

ARTICLE

# Trophic Ecology of Lahontan Cutthroat Trout: Historical Predator–Prey Interaction Supports Native Apex Predator in a Unique Desert Lake

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## Abstract

Pyramid Lake, Nevada, remains one of the last strongholds for lacustrine-strain Lahontan Cutthroat Trout *Oncorhynchus clarkii henshawi* (LCT) following historical declines throughout their native range. Historically the apex predator in this aquatic ecosystem, LCT in Pyramid Lake are now entirely dependent on hatchery programs and are potentially threatened by the introduction of a nonnative piscivore. The purpose of this study was to identify strong food web interactions and potential trophic limitations to the LCT population. Our specific objectives were to estimate seasonal foraging patterns, trophic position (TP), trophic niche space, diet composition, and seasonal depth distributions of LCT relative to prey fish. Additionally, we evaluated the potential for competition between LCT and nonnative, piscivorous Sacramento Perch *Archoplites interruptus* by examining diet overlap and trophic niche space. Our results indicate that LCT are apex predators, with TP (large [ $>400$  mm TL] LCT: TP [mean  $\pm$  1.96-SE] =  $4.30 \pm 0.04$ ) and diet composition indicating high rates of piscivory (average annual rate of piscivory = 77.1% for large LCT) throughout the year. Small (200–400 mm TL) LCT exhibited weak dietary overlap (Schoener's index = 0.55) and large LCT exhibited strong overlap (Schoener's index = 0.72) with Sacramento Perch. These trends were present despite seasonal changes in distribution and catch of Tui Chub *Siphateles bicolor*, the primary prey of LCT. Analysis of isotopic niche space also indicated strong overlap between the trophic niche of large LCT (89%) and that of Sacramento Perch; however, overall catch rates of Sacramento Perch were low. Despite the presence of a potential nonnative competitor, LCT demonstrate high rates of piscivory and are not negatively influenced by Sacramento Perch. Overall, these results demonstrate how trophic niche ecology can be used to evaluate key food web interactions in anthropogenically altered ecosystems.

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Anthropogenic alterations to aquatic environments can have significant effects on aquatic food webs. Throughout western North America, Cutthroat Trout *Oncorhynchus clarkii* subspecies have experienced declines in both population size and geographic distribution, often resulting from habitat alterations and nonnative species introductions. For example, in Bear Lake, Utah–Idaho, introduced Lake Trout *Salvelinus namaycush* contributed to the poor

survival rates of Bonneville Cutthroat Trout *O. clarkii utah* through competition for prey fish (Ruzycki et al. 2001). In Yellowstone Lake, predation on native Yellowstone Cutthroat Trout *O. clarkii bouvieri* by nonnative Lake Trout had a negative effect on the Yellowstone Lake food web (Ruzycki et al. 2003; Koel et al. 2005), thus altering zooplankton biomass and phytoplankton biovolume (Tronstad et al. 2010).

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The rangewide status of Cutthroat Trout provides reason for concern and highlights a need to better identify factors limiting the persistence and viability of Cutthroat Trout (Budy et al., in press). Of the 11 subspecies of Cutthroat Trout, two are now extinct, three are listed as threatened under the Endangered Species Act (USFWS 1975), and three are listed as species of special concern by state or federal agencies (Budy et al., in press). Among those listed as threatened, the Lahontan Cutthroat Trout *O. clarkii henshawii* (LCT) has been extirpated from more than 90% of its historical habitat and more than 99% of its lacustrine habitat (Coffin and Cowan 1995). Historically an apex predator within its range in southern Oregon, eastern California, and northern Nevada, this subspecies has experienced population declines resulting from overfishing (Coffin and Cowan 1995), the loss of spawning habitat (Sigler et al. 1983), and the introduction of nonnative species (Dunham et al. 1999; Vander Zanden et al. 2003). Consequently, the U.S. Fish and Wildlife Service and state and tribal agencies have been engaged in hatchery programs to maintain LCT populations in some lacustrine habitats.

One LCT population that has been maintained through continued conservation efforts resides in Pyramid Lake, Nevada. At the terminal end of the Tahoe-Truckee watershed, Pyramid Lake has been subject to numerous anthropogenic alterations that likely contributed to the loss of naturally reproducing LCT around 1938. Currently, the Pyramid Lake LCT population is made up of two strains: the “contemporary” strain, primarily the descendants of LCT stocks from Independence and Summit lakes; and the Pilot Peak strain. Pilot Peak LCT were re-established in Pyramid Lake after genetic analyses indicated that this stock provided the closest match to museum specimens of pre-extirpation Pyramid Lake LCT (Peacock et al. 2017). The presence of a nonnative piscivore, the Sacramento Perch *Archoplites interruptus*, potentially adds to this altered ecosystem. Sacramento Perch have been described as becoming highly piscivorous at sizes as small as 90 mm TL (Crain and Moyle 2011), and they may directly affect LCT in Pyramid Lake through competition or predation. These types of anthropogenic alterations to aquatic ecosystems can alter community structure (Lodge et al. 2006) through competitive (Douglas et al. 1994; Byers 2000) and predator-prey interactions (Ney 1990; Ruzycski et al. 2003) and ultimately may disrupt otherwise dependent relationships between native predators and prey.

The decline of LCT in other lacustrine food webs subjected to anthropogenic alterations highlights the importance of elucidating food web interactions. Lahontan Cutthroat Trout were once the dominant apex predator in many lakes of the Lahontan drainage (Moyle et al. 1996), which reflected their trophic niche atop lacustrine food webs (Vander Zanden et al. 2003). Although juvenile LCT tend to feed on zooplankton and invertebrates (Juday 1907;

Sigler et al. 1983), they become increasingly piscivorous with growth, and in many lakes, they feed heavily on Tui Chub *Siphateles bicolor* as adults (Juday 1907; Sigler et al. 1983; Vander Zanden et al. 2003). The Tui Chub is a planktivore (Galat and Vucinich 1983) that is commonly found in the same lakes as LCT and has historically been the primary prey of LCT in Pyramid Lake. However, after the introduction of nonnative piscivores, Cutthroat Trout can exhibit altered diets and a decreased trophic niche, and in some cases this trend has preceded extirpation. For example, in Lake Tahoe, the extirpation of naturally reproducing LCT coincided with the introduction of nonnative piscivores occupying a similar niche (Vander Zanden et al. 2003). Prior to their extirpation from Cascade Lake, LCT initially persisted after the introduction of Brown Trout *Salmo trutta* but exhibited a reduced trophic position (TP) in comparison with LCT throughout the subspecies’ native range and prior to nonnative species introductions (Vander Zanden et al. 2003). These cases highlight the need to preserve and effectively manage the Pyramid Lake LCT population, including preserving the LCT’s historical trophic niche as the apex predator in the food web.

Our overall goal was to better understand and quantify the contemporary food web of Pyramid Lake, with emphasis on the trophic ecology of LCT. We utilized several years of comprehensive field data describing diets and isotopic composition to estimate seasonal foraging patterns, TP, trophic niche space, and diet composition. Because we were also interested in the potential interaction and potential for competition between LCT and nonnative Sacramento Perch, we examined diet overlap and relative abundance. Lastly, we compared trends in Tui Chub consumption by LCT as they relate to seasonal fish distributions. In addressing these objectives, we aimed to determine the influence of Sacramento Perch on the LCT population and to quantify the degree of contemporary LCT reliance on Tui Chub, which historically constituted their most important prey item.

## METHODS

*Study site.*—Pyramid Lake is a cool, monomictic lake with summer stratification generally occurring from July through November. The lake has an average depth of 53 m, a maximum depth of 105 m, and a surface area of 488 km<sup>2</sup>. During summer, the metalimnion typically forms between 9 and 22 m below the surface, with a temperature range of 12–22°C. Temperatures in the hypolimnion generally remain at or below 10°C throughout the year (Galat et al. 1981; Chandra and Lawrence 2005). In addition to LCT, the native fish community consists of the Tahoe Sucker *Catostomus tahoensis*; the Cui-ui *Chasmistes cujus*, an endangered sucker species endemic to Pyramid Lake; the Lahontan Redside *Richardsonius egregius*; and the Tui Chub (Vigg 1981).

*Field sampling.*—We sampled the Pyramid Lake food web during three seasons throughout the year from summer 2011 through fall 2012. As Pyramid Lake is monomictic, we focused on sample periods that would best capture temperature variability throughout the year. We sampled fish during the last 2 weeks of late May/early June (spring), the first 2 weeks of August (summer), and late November/December (winter). Spring sampling was conducted once during 2012. Both summer sampling and winter sampling were conducted twice (in 2011 and 2012). Spring sampling occurred while the lake was transitioning from an isothermal state to a stratified state, summer sampling occurred while the lake was stratified, and winter sampling occurred while the lake was again isothermal. During both of the summer sampling periods, the inflection point of the thermocline occurred at or near 16 m below the surface. Temperature data were provided by Pyramid Lake Fisheries and were collected with a Sea-CAT Profiler at Station 96 (Figure 1). Temperatures were recorded at 1-m intervals to a depth of 60 m and were recorded within 1 week of each fish sampling period. We chose sampling locations that were evenly distributed around the lake and that would likely represent a range of habitat types (Figure 1).

*Relative abundance.*—During each sampling period, we conducted overnight gill-net sets at eight locations around the lake. To ensure a sufficient catch for isotope samples, we also set one trap net at each location in 5–10 m of water approximately 200 m away from the nearest gill net. We set nets at dusk and pulled them the following morning after dawn to capture two crepuscular periods. Six variable-mesh gill nets were set on the bottom of the lake at 10-m depth intervals from 10- to 60-m depth. We used sinking horizontal gill nets with variable mesh sizes (24 m long  $\times$  1.8 m tall, with eight monofilament panels of 38-, 57-, 25-, 44-, 19-, 64-, 32-, and 51-mm knot-to-knot bar mesh) according to standard gill-net methods for capturing a representative size distribution of all fishes within Pyramid Lake (Beauchamp et al. 2009). Fish were removed from nets and immediately placed on ice. We calculated CPUE (fish-net<sup>-1</sup>·h<sup>-1</sup>) for each net to quantify seasonal differences in depth distribution by small and large LCT, Sacramento Perch, and Tui Chub. We divided Tui Chub into two size-classes (small:  $\leq 200$  mm TL; large:  $>200$  mm TL) based on LCT gape limitation data. Theoretically, small LCT would only be able to consume Tui Chub up to approximately 200 mm TL (Heredia 2014).

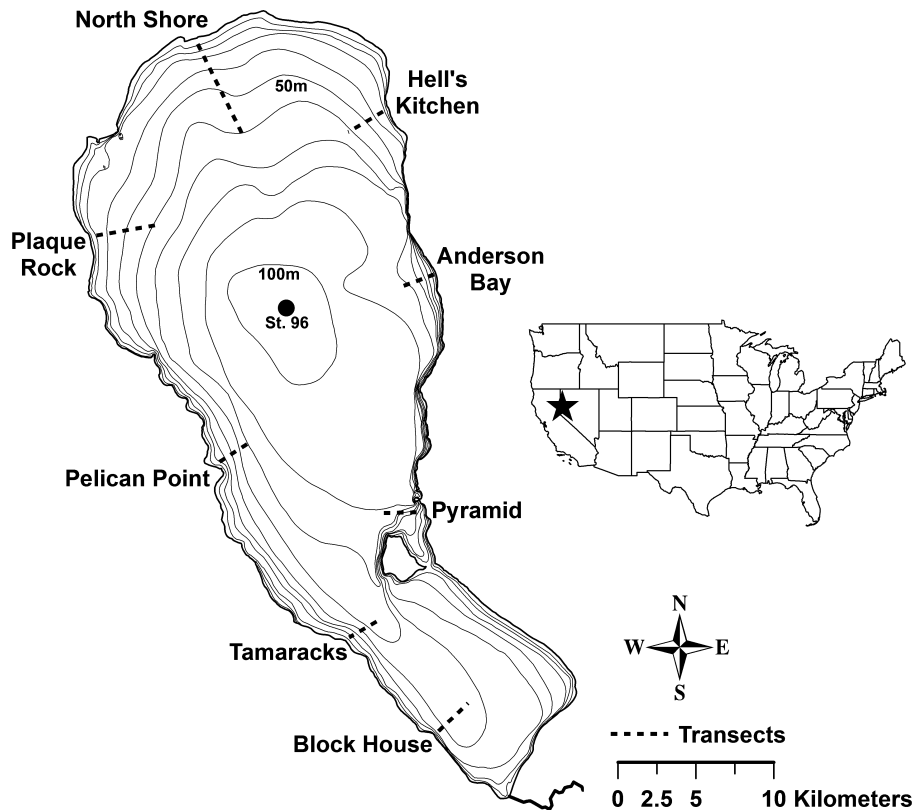


FIGURE 1. Map of Pyramid Lake, Nevada. The labels and dashed lines shown around the perimeter of the lake indicate routine sample transects used for gillnetting (St. 96 = Station 96).

We used a generalized linear mixed-effects model (“glmer” function in R) to assess the significance ( $\alpha = 0.05$ ) of depth and season on catch. We built a negative binomial model for each species separately. We assessed catch as a function of depth and season, with location set as a random effect and the duration of each gill-net set as an offset. For each species, we attempted to model catch with season and depth as factors. However, the models for small LCT and Sacramento Perch failed to converge; therefore, we assessed catch as a function of season. To evaluate pairwise differences between the levels of a significant factor, we performed Tukey’s adjusted post hoc tests by using the “glht” function from the R package “multcomp.”

*Diet composition and overlap.*—We examined diets of LCT and Sacramento Perch collected throughout the study to determine seasonal and ontogenetic transitions in diet composition. For diet analysis (as well as all other analyses throughout), we apportioned LCT into two size categories (small: 200–400 mm TL; large: >400 mm TL) based on diet composition and ontogenetic shift (Nowak et al. 2004). We removed fish stomachs and placed them in ethanol within 5 h of sampling. In the laboratory, we classified prey items into six different categories: Tui Chub, suckers, fish (fish that could not be identified to species), zooplankton, invertebrates, and other (unidentifiable organic matter). We identified partially digested fish prey by using external body and bone morphology. Once all diet items were sorted and their weights were recorded, we calculated diet composition as proportion of the total wet mass (g) of each diet category for each fish. We then used diet proportion by wet weight to calculate seasonal averages for the two LCT size-classes. We did not distinguish between size-classes for Sacramento Perch, as these fish become highly piscivorous at around 90 mm TL and remain so for life (Crain and Moyle 2011).

In Pyramid Lake, Sacramento Perch are the only aquatic piscivores that could potentially compete with LCT for food. We examined diet composition of LCT and Sacramento Perch to assess potential competition for food. We used diet overlap to compare prey consumption between each LCT size-class and Sacramento Perch as well as between the two LCT size-classes across the different seasons. We calculated diet overlap with Schoener’s index  $\alpha$  (Schoener 1970),

$$\text{Schoener's } \alpha = 1 - 0.5 \left( \sum_{i=1}^n |P_{x,i} - P_{y,i}| \right),$$

where  $P_{x,i}$  is the proportion of food item  $i$  used by group  $x$ ;  $P_{y,i}$  is the proportion of food category  $i$  used by group  $y$ ; and  $n$  is the total number of diet categories. A value of zero suggests no overlap, and a value of 1 suggests complete overlap. This approach assumes that all diet items are equally available to all groups of predators being

compared. We used 0.60 as a cutoff representing significant diet overlap, such that values above 0.60 were considered biologically significant (Wallace 1981).

*Stable isotope analysis of food web structure.*—We used carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes to determine a time-integrated representation of the Pyramid Lake food web by employing a measure of species niche space. Based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures, species niche space gives a representation of both TP and where in the lake (i.e., pelagic versus benthic) an individual consumes food (Vander Zanden and Rasmussen 1999; Jackson et al. 2011). We collected tissues during the routine summer sampling periods to evaluate  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures. Benthic invertebrates were collected using a standard Eckman grab (15.24 × 15.24 × 15.24 cm [6 × 6 × 6 in]) at the Pelican Point sampling site (Figure 1). Benthic samples were collected at depths of 5, 10, and 15 m. Zooplankton were collected using a Wisconsin-style zooplankton tow at Station 96 (Figure 1) from the top 50 m of the lake. All benthic invertebrate and zooplankton samples used in isotopic analyses were collected during August 2012, and at least five replicates were collected at each depth or site. We collected a minimum of 10 samples for each fish species or group (small LCT:  $n = 17$ ; large LCT:  $n = 46$ ; Sacramento Perch:  $n = 13$ ), as this has been shown to be adequate for representing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in fish tissues (Vinson and Budy 2011). We used fish tissue samples that were collected in August 2011. Due to the high number of prey categories evaluated, between 5 and 10 samples were processed per prey species for isotopic analysis; the exception was Ephemeroptera, for which we only prepared four samples due to processing error. Other invertebrate prey taxa included were Amphipoda, Cladocera, Diptera, Hemiptera, Odonata, Trichoptera, and the cladocerans *Moina* spp. We also sampled benthic macrophytes and pelagic phytoplankton for analysis of baseline  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures. Macrophyte samples were collected using an Eckman grab at the same times and locations that benthic invertebrate samples were collected. We collected five water samples to capture phytoplankton for isotope analyses. The phytoplankton samples were collected near the middle of the lake and were filtered through ashed fiberglass filters. Once in the laboratory, we dried tissue samples for 48 h at 70°C, ground them into a fine powder using mortar and pestle, and placed them into pre-weighed tin capsules.

Tissue and filter samples were processed at the Stable Isotope Core laboratory, Washington State University, Pullman, for analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and percent composition of both carbon and nitrogen. Isotopic signatures are expressed as ratios ( $^{13}\text{C}:^{12}\text{C}$  and  $^{15}\text{N}:^{14}\text{N}$ ) of per mille (‰) values relative to ratios of standard atmospheric  $\text{N}_2$  and Pee Dee belemnite, respectively.

We used a baseline correction equation for all  $\delta^{15}\text{N}$  data, which scaled  $\delta^{15}\text{N}$  values for all individuals to

baseline values representative of primary production as represented by  $\delta^{13}\text{C}$  (Vander Zanden and Rasmussen 1999). The baseline correction accounts for  $\delta^{13}\text{C}$  among pelagic primary producers being isotopically depleted relative to that of benthic primary producers (Hecky and Hestlein 1995). The correction is calculated as

$$\delta^{15}\text{N}_{i,\text{correction}} = -0.148(\delta^{13}\text{C}_i) - 0.303,$$

where  $\delta^{15}\text{N}_{i,\text{correction}}$  is the lake-corrected baseline  $\delta^{15}\text{N}$  value for individual  $i$ ; and  $\delta^{13}\text{C}_i$  is the  $\delta^{13}\text{C}$  for individual  $i$ . We then used the baseline-corrected data to assess TP.

We calculated TP of the three piscivore groups (small LCT, large LCT, and Sacramento Perch) as

$$\text{TP}_i = \left( \frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{baseline}}}{3.4} \right) + 1,$$

where  $\text{TP}_i$  is the trophic position of species  $i$ ;  $\delta^{15}\text{N}_i$  is the nitrogen signature of species  $i$ ; and  $\delta^{15}\text{N}_{\text{baseline}}$  is the nitrogen signature for primary producers (Vander Zanden and Rasmussen 1999). We assumed that primary producers represented a TP of 1 and a  $\delta^{15}\text{N}$  trophic fractionation value of  $3.4 \pm 1.1\text{‰}$  (Minagawa and Wada 1984). We modified the Vander Zanden and Rasmussen (1999) equation to account for the use of benthic macrophytes and phytoplankton as baseline nitrogen values rather than collector-filterer invertebrates because those values produced a better carbon-to-nitrogen fit across a gradient of pelagic to benthic carbon signatures (Post 2002). Benthic macrophytes and pelagic phytoplankton served as the benthic and pelagic end-members that were used to calculate baseline nitrogen values. We used Student's  $t$ -tests to compare TP. Additionally, we used  $\delta^{13}\text{C}$  values to calculate percent benthic reliance (BR), a measure of prey origin wherein low values indicate a reliance on pelagic prey and higher values indicate a reliance on benthic prey (Vander Zanden and Rasmussen 1999). As the  $\delta^{13}\text{C}$  of pelagic primary producers is isotopically enriched relative to benthic primary producers, we used mean benthic macrophyte and mean pelagic phytoplankton values to create a two-end-member mixing model of benthic versus pelagic reliance. Percent BR was calculated as

$$\text{Percent BR} = (\delta^{13}\text{C}_i - \delta^{13}\text{C}_{\text{pelagic}}) / (\delta^{13}\text{C}_{\text{benthic}} - \delta^{13}\text{C}_{\text{pelagic}}) \times 100,$$

where  $\delta^{13}\text{C}_i$  is the carbon signature of individual  $i$ ; and  $\delta^{13}\text{C}_{\text{pelagic}}$  and  $\delta^{13}\text{C}_{\text{benthic}}$  are the pelagic and benthic end-member values.

The SIBER (Stable Isotope Bayesian Ellipses in R) model, which employs Bayesian inference techniques to

describe niche and community metrics (Jackson et al. 2011), was used to infer characteristics of community structure and niche overlap of community members. For all stable isotope analyses described hereafter, we used program R (R Development Core Team 2011). The SIBER model uses bivariate  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data to represent isotopic niche space for a species or group. The Shapiro–Wilk test conducted via the `mshapiro.test()` function in R was used to test for normality. All analyzed species or groups met the assumption that the isotope data used were sufficiently described by a multivariate normal distribution (all species: Shapiro–Wilk  $W \geq 0.91$ ,  $P \geq 0.14$ ; Royston 1982). The SIBER model fits a standard ellipse to bivariate data using maximum likelihood estimators (Jackson et al. 2011). We then employed the intersection of ellipse areas to calculate percent species (or group) overlap.

*Prey-to-predator contribution.*—We used the Bayesian stable isotope mixing model from the SIAR (Stable Isotope Analysis in R) package (Parnell et al. 2008) to further understand the relative contributions of the different food sources to upper-level consumers. The SIAR mixing model allows for the estimation of prey-to-consumer contributions of food for any number of potential source items, regardless of the number of isotopes analyzed. The model requires that the isotopic values for food sources be adjusted by using trophic enrichment factors (Gannes et al. 1998). We used trophic enrichment factors of  $1.3 \pm 1.7\text{‰}$  (mean  $\pm 1$  SD) for  $\delta^{13}\text{C}$  and  $3.4 \pm 1.1\text{‰}$  for  $\delta^{15}\text{N}$  (Minagawa and Wada 1984; Vander Zanden and Rasmussen 1999; McCutchan et al. 2003) for all prey species adjustments to account for changes in isotope enrichment from one trophic level to the next. Additionally, the SIAR mixing model allows for the inclusion of elemental concentrations from both predator and prey, which has been shown to further improve the accuracy of estimating dietary trends from stable isotopes (Phillips and Koch 2002). The SIAR model uses the aforementioned inputs to estimate Bayesian 95% credible intervals (CIs) representing percent diet contribution. We collected prey fish tissue samples as well as all of the major benthic invertebrate orders found during gut content analysis and included their carbon and nitrogen signatures in the SIAR analysis. However, among the various zooplankton taxa collected, only *Moina* spp. were included in this analysis. The other zooplankton taxa exhibited extremely high and variable  $\delta^{15}\text{N}$  values due to their small sizes and short life spans (Toda and Wada 1990; Yoshioka et al. 1994; Cabana and Rasmussen 1996).

## RESULTS

### Relative Abundance

Catch data indicated seasonal shifts in Tui Chub and LCT distributions throughout the year (Figure 2). The

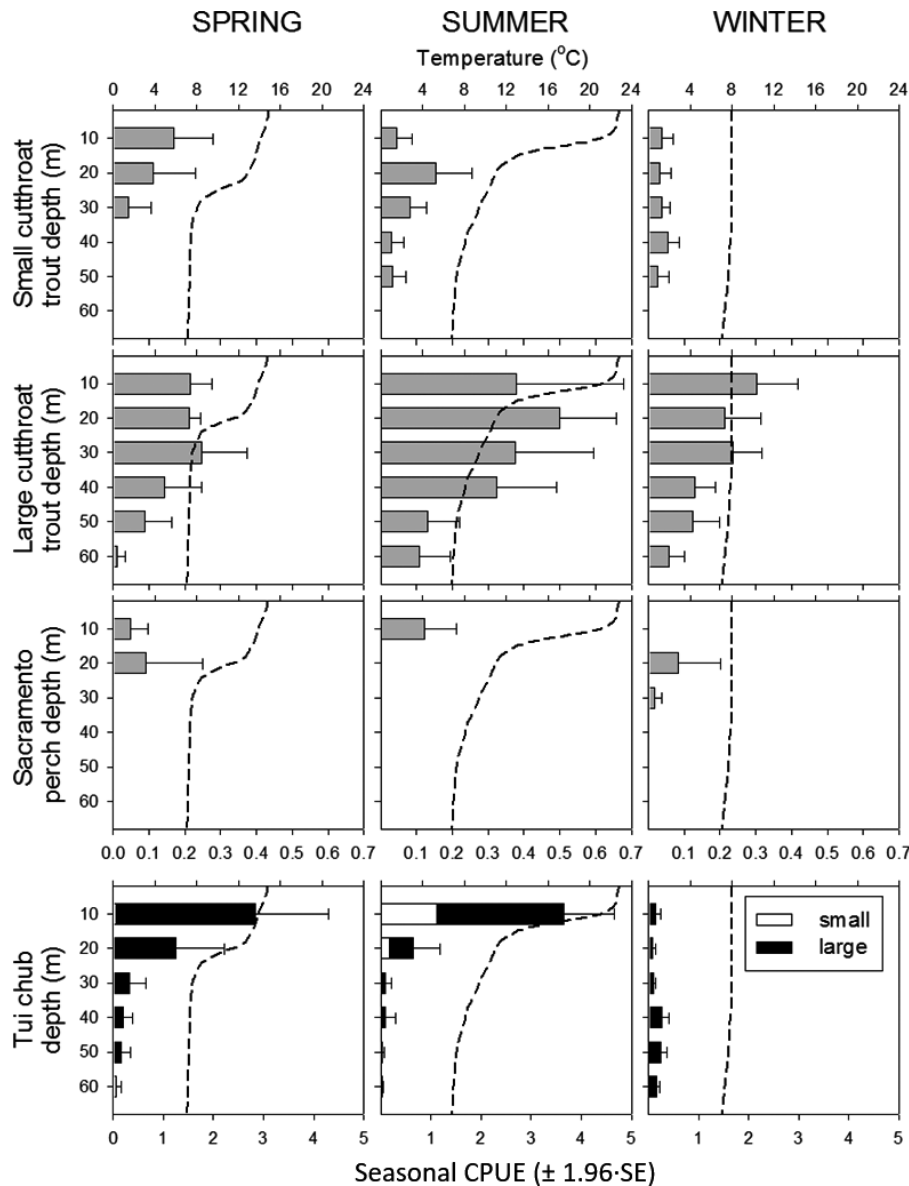


FIGURE 2. Catch per unit effort (fish·net<sup>-1</sup>·h<sup>-1</sup>; bars) by season for small (200–400 mm TL) Lahontan Cutthroat Trout, large (>400 mm TL) Lahontan Cutthroat Trout, Sacramento Perch, and Tui Chub. Dashed lines represent temperature profiles. Data are from gill-net catches in Pyramid Lake, Nevada, obtained during June 2011 through December 2012. Note that the *x*-axis for Tui Chub is scaled differently than those of the other three groups. Error bars represent 2 SEs. Optimum temperature ranges for Lahontan Cutthroat Trout and Tui Chub are 13–20°C and 24–30°C, respectively.

generalized linear mixed-effects models revealed that catches differed significantly by depth for large LCT and by depth and season for Tui Chub (Table 1). Post hoc tests (Table 2) suggested the same pattern as seen in Figure 2. The small LCT and Sacramento Perch models yielded no significant trends. During spring, Tui Chub catch appeared to be highest at 10 m (CPUE [mean ± 1.96·SE] = 2.77 ± 1.44 fish·net<sup>-1</sup>·h<sup>-1</sup>; Table 1; Figure 2), where surface temperatures approached those more suitable for Tui Chub metabolic rates (24–30°C; McClanahan et al. 1986). Similarly, the majority of large LCT catch occurred

between 10- and 30-m depths, much of which reflected optimum temperatures for LCT growth (13–20°C; Dickerson and Vinyard 1999). Summer sampling took place during thermal stratification, when 86.8% of small LCT catch and 79.1% of large LCT catch occurred at or below 20 m (Figure 2). During the same period, 81% of Tui Chub catch occurred at 10-m depth. During winter, Tui Chub catch was relatively low across all depths, while large LCT catch generally decreased with depth (Figure 2). Sacramento Perch catch was restricted to the upper 30 m of the water column, was not significantly different between seasons (Table 1),

and was relatively low throughout the year compared to LCT and Tui Chub catch (Figure 2).

### Diet Composition and Overlap

Diets of both small LCT ( $n = 44$ ) and large LCT ( $n = 209$ ) indicated that Tui Chub were a primary food source for LCT. During spring, a combination of nonfish prey (zooplankton and invertebrates) made up the majority of the diet by wet weight for small LCT ( $n = 24$ ), and the proportion of fish in the diets of small LCT increased throughout the year. The percentage of the diet that was composed of fish prey peaked in summer for large LCT ( $n = 54$ ) and was lowest during spring ( $n = 91$ ), but the difference was only 12%. During winter, more than 80% of the diet for small LCT ( $n = 8$ ) consisted of a combination of Tui Chub (58%) and unidentifiable fish prey (25%; Figure 3A), while diet composition for large LCT was fairly consistent throughout the year (Figure 3B). The diet consumed by large LCT comprised a minimum of 70% fish, mostly Tui Chub, during all three seasons. Sacramento Perch were highly piscivorous during spring ( $n = 42$ ) and summer ( $n = 19$ ), whereas they shifted to consuming more benthic invertebrates during winter ( $n = 10$ ; Figure 3C).

TABLE 1. Results from negative binomial generalized linear mixed-effects models used to assess fish catch for each studied species in Pyramid Lake, Nevada (small Lahontan Cutthroat Trout: 200–400 mm TL; large Lahontan Cutthroat Trout: >400 mm TL).

Fixed effect	$\chi^2$	df	<i>P</i>
<b>Small Lahontan Cutthroat Trout</b>			
Season	2.15	2	0.34
<b>Large Lahontan Cutthroat Trout</b>			
Season	5.7	2	0.06
Depth	77.4	5	<0.01
Season × Depth	11.62	10	0.3
<b>Tui Chub</b>			
Season	7.3	2	0.03
Depth	71.3	5	<0.01
Season × Depth	80.3	10	<0.01
<b>Sacramento Perch</b>			
Season	0.51	2	0.77

TABLE 2. Post hoc pairwise comparisons of fixed-effects levels influencing catch (large LCT = >400 mm TL Lahontan Cutthroat Trout; ns = not significant). Within a row, levels without a letter in common are significantly different.

Species	Depth (m)						Season		
	10	20	30	40	50	60	Spring	Summer	Winter
Large LCT	z	z	z	zy	zy	y	ns	ns	ns
Tui Chub	z	zy	yx	yx	yx	x	z	z	y

Dietary overlap between large LCT and nonnative Sacramento Perch ( $n = 19$ ) was significant across all seasons and highest during summer (Table 3). Overlap between small LCT and Sacramento Perch was also significant during summer but was biologically insignificant during spring and winter (Table 3). Intraspecific dietary overlap between small and large LCT was insignificant during spring, when small LCT were not yet highly piscivorous, but overlap between the two LCT size-classes was significant during summer and winter, as small LCT ( $n = 13$ ) transitioned to higher rates of piscivory (Table 3).

### Stable Isotope Analysis of Food Web Structure

Lahontan Cutthroat Trout and Sacramento Perch exhibited similar TPs at the top of the food web (Figure 4). Large LCT (TP [mean ± 1.96-SE] = 4.30 ± 0.04) and Sacramento Perch (TP = 4.38 ± 0.11) occupied similar TPs ( $t$ -value = 2.13,  $P = 0.19$ ), exhibited similar carbon signatures ( $t$ -value = 2.1,  $P = 0.44$ ), and thus exhibited similar percent BR. Small LCT (TP = 4.13 ± 0.17) exhibited a lower TP than large LCT ( $t$ -value = 2.10,  $P = 0.086$ ) and a significantly lower TP than Sacramento Perch ( $t$ -value = 2.06,  $P = 0.026$ ). Tui Chub (TP = 3.40 ± 0.17) and suckers (Tahoe Suckers; TP = 3.01 ± 0.22) demonstrated significantly different TPs ( $t$ -value = 2.11,  $P = 0.016$ ) but similar carbon signatures ( $t$ -value = 2.07,  $P = 0.48$ ). Benthic reliance values for small LCT (BR [mean ± 1.96-SE] = 41.7 ± 3.7%), large LCT (BR = 45.0 ± 2.3%), Sacramento Perch (BR = 46.1 ± 4.7%), suckers (BR = 47.6 ± 7.2%), and Tui Chub (BR = 43.3 ± 9.2%) were not significantly different (ANOVA:  $F = 2.47$ ,  $P = 0.65$ ).

Strong isotopic niche space overlap between large LCT and Sacramento Perch reflected similar isotopic niche occupancy, while small LCT exhibited a broader  $\delta^{15}\text{N}$  range (Figure 5), indicating wider dietary breadth. Although small LCT, large LCT, and Sacramento Perch exhibited similar  $\delta^{13}\text{C}$  ranges, 32% of small LCT trophic niche space was overlapped by Sacramento Perch (36% was overlapped by a combination of Sacramento Perch and large LCT). In comparison, 89% of large LCT niche space was overlapped by Sacramento Perch niche space, and 100% of large LCT niche space was overlapped by a combination of Sacramento Perch and small LCT. A combination of large LCT (50%) and small LCT (50%) niche

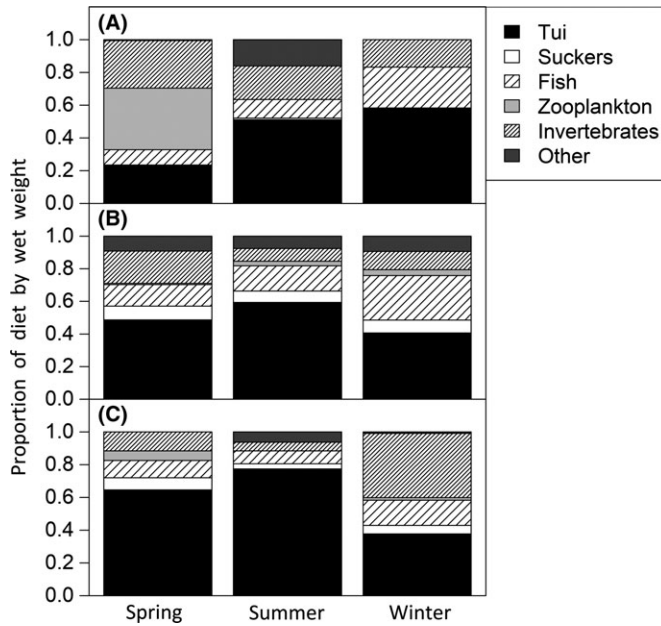


FIGURE 3. Seasonal diet composition (proportion of wet weight) for (A) small (200–400 mm TL) Lahontan Cutthroat Trout, (B) large (>400 mm TL) Lahontan Cutthroat Trout, and (C) Sacramento Perch in Pyramid Lake, Nevada (Tui = Tui Chub; Suckers = mix of Tahoe Suckers and Cui-ii; Fish = fish that were too digested to be identified to species; Invertebrates = terrestrial and aquatic macroinvertebrates; Other = mixture of unidentifiable organic matter).

TABLE 3. Seasonal estimates of Schoener's index of diet overlap for predator species in Pyramid Lake, Nevada (small LCT = 200–400 mm TL Lahontan Cutthroat Trout; large LCT = >400 mm TL Lahontan Cutthroat Trout; SAP = >100 mm TL Sacramento Perch). Values higher than 0.60 (the cutoff for significance) are shown in bold italics.

Comparison	Spring	Summer	Winter	Mean
Small LCT versus SAP	0.41	<b>0.72</b>	0.53	0.55
Large LCT versus SAP	<b>0.73</b>	<b>0.79</b>	<b>0.63</b>	<b>0.72</b>
Small LCT versus large LCT	0.47	<b>0.76</b>	<b>0.69</b>	<b>0.64</b>
Mean	0.54	<b>0.75</b>	<b>0.62</b>	

space overlapped 62% of Sacramento Perch niche space. Tui Chub niche space overlapped 48% of sucker niche space, and sucker niche space overlapped 28% of Tui Chub niche space.

### Prey-to-Predator Contribution

Similar to diet data, the SIAR mixing model suggested that all three groups (small LCT, large LCT, and Sacramento Perch) were highly piscivorous and that Tui Chub were the most important contributors to the diets of small and large LCT (Figure 6). Large LCT reflected a diet consisting of primarily Tui Chub (95% CI = 33–79%) and a

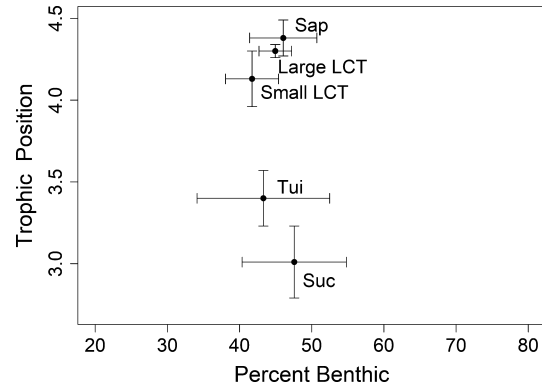


FIGURE 4. Trophic position and percent benthic reliance (mean  $\pm$  1.96-SE) for fishes in Pyramid Lake, Nevada (small LCT = 200–400 mm TL Lahontan Cutthroat Trout; large LCT = >400 mm TL Lahontan Cutthroat Trout; Sap = Sacramento Perch; Tui = Tui Chub; Suc = Tahoe Suckers). Values were calculated as described by Vander Zanden et al. (1999).

smaller amount of suckers (95% CI = 5–37%). Six of the remaining seven diet items included in the analysis returned a lower bound of zero for the 95% CIs, suggesting that invertebrate prey contributed relatively little to the diets of large LCT. Pelagic zooplankton made a small but significant contribution to large LCT diets (*Moina* spp.: 95% CI = 5.6–19%).

Small LCT exhibited trends similar to those of large LCT, with a slightly lower emphasis on fish prey and a slightly higher emphasis on invertebrate prey, but still consumed mostly Tui Chub and suckers (95% CI = 13–54% and 14–50%, respectively; Figure 6). Consistent with large LCT, six of the seven remaining taxa included in the analysis produced CIs that included zero (Amphipoda: 0–18%; *Moina* spp.: 0–8.6%; Diptera: 0–13%; Ephemeroptera: 0–10%; Hemiptera: 0–8.9%; Odonata: 0–16%; Trichoptera: 0–14%). However, all of these taxa consistently resulted in CI upper bounds that were larger than those produced for the same prey items of large LCT.

Based on the SIAR mixing model for Sacramento Perch, diet contributions were similar to those of both large and small LCT (Figure 6). Sacramento Perch fed mostly on Tui Chub and suckers (95% CI = 19–70% and 12–58%, respectively), and all of the remaining diet items exhibited 95% CIs that included zero. These modeled diet proportions indicate that, similar to LCT, Sacramento Perch consumed primarily fish.

### DISCUSSION

Despite the current fragmented and imperiled status of LCT throughout their native range (Coffin and Cowan 1995), the LCT in Pyramid Lake remains an apex predator and is reliant on its historical prey base. The presence



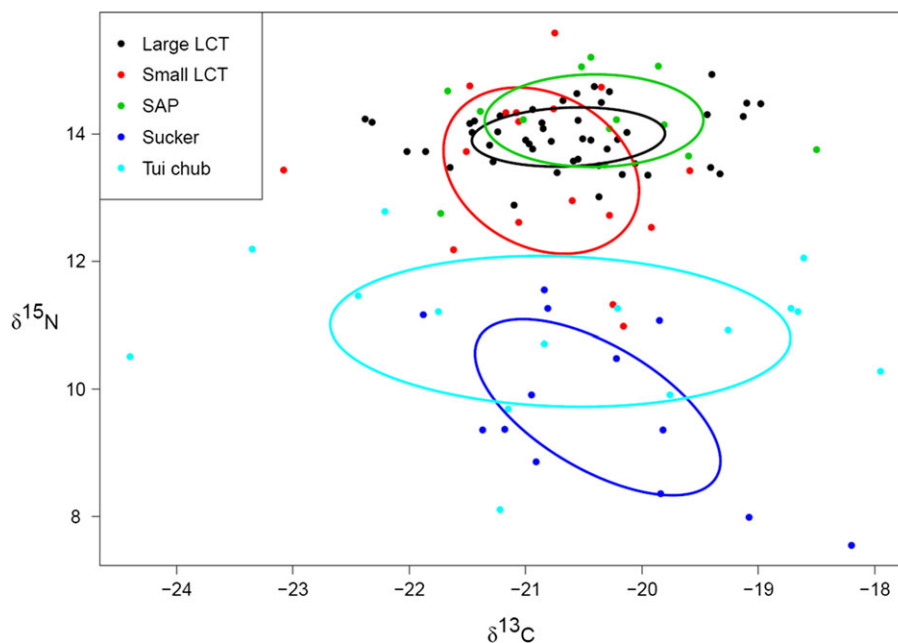


FIGURE 5. Trophic niche spaces occupied by fish species of Pyramid Lake, Nevada (red = small [200–400 mm TL] Lahontan Cutthroat Trout [LCT]; black = large [ $>400$  mm TL] LCT; green = Sacramento Perch [SAP]; blue = Tahoe Sucker [Sucker]; cyan = Tui Chub). Points represent empirical  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (‰). Ellipses encompass  $\pm 1$  SD around the centroid.

of nonnative Sacramento Perch and the fact that LCT are now entirely dependent on stocking programs in Pyramid Lake create the potential for an altered trophic niche and, subsequently, an altered Pyramid Lake food web. However, both diet and isotope analyses indicated a strong predator–prey relationship between LCT and Tui Chub, as would have occurred historically. This dependence on Tui Chub persists despite the potential for competition with Sacramento Perch and despite seasonal shifts in species depth distributions. Additionally, as also indicated by isotope analysis, the LCT remains an upper-trophic-level predator within this unique desert lake. The Tui Chub was the most abundant species caught and the most common diet item for LCT, thus resulting in a high TP. These trends, in combination with bioenergetic simulations (Heredia 2014), suggest that LCT still rely strongly on Tui Chub as a primary food source throughout the year and are currently unlikely to be limited by food availability. In addition, the strong link between predator and prey has not been disrupted by the reliance on hatchery stocking of LCT or by the presence of nonnative Sacramento Perch.

Seasonal depth distributions may reflect temperature preferenda for LCT, Sacramento Perch, and Tui Chub. During the spring sampling period, all of the small LCT and Sacramento Perch as well as the majority of both large LCT and Tui Chub were caught at or above 30 m, where temperatures ranged from  $8^{\circ}\text{C}$  to  $15^{\circ}\text{C}$ . While these distributions likely reflect temperature preferenda for Sacramento Perch and Tui Chub, there does not appear

to be as strong of a relationship between temperature and LCT. May marks the transition from an isothermal state to a stratified state in the lake (Galat et al. 1981; Chandra and Lawrence 2005) and represents the period when surface temperatures approach those more suitable for LCT (Dickerson and Vinyard 1999; Meeuwig et al. 2004), Sacramento Perch (Knight 1985; Woodley 2007), and Tui Chub (Vigg 1978; McClanahan et al. 1986) alike. Summer depth distributions further reflected differences in distribution, with the majority of LCT catch occurring below the thermocline and the majority of Tui Chub and Sacramento Perch occurring in the warmer littoral regions. Despite the differences in habitat occupied by predator and prey, both large LCT and Sacramento Perch consumed a higher proportion of Tui Chub during summer than during spring or winter.

In summer, Tui Chub appeared to preferentially occupy epilimnion habitat, where temperatures are more suitable for both metabolic processes (Castleberry and Cech 1986; McClanahan et al. 1986) and spawning (Kucera 1978). Conversely, the majority of both small and large LCT were below the epilimnion, spatially separating predators from prey. Laboratory studies of LCT demonstrated that they can maintain reduced yet positive growth rates while subject to temperature fluctuations similar to what would be experienced by a fish making diel migrations from the hypolimnion into the epilimnion of Pyramid Lake (Dickerson and Vinyard 1999). Although our data are too coarse to investigate diel migrations, the high variability

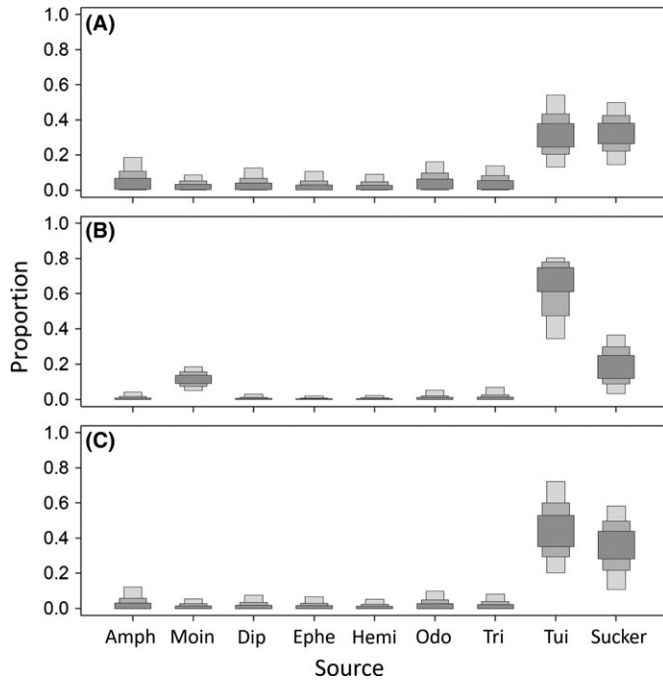


FIGURE 6. Results of the SIAR (Stable Isotope Analysis in R) mixing model (95, 75, and 50% credible intervals) showing the estimated prey contributions to the diets of (A) small (200–400 mm TL) Lahontan Cutthroat Trout, (B) large (>400 mm TL) Lahontan Cutthroat Trout, and (C) Sacramento Perch in Pyramid Lake, Nevada (Amph = Amphipoda; Moin = *Moina* spp.; Dip = Diptera; Ephe = Ephemeroptera; Hemi = Hemiptera; Odo = Odonata; Tri = Trichoptera; Tui = Tui Chub; Sucker = Tahoe Suckers and Cui-UI). Results were calculated from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope signatures and elemental concentrations of consumer and prey sources alike.

in LCT summer catch at 10-m depth, in combination with a diet high in Tui Chub for the same period, suggests either that LCT can make migrations to forage in warmer water or that Tui Chub abundance in the deeper, cooler waters is sufficient for LCT to maintain a high-fish diet. In contrast, Sacramento Perch catch was restricted to the epilimnion, reflecting heavy overlap with their prey base. Nonetheless, the low total catch of Sacramento Perch considered along with the high Tui Chub diet for LCT during this period suggests little competitive pressure from Sacramento Perch for food. Cold winter temperatures and the transition to an isothermal state (Galat et al. 1981; Chandra and Lawrence 2005) brought more than a fourfold decrease in Tui Chub CPUE, yet large LCT still maintained a piscivorous diet similar to that in summer, suggesting ample fish prey for LCT throughout the year.

The large dietary overlap between native LCT and non-native Sacramento Perch, most notably during summer, could indicate the potential for competitive interactions between the two species. However, the high amount of overlap between the two species and the lack of significant differences between  $\delta^{13}\text{C}$  signatures are indicative of little

to no resource partitioning. This overlap appears to occur despite the presence of abundant alternative prey items and further suggests that food resources are not limiting (e.g., Grossman 1986; Correa and Winemiller 2014). Moreover, isotopic niche space data reflect little to no trophic separation among piscivores, with the strongest overlap occurring between large LCT and Sacramento Perch. In addition, both LCT and Sacramento Perch in Pyramid Lake obtain the largest sizes observed throughout their respective geographic ranges (Trotter 2008; Crain and Moyle 2011); however, as noted above, catch rates of Sacramento Perch remain very low and localized. In other systems where upper-trophic-level piscivores are introduced, competitive interactions commonly result in altered foraging habits of native or historical counterparts and a corresponding reduction in performance (Vander Zanden et al. 1999, 2003; Winters and Budy 2015), a phenomenon that does not appear to be true for LCT in Pyramid Lake.

In contrast, during winter, small LCT and Sacramento Perch exhibited weak dietary overlap, potentially indicating competitive exclusion or a lack of available fish prey. However, this weak overlap was the result of a reduction in the percentage of Sacramento Perch diet made up of fish, while small LCT continued to feed on the more energetically rich fish prey, potentially indicative of the ontogenetic diet shift by LCT as they transition to consuming a higher proportion of fish prey. Although both LCT and Sacramento Perch are highly piscivorous in Pyramid Lake, we found no indication of predation on one piscivore by the other. Additionally, of the 253 LCT diets analyzed, only one LCT was found in the diet of another LCT, and no Sacramento Perch were found in conspecific diets. These results suggest that little to no cannibalism is occurring and provide yet another indication that food resources are not limiting (Hecht and Pienaar 1993). There appears to be an alternative factor (i.e., not food availability) limiting Sacramento Perch expansion in Pyramid Lake. Based on the distribution of our catch data and the bathymetry of Pyramid Lake, we suspect that a lack of physical structure limits their expansion and further integration into the fish community at a lake-wide scale. Other work has hypothesized that given their deep body shape, Sacramento Perch are highly dependent on shallow physical structure (Crain and Moyle 2011). Given the relatively small littoral zone and the lack of a well-developed macrophyte community (Galat et al. 1981) in Pyramid Lake, Sacramento Perch are likely restricted to the calcium carbonate formations found in localized regions of the lake.

While few empirical comparisons between current and historical fish communities of Pyramid Lake exist, the TP of LCT in Pyramid Lake is currently higher than LCT TPs observed historically in Lake Tahoe, even when the native fish community was still intact (Vander Zanden

et al. 2003). Over the last century, LCT in Lake Tahoe progressively exhibited a lower TP as the number of non-native piscivores increased, eventually leading, in part, to their extirpation. Although Pyramid Lake and Lake Tahoe differ in many characteristics, their fish communities were similar prior to human disturbance, and the LCT populations of the two lakes likely intermixed (Juday 1907). Currently, the Pyramid Lake LCT population bears a higher percent benthic signature than at any recorded point in Lake Tahoe. This trend is likely a result of the large dietary contribution of Tui Chub, which feed both on zooplankton and benthic invertebrates (Galat and Vucinich 1983; our unpublished data). Similarly, the LCT population in Cascade Lake near Lake Tahoe exhibited a lower TP than both the historical Lake Tahoe population and the current Pyramid Lake population, a trend attributed to competitive displacement by nonnative Brown Trout (Vander Zanden et al. 2003). The LCT's reliance on Tui Chub is further exemplified by the narrow scope of  $\delta^{13}\text{C}$  signatures from prey to predator throughout the food web and suggests a shared reliance on both benthic and pelagic production.

Our study provides clear evidence that LCT are apex predators, currently not likely to be food limited (see also Heredia 2014), and that competition for food with nonnative Sacramento Perch is minimal. However, there were some limitations to our study. For example, prey source contributions developed using the SIAR mixing model only included the major prey items previously found in the diets of LCT and Sacramento Perch. Nitrogen fractionation values ( $\delta^{15}\text{N}$ ) for some calanoid and copepod zooplankton were high and variable, likely due to high rates of nitrogen turnover or analytical error (Toda and Wada 1990; Yoshioka et al. 1994; Cabana and Rasmussen 1996), and were therefore left out of this analysis. In addition, using CPUE as a measure of species distribution within Pyramid Lake could also be somewhat misleading, as certain fish species and sizes are more susceptible than others to gill nets (Hamley 1975; Jonsson et al. 2013), and catch will vary with light intensity and depth. Furthermore, since our nets were always set on benthic substrate, they did not necessarily sample the pelagic regions of the lake. Lastly, while we were limited in making comparisons between the two strains of LCT stocked in Pyramid Lake, future work should focus on this aspect as the numbers of stocked and recaptured Pilot Peak LCT increase. Nonetheless, our multifaceted and comprehensive study provides a robust weight-of-evidence-type approach that allows us to eliminate potential limiting factors for LCT in Pyramid Lake and thus addresses important conservation challenges (Hilborn and Walters 1992; Marmorek and Peters 2002).

Although our results for the different groups of fish indicate similarities in diet and resource use, we found evidence that piscivores in the lake share very high TPs,

indicating successful foraging on high-trophic-level prey. The distribution and diet of LCT in Pyramid Lake are characterized by a clear reliance on Tui Chub as the main source of food during both stratified and nonstratified times of the year. Although the vertical distribution and overall catch of Tui Chub appear to vary by season, the Tui Chub still remains the primary diet item for LCT throughout the year, allowing this native piscivore to maintain its historical TP atop the food web. Our results highlight the food web relationships that are unique to Pyramid Lake and underscore the importance of a historical prey base for LCT persistence and viability. As such, managing for LCT performance and conservation inherently means managing Tui Chub. Our results have important implications for conservation and management of large-bodied, lentic trout in other systems where conservation strategies are similar and the target species face similar common threats.

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