yellowstone Cutthroat Trout's shift from zooplanktivory to the consumption of benthic amphipods was the result of increased amphipod availability after the Yellowstone Cutthroat Trout population declined.

Similar shifts in the prey types consumed (i.e., shifts from zooplankton to benthic amphipods) were detected for Bloaters *Coregonus hoyi*, Alewives *Alosa pseudoharengus*, and Slimy Sculpins *Cottus cognatus* in Lake Michigan when the availability of amphipods *Diporeia* spp. increased (Hondorp et al. 2005). Additionally, the occurrence of *Diporeia* spp. in the diets of Lake Whitefish *Coregonus clupeaformis* in Lake Michigan decreased and planktivory increased when *Diporeia* abundance declined from 1980 through 1999, corresponding to a decrease in Lake Whitefish body condition and

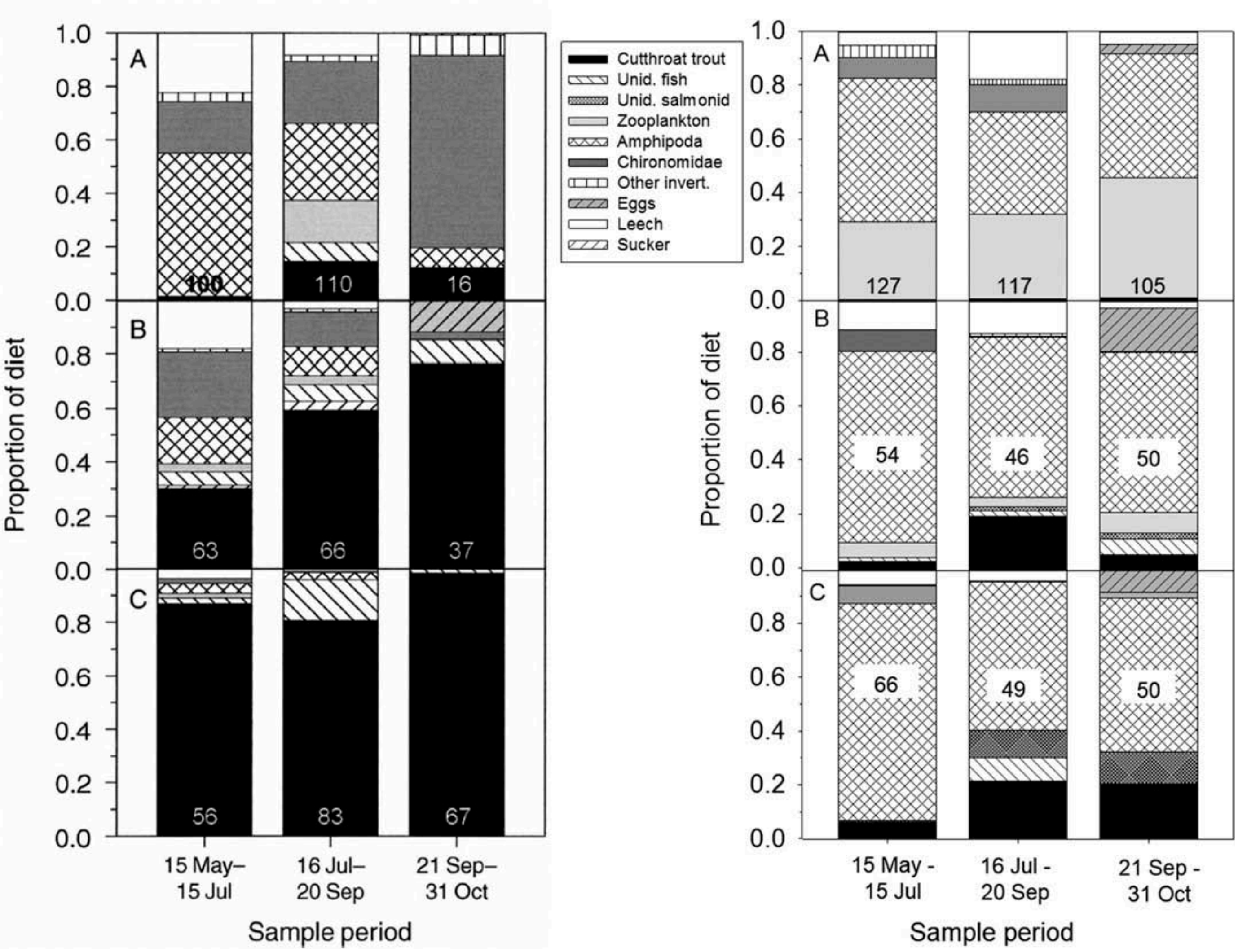

FIGURE 8. Diet composition (proportion by weight) for Lake Trout sampled during three periods of thermal stratification in 1996–1999 (left panel; Ruzycki et al. 2003) and 2011–2013 (right panel; present study). Data are presented for each Lake Trout age-class (left panel: A = ages 3–4, B = ages 5–8, and C = ages 9–23; right panel: A = ages 2–4, B = ages 5–7, and C = ages 8–17). Numbers within bars are sample sizes (Cutthroat Trout = Yellowstone Cutthroat Trout; unid = unidentified; invert = invertebrates; left panel reprinted from Ruzycki et al. 2003, with permission from the Ecological Society of America).

growth (Pothoven et al. 2001). In Lake Michigan, *Diporeia* spp. contain greater energy density than other macroinvertebrates (Gardner et al. 1985), and *Diporeia* availability influences fish body condition, distribution, and abundance (Pothoven et al. 2001; Hondorp et al. 2005). The large proportional contribution of amphipods to the diets of Yellowstone Cutthroat Trout and Lake Trout during 2011–2013 suggests that amphipods could constitute a keystone species in the Yellowstone Lake food web, similar to the role of *Diporeia* spp. in Lake Michigan.

The combination of diet analysis and stable isotope analysis provided greater power for assessing trophic dynamics in Yellowstone Lake than would have been obtained by the use of either approach alone. Diet overlap was substantial between Lake Trout larger than 300 mm TL and all length-classes of Yellowstone Cutthroat Trout. However, stable isotope analyses indicated that overlap in core niche areas only occurred between the largest Yellowstone Cutthroat Trout length-class (476–575 mm) and 301–575-mm Lake Trout. Substantial diet overlap was caused by the consumption of similar prey taxa, but stable isotope analyses revealed that the prey consumed by Lake Trout were from more profundal sources relative to the prey consumed by Yellowstone Cutthroat Trout.

On average, the δ^{15}N of consumers is enriched by 3.4‰ relative to their prey, but values of δ^{15}N can increase by 2–5‰ per trophic level (Minigawa and Wada 1984; Post 2002) and differences in δ^{15}N tend to become narrower with increasing trophic level (Hussey et al. 2014). Assuming that

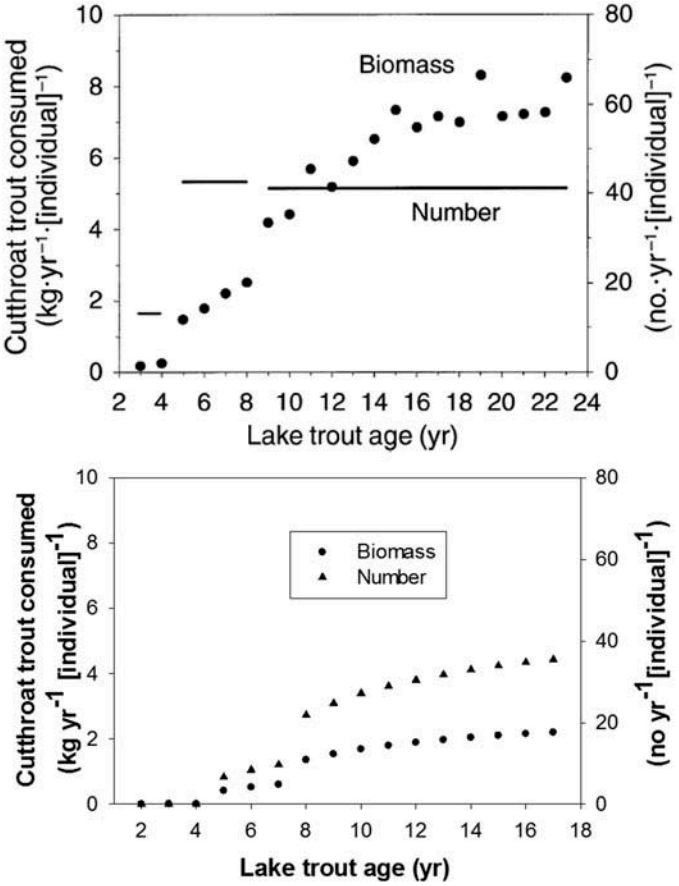

FIGURE 9. Per capita consumption of Yellowstone Cutthroat Trout biomass (kg/year) and Yellowstone Cutthroat Trout individuals by Lake Trout of each age-class (years) in Yellowstone Lake during 1996–1999 (top panel; Ruzycki et al. 2003) and 2011–2013 (bottom panel; present study), as estimated with bioenergetics models (top panel: circles = biomass consumed, lines = individuals consumed; bottom panel: circles = biomass consumed, triangles = individuals consumed). Estimates for 2011–2013 include unidentified salmonids (see Methods; top panel reprinted from Ruzycki et al. 2003, with permission from the Ecological Society of America).

$\delta^{15}N$ increases by about 3‰ per trophic level, the variation in baseline $\delta^{15}N$ from amphipods in the littoral zone versus the profundal zone represents the equivalent of two trophic levels. Relative to amphipods, mean $\delta^{15}N$ was enriched by nearly a trophic level (2–3‰) for all Lake Trout length-classes and for 476-mm and larger Yellowstone Cutthroat Trout. Yellowstone Cutthroat Trout that were smaller than 476 mm were enriched in $\delta^{15}N$ by 3‰ relative to the amphipod baseline in the littoral zone (at less-negative $\delta^{13}C$ values), but the $\delta^{15}N$ for these fish declined relative to the baseline as $\delta^{13}C$ decreased. Juvenile Yellowstone Cutthroat Trout become increasingly pelagic rather than benthic as distance from the shore increases (Gresswell and Varley 1988). Baseline $\delta^{15}N$ is likely greater in the profundal zone than in the pelagic zone (Vander Zanden and Rasmussen 1999); therefore, the use of amphipods to establish a baseline may have been inappropriate for small Yellowstone Cutthroat Trout. Given the similarity in $\delta^{15}N$ values for small Yellowstone Cutthroat Trout and amphipods, stable isotope analyses could not be used to distinguish whether large Lake Trout were consuming Yellowstone Cutthroat Trout or amphipods; however, analysis of stomach contents indicated that both Yellowstone Cutthroat Trout and amphipods were important energy sources for large Lake Trout.

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

In addition to the dietary shift 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, whereas they consume smaller individuals after larger fish are depleted (Matuszek et al. 1990; Rand and Stewart 1998). In Yellowstone Lake, the changes in prey sizes consumed caused the difference in numerical predation losses between time periods to be lower than expected based on the estimated change in biomass consumed. For example, the annual biomass of Yellowstone Cutthroat Trout and unidentified salmonids consumed by Lake Trout that were considered fully piscivorous (age ≥ 9) declined by 67%, whereas the number of individuals consumed only declined by 32%.

To maintain piscivorous diets, Lake Trout can switch prey species after declines in preferred prey (Rand and Stewart 1998). Lake Trout are opportunistic predators and consume prey fish species in proportion to their relative abundances in the environment (Elrod and O'Gorman 1991). Nonnative Lake Trout in Lake Chelan consumed several different prey taxa (salmonids, cyprinids, Threespine Sticklebacks *Gasterosteus aculeatus*, and Burbot *Lota lota*) after the decline of their preferred prey species (kokanee *O. nerka* [lacustrine Sockeye Salmon]; Schoen et al. 2012). After the kokanee population's collapse in Flathead Lake, Montana (Spencer et al. 1991), Lake Trout consumed a variety of salmonid species as well as Yellow Perch *Perca flavescens* (Beauchamp et al. 2006). In contrast, the diets of Lake Trout in Yellowstone Lake during 2011–2013 did not include a substantial proportion of fishes other than Yellowstone Cutthroat Trout. Alternative prey fishes for Lake Trout in Yellowstone Lake include cyprinids and Longnose Suckers, which occupy the littoral zones of the lake (Gresswell and Varley 1988) and therefore may have been unavailable to Lake Trout during the stratification season.

Given the lack of alternative prey fish species in Yellowstone Lake, we expected to observe cannibalism in Lake Trout. However, Lake Trout diets did not include conspecific prey. Throughout the nonnative range of Lake Trout, the observed incidence of cannibalism varies among lakes. In Flathead Lake, cannibalism was considered an important mechanism for Lake Trout population regulation (Beauchamp et al. 2006). Cannibalism was similarly observed in Lake Chelan: during thermal stratification, 84% of the diet for Lake Trout larger than 551 mm consisted of conspecifics (Schoen et al. 2012). In contrast, cannibalism was not observed in four Colorado reservoirs where the predatory demand of stocked Lake Trout exceeded the forage base (Johnson and Martinez 2000).

Our results indicate that cannibalism does not currently provide a mechanism for Lake Trout population regulation in Yellowstone Lake; however, dietary shifts toward lower trophic levels may ultimately result in a decreased Lake Trout population growth rate through decreases in individual growth rate, body condition, and fecundity (Matuszek et al. 1990; Pazzia et al. 2002). In contrast, the increase in Yellowstone Cutthroat Trout consumption of a preferred prey type (amphipods) may lead to an increased population growth rate via enhanced individual growth and body condition. Therefore, the dietary shifts displayed by Yellowstone Cutthroat Trout and Lake Trout likely have implications for the success of Lake Trout removal efforts and Yellowstone Cutthroat Trout recovery efforts in Yellowstone Lake.

A limitation of our study was the lack of diet data representing the winter months. Given logistical constraints, diet studies for Lake Trout in Yellowstone Lake have only been conducted during the ice-free season (May–October). The occurrence of Lake Trout in the littoral zone often increases when thermal barriers subside during the winter (Martin and Olver 1980). The increased occurrence of Lake Trout in the littoral areas of Yellowstone Lake could lead to higher consumption of Yellowstone Cutthroat Trout, cyprinids, or catostomids during the winter. Fish were common in the winter diets of Lake Trout in Lake Opeongo, Ontario (Martin 1954), and nonnative Lake Trout in Lake Chelan (Schoen et al. 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 assess Lake Trout diets in Yellowstone Lake during the winter.

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 focused on nonnative fishes are commonly conducted to evaluate trophic overlap or the effects of piscivory on native fish species (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 changing food web after a nonnative species introduction. Diet shifts for Yellowstone Cutthroat Trout and Lake Trout highlight the drastic changes that can occur in simple food webs after the establishment of a nonnative apex piscivore.

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REFERENCES

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, Pablo, Montana.

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.

Behnke, R. J. 2002. Trout and salmon of North America. Free Press, New York.

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

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 Internationale Vereinigung für Theoretische und Angewandte Limnologie 18.

Donald, D. B., and D. J. Alger. 1993. Geographic distribution, species displacement and niche overlap for Lake Trout and Bull Trout in mountain lakes. Canadian Journal of Zoology 71:238–247.

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 of the USA 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.

Fredenberg, W. 2002. Further evidence that Lake Trout displace Bull Trout in mountain lakes. Intermountain Journal of Sciences 8:143–152.

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 Journal of 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, Maryland.

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., and J. D. Varley. 1988. Effects of a century of human influence on the Cutthroat Trout of Yellowstone Lake. Pages 45–52 *in* R. E. Gresswell, editor. Status and management of interior stock of Cutthroat Trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

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.

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.

Hussey, N. E., M. A. MacNeil, B. C. McMeans, J. A. Olin, S. F. J. Dudley, G. Cliff, S. P. Wintner, S. T. Fennessy, and A. T. Fisk. 2014. Rescaling the trophic structure of marine food webs. Ecology Letters 17:239–250.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER – stable isotope Bayesian ellipses in R. Journal of Animal Ecology 80:595–602.

Jackson, M. C., I. Donahue, A. L. Jackson, J. R. Britton, D. M. Harper, and J. Grey. 2012. Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLoS (Public Library of Science) ONE [online serial] 7(2):e31757.

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, R. E. Gresswell, D. L. Mahoney, and S. E. Relyea. 1990. Fishery and aquatic management program in Yellowstone National Park. 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(3):16–20.

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(11):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, YCR-2007-04, Yellowstone National Park, Wyoming.

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, YCR-2012-03, Yellowstone National Park, Wyoming.

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, Hingham, Massachusetts.

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.

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(8):6–13.

Minigawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N 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.

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.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

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. 2004. Impact of Lake Trout introductions on Cutthroat Trout of selected western lakes of the continental United States. Doctoral dissertation. Utah State University, Logan.

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. Gresswell, P. Dwyer, and R. H. Hamre, editors. Wild trout VI: putting the native back in wild trout. Wild Trout Symposium, Bozeman, Montana.

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. 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.

Satterfield, F. R. IV, and B. P. Finney. 2002. Stable isotope analysis of Pacific salmon: insight into trophic status and oceanographic conditions over the last 30 years. Progress in Oceanography 53:231–246.

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.

Schullery, P., and J. D. Varley. 1995. Cutthroat Trout and the Yellowstone Lake ecosystem. Pages 12–21 *in* J. D. Varley and P. Schullery, editors. The Yellowstone Lake crisis: confronting a Lake Trout invasion. Report to the Director of the National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

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 41:14–21.

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, USA. 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., M. C. Clayton, E. K. Moody, C. T. Solomon, and B. C. Weidel. 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS (Public Library of Science) ONE [online serial] 10(1):e0116182.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer $\delta^{15}N$ and $\delta^{13}C$ 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.