Trophic Status, Energetic Demands, and Factors Affecting Lahontan Cutthroat Trout Distribution in Pyramid Lake, Nevada

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TROPHIC STATUS, ENERGETIC DEMANDS, AND FACTORS AFFECTING
LAHONTAN CUTTHROAT TROUT DISTRIBUTION IN
PYRAMID LAKE, NEVADA

by

Nicholas A. Heredia

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

2014
ABSTRACT

Trophic Status, Energetic Demands, and Factors Affecting 
Lahontan Cutthroat Trout Distribution in 
Pyramid Lake, Nevada

by

Nicholas A. Heredia, Master of Science 
Utah State University, 2014

Major Professor: Dr. Phaedra Budy 
Department: Watershed Sciences

Through a myriad of practices, anthropogenic land and water use has caused the localized extirpation or complete elimination of many native fishes throughout North America. Specifically, native salmonids have seen substantial declines in population sizes and geographic distributions due to a number of factors, including habitat loss or degradation, overharvest, or the introduction of non-native competitors and predators. Among those affected, the 14 subspecies of cutthroat trout found across western North America have been subject to two extinctions and five listings as Threatened as per the Endangered Species Act.

Lahontan cutthroat trout *Oncorhynchus clarkii henshawi* have experienced marked reductions throughout their native range in the western Great Basin, U.S. In Pyramid Lake, Nevada, where they were once locally extirpated due to overfishing, water loss, and degraded spawning habitat, Lahontan cutthroat trout have been successfully
stocked and managed, though they do not routinely reach their pre-extirpation sizes. With little research to determine the factors influencing Lahontan cutthroat trout in Pyramid Lake, I used a suite of modeling tools and empirical data to elucidate the influence of the current surrounding environment on Lahontan cutthroat trout in Pyramid Lake.

To identify important food web interactions that may affect the availability of food to Lahontan cutthroat trout, I used diet composition and stable isotope analyses of carbon and nitrogen to understand dietary trends. Large Lahontan cutthroat trout (>400 mm TL), along with non-native Sacramento perch *Ambloplites interruptus*, relied most heavily on fish prey, yet neither species showed signs of cannibalism or preying on the other species. Diet composition and stable isotope analyses also indicated that Lahontan cutthroat trout rely mostly on tui chub *Gila bicolor* and other fish for food. I also used results from bioenergetic and hydroacoustic analyses to compare the number of tui chub consumed by trout to the number of tui chub in the lake, during the time of this study. Results from these analyses suggest that trout consume well below the number of tui chub available in the lake, indicating that trout are not limited by the availability of tui chub. Lastly, I used a number of biotic and abiotic predictors to determine which factors influence the distribution, and subsequently abundance, of trout in Pyramid Lake and found that biotic factors were very weak predictors of trout distribution, further indicating that trout are not limited by food resources in Pyramid Lake.
PUBLIC ABSTRACT

Food Web Interactions and Evaluation of the Potentially Limiting Factors to a Valuable Sport and Subsistence Fishery

Nicholas A. Heredia

The progression of human development across the landscape has caused declines to both terrestrial and aquatic fauna. Many fishes, specifically native salmonids, have seen reductions in both population size and geographic distribution resulting from reduced habitat, overharvest, and the introduction of non-native predators and competitors. A native North American fish particularly hard hit by these types of actions, Lahontan cutthroat trout, are now limited to less than 10% of their historical habitat, and currently occupy only half of the lakes that they once occupied.

In Pyramid Lake, Nevada, where Lahontan cutthroat trout were once locally extinct, due to overfishing, water loss, and loss of spawning habitat, stocking and proper management have helped to maintain a healthy fishery. However, since their reintroduction, little research has been conducted to determine which, if any, factors limit the production of Lahontan cutthroat trout in Pyramid Lake, one of their last remaining strongholds. For my thesis, I used a number of analytical tools, accompanied with field data, to assess whether Lahontan cutthroat trout in Pyramid Lake are potentially limited by food availability.
To understand dietary trends of Lahontan cutthroat trout and other prey fish in the lake, I used diet composition from three different seasons throughout the year, as well as stable isotope data, which give insight to long-term dietary trends. These results suggest that trout, and other predatory fish, primarily rely on tui chub, an abundant native prey fish, for food. I combined these dietary data with temperature and growth rate data to estimate the number of tui chub consumed by trout on an annual basis. These results, coupled with abundance estimates from acoustic sampling, allowed me to compare the number of chub consumed by trout to the number of chub available within the lake. Consumption and abundance estimates indicated that trout consume less than one third of the standing biomass of tui chub on an annual basis. Results from these analyses suggest that trout consume well below the number of tui chub available in the lake, and indicate that trout are not limited by the availability of tui chub. In addition, I used data on physical and biological characteristics of the Pyramid Lake environment to understand which factors influence trout distribution and abundance. This approach confirmed the previously described results that suggest trout do not appear to be limited by food resources. These results will help aid in the management and conservation of this important sport and subsistence fishery, and add to the existing body of research on Lahontan cutthroat trout throughout their native range.
DEDICATION

I dedicate this thesis to my parents, Robin and Greg Graham, and John Heredia.
ACKNOWLEDGMENTS

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The findings and conclusions in this thesis do not necessarily reflect the views of Pyramid Lake Fisheries or U.S. Fish and Wildlife Service.

Nicholas A. Heredia
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CHAPTER 1

INTRODUCTION AND PROBLEM STATEMENT

While past aquatic ecosystem restoration efforts have generally focused on influences of abiotic factors, reconstructing self-sustaining native communities has become a growing trend in fisheries management (Kitchell et al. 2000; Vander Zanden et al. 2003; Al-Chokhachy et al. 2009). This approach incorporates an understanding of direct and indirect interactions between community members. Past food web studies demonstrate the importance of individual species which structure aquatic communities through highly connected linkages in food webs (Carpenter et al. 1985; Paine 1992; Power et al. 1996), which quantify the influences of one species on surrounding members of their respective food webs. The main purpose of my study was to determine food web interactions that may act to negatively influence Lahontan cutthroat trout (Oncorhynchus clarkii henshawi, LCT) growth and production in Pyramid Lake, Nevada and to identify factors influencing their distribution throughout the lake.

Lahontan cutthroat trout have experienced marked reductions in population size and distribution over the last century throughout much of their native range in the Great Basin (Williams et al. 1989; Dunham et al. 1997). Lahontan cutthroat trout currently occupy only 10.7% of their native lotic and 0.4% of their native lacustrine habitat (Coffin & Cowan 1995), and Pyramid Lake, Nevada, is one of their last remaining strongholds. Population reductions reflect anthropogenic habitat alterations in the forms of altered flow regimes, restricted habitat, and overfishing (Sigler et al. 1983). Additionally, interactions with nonnative species have altered LCT distributions and population densities via competition (Vander Zanden et al. 2003), predation (Vander Zanden et al.
2003; Al-Chokhachy et al. 2009), and hybridization with other salmonids (Peacock & Kirchoff 2004). An important native, top predator, and game fish in Pyramid Lake, LCT are listed as threatened under the Endangered Species Act (ESA). For my thesis research, I quantified predator-prey and competitive interactions that may limit LCT growth and production in Pyramid Lake.

Over the last 130 years, Pyramid Lake has undergone multiple alterations which may have reduced the size and condition of LCT. Overfishing, the introduction of Sacramento perch (*Ambloplites interruptus*), the building of Derby Dam on the Truckee River, which reduced water levels and spawning success, and the eventual extirpation of naturally-reproducing LCT in 1942 have all likely contributed to the current threatened status of this important native, predator. Many historic changes have altered the habitat in Pyramid Lake and influenced the food web such that the magnitude of interactions between community members, from basal resources to top-level predators, is poorly understood. Understanding these competitive and predator-prey relationships between community members will aid in managing for improved LCT growth and production.

Past studies on Pyramid Lake have focused primarily on water quality issues, some of which have documented effects on members of the fish community. These studies examined, or focused on, the role of nitrogen fixation, pH, and total dissolved solids (TDS) on primary production, LCT survival, and LCT acclimation to saline waters (Horne & Galat 1985; Wilkie et al. 1993; Dickerson & Vinyard 1999). Pyramid Lake is nitrogen limited (Galat et al. 1981; Horne & Galat 1985), likely as a result of little surrounding terrestrial vegetation combined with low precipitation. The nitrogen-fixing blue-green algae, *Nodularia spumigena*, can provide up to 81% of the lake’s annual
nitrogen input, although contributions of this magnitude are thought to be uncommon (Galat et al. 1981; Horne & Galat 1985). This process is particularly important for primary production of non-nitrogen fixing algae. Nitrogen released to the water column following *N. spumigena* die-offs subsequently becomes available for non-nitrogen fixing algae. Zooplankton are influenced by this N-fixing process, as they feed on the many phytoplankton which benefit from the *N. spumigena* die-offs. Tui chub (*Gila bicolor*), the primary forage item of LCT, and Sacramento perch, rely heavily on zooplankton for food (Galat & Vucinich 1983; Monda 1999; Chandra & Lawrence 2005). While knowledge of these food web interactions gives insight to some linkages in the food web in Pyramid Lake, less is known of the interactions of higher trophic level members.

While studies pertaining to the effects of abiotic factors on LCT are insightful, little is known about the contemporary predator-prey and competitive dynamics of the Pyramid Lake food web. Previous research has established that tui chub are an important diet item for LCT in Pyramid Lake (Monda 1999; Chandra & Lawrence 2005) as well as various surrounding lakes (Vander Zanden et al. 2003; Al-Chokhachy et al. 2009). Despite these findings, questions remain regarding population abundances and distributions of tui chub, Sacramento perch, and LCT, and whether or not these abundances or distributions limit LCT growth and abundance.

The purpose of this study was to determine if predator-prey and competitive interactions limit LCT growth or production. The broad goals of the study were to: 1) determine which prey is most important to LCT, 2) is prey supply potentially limiting to the population in Pyramid Lake, 3) are there any competitive interactions that may reduce the amount of prey available to LCT, and 4) to determine which factors most influence
the distribution of LCT. Results from this study are intended to inform managers and conservationists of key resources and environmental traits that are important for the continued success of LCT in Pyramid Lake.

References


CHAPTER 2

PREDATOR-PREY INTERACTIONS AND FEEDING ECOLOGY: IMPLICATIONS FOR THE TROPHIC STATUS AND RESOURCE RELIANCE OF LAHONTAN CUTTHROAT TROUT ONCORHYNCHUS CLARKII HENSHAWI IN PYRMID LAKE, NV

Abstract

Pyramid Lake, Nevada is one of the last remaining strongholds for lacustrine Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*; LCT); almost all other large lake populations have undergone population declines or extirpation as a result of invasive species interactions and habitat degradation. In Pyramid Lake, LCT have persisted despite anthropogenic alterations, but the population now depends entirely on stocking programs and efficient management. The purpose of this study was to identify important food-web interactions. The objectives were to 1) compare seasonal depth distributions, seasonal diet overlap, and trophic niche overlap between LCT and non-native Sacramento perch (*Archoplites interruptus*); and 2) to evaluate the seasonal depth distribution patterns of LCT and native tui chub (*Gila bicolor*), seasonal changes in LCT diet, and current LCT trophic position (TP). LCT remain apex predators, with both trophic position (large LCT TP = 4.30 ± 0.04 [mean±1.96SE]) and diet composition indicating high rates of piscivory (average annual rate of piscivory = 77.1% for large LCT; > 400mm TL). Small LCT (200 - 400mm TL) exhibited weak dietary overlap (Schoener’s Index = 0.55) and large LCT exhibited strong overlap (0.72) with Sacramento perch. Small and large LCT, and Sacramento perch, preyed most heavily on tui chub. Isotope data indicates strong overlap between large LCT and Sacramento perch niche space (large LCT 88.6%);
however, catch rates indicate that Sacramento perch are only present in small numbers throughout the lake. LCT demonstrate high rates of piscivory, which subsequently suggests that they are not negatively influenced by the presence of Sacramento perch and do not appear to be exceeding carrying-capacity.

**Introduction**

Anthropogenic alterations to aquatic ecosystems through habitat alteration, or by introduction of invasive species, can alter community structure (Lodge et al. 2006) through modified competitive (Douglas et al. 1994; Byers 2000) and predator-prey interactions (Ney 1990; Ruzycki et al. 2003). These habitat alterations, the introduction of, or loss of species, can alter life-history strategies, feeding success of remaining native species, and thus, alter food-web interactions and the flow of energy throughout a community. Additionally, altered habitat and community assemblages can cause trophic cascades (Paine 1980), alter food chain length (Post 2002; Walsworth et al. 2013), or regime shifts (Carpenter & Scheffer 2009). While many habitat and species composition alterations do result in negative effects on native fish communities, a limited number of studies have reported few to no negative effects (Moyle & Light 1996; Eby et al. 2006), and occasionally positive effects (Gozlan 2008). Elucidating food web interactions in light of habitat alteration and altered community composition, will aid in preventing extirpation, and in informing future water resource and fisheries management decisions.

Throughout western North America, cutthroat trout subspecies have experienced dramatic declines in both population size and geographic distribution, resulting from habitat alterations and non-native species invasions. Of the 14 subspecies of cutthroat trout, two are now extinct, and five are listed as threatened (Trotter 2008). Among those
listed as Threatened by ESA, the Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*; LCT hereafter) has been extirpated from more than 90% of its historical habitat (Coffin & Cowan 1995; Dunham et al. 1997), and of the 11 historical lake populations, only 5 remain. LCT are a federally listed Threatened subspecies (Office of the Federal Register 40[1975]:29864, Coffin & Cowan 1995), of cultural significance to the Pyramid Lake Paiute Tribe and an important game fish in Pyramid Lake, NV. LCT were historically an apex predator in nearby Lake Tahoe, however, following the introduction of multiple salmonids and other cool and cold water piscivores, they were extirpated (Vander Zanden et al. 2003). The same study also indicated that the LCT population in Cascade Lake persisted after the introduction of brown trout *Salmo trutta*, but exhibited a reduced trophic position when compared to LCT throughout their native range, prior to non-native species introductions. Additionally, the Walker Lake population of LCT demonstrated a significant reduction in population size following rapid water loss and significant increases in total dissolved solids, due to agricultural demands and continued evaporative water loss (Dickerson & Vinyard 1999). These cases highlight the need to preserve and effectively manage the few remaining lacustrine populations of LCT.

Heavy fishing pressure, potential interactions with non-native Sacramento perch, and water diversions, which subsequently reduced accessibility to spawning habitat, led to the extirpation of LCT from Pyramid Lake. Sacramento perch *Ambloplites interruptus*, a non-native piscivore, was introduced to Pyramid Lake in the late 19th century (Parker 1881). While Sacramento perch have long been established in Pyramid Lake, their population size has remained low, relative to LCT (Vigg 1980; Vigg 1981;
Monda 1999), and their laterally-compressed body shape in combination with catch data suggests that these fish are limited to littoral habitat near physical structure (Crain & Moyle 2011). Since their extirpation, no natural reproduction has been documented, and is unlikely in the future, given a number of barriers that block access to spawning habitat. Since 1942 LCT have been, and remain, entirely dependent upon stocking programs for their continued persistence, and this reliance on stocking has potentially removed density-dependent constraints on the population. Thus, the loss of natural reproduction may have decoupled the historical predator-prey relationship between LCT and native tui chub *Gila bicolor*, two species that have adapted together in Pyramid Lake as pluvial Lake Lahontan receded.

In this study, I focused on understanding seasonal foraging patterns and trophic position, with emphasis on the interaction between LCT and their most abundant native food item, tui chub, in Pyramid Lake, NV. In addition, I also aimed to evaluate the current relationship between LCT and Sacramento perch. The specific objectives of this study were to 1) compare seasonal depth distributions, seasonal diet overlap, and trophic niche overlap between LCT and Sacramento perch; and 2) to evaluate the seasonal depth distribution patterns between LCT and tui chub, seasonal changes in LCT diet, and current trophic position of LCT. In addressing these objectives, I was able to determine the influence of Sacramento perch on the LCT population and quantify LCT reliance on tui chub.
Methods

Study Area

Pyramid Lake is a cool monomictic lake with summer stratification generally occurring from July through November. The maximum depth is 105 m deep, it averages 53 m deep, and covers an area of approximately 488 km². During summer, the metalimnion typically forms between 9-22 m with a temperature range of 12-22°C. Hypolimnetic temperatures generally remain at or below 10°C throughout the year (Galat et al. 1981; Chandra & Lawrence 2005; this study).

The Pyramid Lake fish community is dominated by tui chub, which have historically been the primary forage of LCT. According to a past study, the five most abundant species make up more than 99.9% of the fish catch in Pyramid Lake (Vigg 1981). The two other prey fish for LCT are benthically-oriented suckers, the Tahoe Catostomus tahoensis and cui-ui Chasmistes cujus. The only potential competitor with LCT is the non-native Sacramento perch. While described as being well established in Pyramid Lake following their introduction sometime around 1880 (Crain & Moyle 2011), previous studies have suggested that Sacramento perch appear to have little impact on the LCT population (e.g., Monda 1999; Chandra & Lawrence 2005). In this chapter, I address the seasonal foraging habits of LCT, and identify key food-web relationships necessary for their continued success in Pyramid Lake.

Routine sampling

I sampled the Pyramid Lake food-web during three seasonally-different time periods throughout the year, from summer 2011 to spring 2013. As Pyramid Lake is monomictic, I focused on sample periods that would best represent the dynamic nature of
the temperature regime. I sampled during the last two weeks of late-May/early-June (spring), the first two weeks of August (summer), and late-November/December (winter). Throughout the study, the spring sampling was conducted once during 2012, whereas both summer and winter sampling was conducted twice, in 2011 and 2012. Spring sampling occurred while the lake was transitioning from an isothermal to stratified state, summer sampling occurred while the lake was stratified, and the winter sampling occurred while the lake was isothermal. I chose sampling locations that were relatively evenly distributed around the lake and that would likely represent a range of habitat types (Figure 2-1).

*Relative abundance of fish by depth and season*

During each sampling period, I conducted overnight gill net sets at 8 locations around the lake. I also set one Fyke net at each location in 5 – 10m of water. I set nets at dusk and pulled them the following morning after dawn to capture two crepuscular periods. To capture both littoral and pelagic habitats, I set 6 variable-mesh gill nets on the bottom of the lake, which increased in depth at 10m intervals, starting at 10m deep and ending at 60m deep. To attain representative size distributions of all fishes within Pyramid Lake, I used sinking horizontal gill nets with variable mesh sizes (24 m long × 1.8 m tall with eight monofilament panels of 38, 57, 25, 44, 19, 64, 32, and 51 mm knot-to-knot bar mesh). To quantify seasonal differences in depth distribution by small and large LCT, Sacramento perch, and tui chub, I calculated catch per unit effort (CPUE; fish per net per hour) for each net. Additionally, I divided tui chub into two size classes, small (≤200 mm TL), and large (>200 mm TL) based on gape limitation data.
Theoretically, small LCT would only be able to consume tui chub up to approximately 200 mm TL.

**Diet composition and overlap between LCT and Sacramento perch**

To determine seasonal and ontogenetic transitions in diet composition, I examined diets of LCT and Sacramento perch collected during routine sampling work in 2011 and 2012. For diet analysis (as well as all other analysis throughout), I apportioned LCT into two size categories, small (200 – 400 mm TL) and large (>400 mm TL) fish, based on diet composition, growth rates, and reproductive status. I removed fish stomachs and placed them in ethanol within 5 hours of sampling. In the lab, I classified prey items into 6 different categories: tui chub, suckers, fish (fish that could not be identified to species), zooplankton, invertebrates, and other (unidentifiable organic matter). I identified partially-digested fish prey using external body and bone morphology. Once all diet items were sorted, and lengths and weights were recorded, I calculated diet composition as proportion of the total wet mass (g) of each diet item for each fish. I then used diet proportion by wet weight to calculate seasonal averages for the two stage classes. I did not distinguish between stage classes for Sacramento perch, as these fish become highly piscivorous around 100 mm TL, and remain so for life (Crain & Moyle 2011).

Understanding the contributions of shared prey resources is integral to evaluate potential competitive interactions between species. In Pyramid Lake, Sacramento perch are the only aquatic piscivores that could potentially compete with LCT for food. I examined diet composition of LCT and Sacramento perch to assess potential competition for food. I used diet overlap to compare prey consumption between both stage classes of
LCT and Sacramento perch, and between the two stage classes of LCT, across the different seasons. I calculated diet overlap with Schoener’s Index (1970) as:

\[
\alpha = 1 - 0.5 \left( \sum_{i=1}^{n} |P_{x,i} - P_{y,i}| \right)
\]

where \(P_{x,i}\) is the proportion of food item \(i\) used by group \(x\), \(P_{y,i}\) is the proportion of food item \(i\) used by group \(y\) and \(n\) is the total number of diet items. 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. I used 0.60 as a cut-off representing significant diet overlap, where values above which were considered biologically significant (Wallace 1981).

Stable isotope analysis of food-web structure

I used carbon (\(\delta^{13}C\)) and nitrogen (\(\delta^{15}N\)) isotopes to determine a time-integrated representation of the Pyramid Lake food-web, and to assess species niche breadth. Species niche breadth gives a representation of where in the lake, pelagic vs. benthic, an individual consumes food and is based on \(\delta^{13}C\) signatures. Predator \(\delta^{13}C\) signatures will reflect signatures for carbon found in diet items. I used dorsal fin clips from fish, and whole benthic invertebrate and zooplankton samples, which I collected during the routine summer sampling periods to evaluate \(\delta^{13}C\) and \(\delta^{15}N\) signatures. Benthic invertebrates were collected using a standard Eckman grab (6 \(\times\) 6 \(\times\) 6 inches) at the Pelican Point sample site (Fig. 1). Benthic samples were collected at depths of 5, 10, and 15m. Zooplanktons were collected using a Wisconsin-style zooplankton tow at Station 96 (Fig. 1) from the top 50m of the lake. All benthic invertebrate and zooplankton samples used
in isotopic analyses were collected in August 2012 and at least 5 replicates were collected at each depth or site. I collected a minimum of 10 samples for each fish species or group (small LCT = 17, large LCT = 46, and Sacramento perch = 13) as this has been shown to be adequate for representing $\delta^{13}C$ and $\delta^{15}N$ signatures for fish tissues (Vinson & Budy 2011). Due to the high number of prey items evaluated, between 5 and 10 samples were processed per prey species for isotopic analysis, except Ephemeroptera, which only had 4 samples due to processing error. Other invertebrate prey taxa included were Amphipoda, Cladocera, Diptera, Hemiptera, Odonata, Trichoptera, and Moina spp. I also sampled benthic macrophytes and pelagic phytoplankton, for analysis of base-line $\delta^{13}C$ and $\delta^{15}N$ signatures. Macrophyte samples were collected using an Eckman grab at the same time and locations that benthic invertebrate samples were collected. During the same period, I collected five water samples near the middle of the lake and filtered them through ashed fiberglass filters. Once in the lab, I dried tissue samples for 48 hrs at 70°C, ground them into a fine powder using mortar and pestle, and placed them into pre-weighed tin capsules. Water filters were dried, but no further processing was done at USU.

Tissue and filter samples were processed at the Washington State University Stable Isotope Core laboratory for analysis of $\delta^{13}C$ and $\delta^{15}N$, and percent composition of both carbon and nitrogen. Isotopic signatures are reported in $\delta$-notation:

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

where $R_{\text{sample}}$ is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ found in the tissue or filter sample, and $R_{\text{standard}}$ is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ found in the standard sample. The standard for $\delta^{13}C$ is PeeDee belemnite and the standard for $\delta^{15}N$ is atmospheric nitrogen.
I used a baseline-correction equation for all δ^{15}N data, which scaled δ^{15}N values for all individuals to baseline values representative of primary production, as represented by δ^{13}C. The correction is calculated as:

\[ \delta^{15}N_{i,\text{correction}} = -0.148(\delta^{13}C_i) - 0.303 \]

where \( \delta^{15}N_{i,\text{correction}} \) is the lake-corrected baseline δ^{15}N value for individual \( i \), and \( \delta^{13}C_i \) is the δ^{13}C for individual \( i \). I then used the baseline-corrected data for all further food-web analysis using stable isotopes. This baseline correction accounts for differences in δ^{13}C in primary producers on a scale from pelagic to benthic regions of the lake.

**Trophic position, benthic reliance, and niche space overlap**

To calculate trophic position of the three piscivore groups (small LCT, large LCT, and Sacramento perch), I used the following equation:

\[ TP_i = \left( \frac{\delta^{15}N_i - \delta^{15}N_{\text{baseline}}}{3.4} \right) + 1 \]

where \( TP_i \) is the trophic position of species \( i \), \( N_i \) is the nitrogen signature of species \( i \), and \( N_{\text{baseline}} \) is the nitrogen signature for primary producers (Vander Zanden & Rasmussen 1999). I assumed that primary producers had a trophic position of 1 and a δ^{15}N trophic fractionation value of 3.4 ± 1.1‰ (Minagawa & Wada 1984). I 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. I used benthic macrophytes and pelagic phytoplankton as
the benthic and pelagic end-members used to calculate baseline nitrogen values. I used
Student’s t-test’s to compare trophic position. Additionally, I calculated percent benthic
resource use using $\delta^{13}C$ (Vander Zanden & Rasmussen 1999). As the $\delta^{13}C$ of pelagic
primary producers is isotopically enriched relative to benthic primary producers, I used
mean benthic macrophyte and mean pelagic phytoplankton values to create a two end-
member mixing model of benthic versus pelagic reliance. Percent benthic reliance was
calculated as:

\[
\text{Percent Benthic} = \left( \delta^{13}C_i - \delta^{13}C_{pelagic} \right) / \left( \delta^{13}C_{benthic} - \delta^{13}C_{pelagic} \right) \times 100
\]

where $\delta^{13}C_i$ is the carbon signature of individual $i$, and $\delta^{13}C_{pelagic}$ and $\delta^{13}C_{benthic}$ are the
pelagic and benthic end-member values.

To infer characteristics of community structure and niche overlap of community
members, I used SIBER (Stable Isotope Bayesian Ellipses in R), which uses Bayesian
inference techniques to describe niche and community metrics (Jackson et al. 2011). For
all stable isotope analyses described hereafter, I used the R statistical computing package
(R Development Core Team 2011). The SIBER model uses bivariate $\delta^{13}C$ and $\delta^{15}N$ data
to represent isotopic niche space for a species or group. I used the Shapiro-Wilk test,
with the mshapiro.test() function in R, to test for normality. All species or groups
analyzed met the assumption that the isotope data used were sufficiently described by a
multivariate normal distribution (all species: $W \geq 0.91$, $p \geq 0.14$; Royston 1982). The
SIBER model produces ellipses around the centroid that include $\pm 1$ s.d. For a metric of
niche space overlap, I used the intersection of ellipse areas to calculate percent species
(or group) overlap.
Prey-to-consumer mixing model

To further understand the relative contributions of the different food sources to upper-level consumers, I used the Bayesian stable-isotope mixing model, Stable Isotope Analysis in R (SIAR; Parnell et al. 2008). 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 using trophic enrichment factors (Gannes et al. 1998). I used trophic enrichment factors of 1.3‰ ± 1.7 (mean ± 1sd) and 3.4‰ ± 1.1 for δ^{13}C and δ^{15}N respectively (Minagawa & Wada 1984; Vander Zanden & Rasmussen 1999; McCutchan et al. 2003) for all prey species adjustments. 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 using stable isotopes (Phillips & Koch 2002). The SIAR model uses the aforementioned inputs to estimate ±95% Bayesian credibility intervals which represent percent diet contribution. I collected prey fish tissue samples as well as all the major benthic invertebrate Orders found during gut content analysis and included these carbon and nitrogen signatures in the SIAR analysis. However, of the various zooplankton taxa collected, only *Moina spp.* were included in this analysis. This was due to the other zooplankton taxa exhibiting extremely high and variable δ^{15}N values, due to their small sizes and short life spans (Toda & Wada 1990; Yoshioka et al. 1994; Cabana & Rasmussen 1996).
Results

Relative abundance of fish by depth and season

Catch data indicated seasonal shifts in species distribution of tui chub and LCT. During spring, a combination of large (60%) and small (3.3%) tui chub made up the majority of catch followed by suckers (a combination of Tahoe and cui-ui). A combination of small LCT (4.5%) and large LCT (12.0%) made up the third largest portion of catch and Sacramento perch (2.2%) accounted for the smallest portion of catch. Large tui chub catch was highest at 10m (CPUE = 2.77 ± 1.44) [mean ± 1.96*SE]) and decreased with depth (Fig. 2-2). Small tui chub catch was low across all depths (CPUE ≤ 0.06 ± 0.06). Large LCT catch was highest from 10m to 30m and decreased with depth (Fig. 2-2). Small LCT were only caught at 30m or shallower, and CPUE decreased with depth (Fig. 2-2). Sacramento perch catch was limited to 10m and 20m (Fig. 2-2).

During summer, tui chub still made up the largest proportion of total catch (small tui chub = 19.9% and large tui chub = 42.9%), LCT mad up the second largest proportion (smallLCT = 3.7% and large LCT = 18.6%), suckers (Tahoe and cui-ui) made up the third largest proportion (13.3%), and Sacramento perch made up the smallest proportion (1.6%). Summer sampling took place during thermal stratification, and during this period, 86.8% of small and 79.1% of large LCT catch occurred at or below 20 m, while 81% of total tui chub catch and all the Sacramento perch catch occurred at 10 m deep. For both large (CPUE = 2.55 ± 0.68; Fig. 2-2) and small tui chub (CPUE = 1.11 ± 0.48) catch rates were highest at 10m and decreased with depth (Fig. 2-2). At 10m deep, large LCT (CPUE = 0.38 ± 0.29) had relatively high catch rates, while small LCT (CPUE =
0.05 ± 0.04) exhibited relatively low catch rates and were also variable (Fig. 2-2). At
20m deep, both large LCT (CPUE = 0.50 ± 0.16) and small LCT (CPUE = 0.15 ± 0.10)
catch rates peaked, and decreased with depth (Fig 2-2). I only caught Sacramento perch
in 10m nets (CPUE = 0.12 ± 0.09), during summer (Fig. 2-2).

Winter catch rates were less than half of what was caught during spring or
summer, and much of the reduction in catch was associated with tui chub (Fig. 2-2).
Additionally, tui chub percent catch was much lower, for both small (2.3%) and large
(29.6%) individuals, during winter. Large (35.3%) and small LCT (6.3%) made up fairly
large percentages of the total catch but the catch rates were similar to those found in
spring and summer. Suckers made up 22.9% of total catch, and Sacramento perch again
made up the smallest proportion at 3.6%. Relative to spring and summer, winter catch
rates of both small and large tui chub were much lower, and were generally higher from
30m to 60m, than 10m to 30m. Large tui chub catch rates were highest from 30m to 60m
(CPUE = 0.25 ± 0.15 to 0.15 ± 0.05; Fig. 2-2) and considerably lower between 10m and
30m (CPUE = 0.07 ± 0.06 to 0.14 ± 0.09; Fig 2-2). Small tui chub catch was low at all
depths (Fig. 2-2). Large LCT catch generally decreased with depth while small LCT
catch was zero at 60m and Low across all other depths (Fig. 2-2). Sacramento perch
were only caught at 20m and 30m during winter sampling.

*Diet composition and overlap between LCT and Sacramento perch*

Diets of both small and large LCT indicated that tui chub are a primary food
source. However, small LCT diets were dominated by invertebrates and zooplankton
during spring sample periods, but these small LCT became increasingly piscivorous
throughout the year (Fig. 2-3A). During spring, a combination of non-fish prey
(zooplankton and invertebrates) made up the majority of small LCT diet composition by wet weight. The proportion of fish in the diets of small LCT increased throughout the year. During winter, more than 80% of small LCT diet consisted of a combination of tui chub (58%) and unidentifiable fish prey (25%; Fig. 2-3A). Large LCT diets were more consistent across seasons than were the diets of small LCT (Fig. 2-3B). Diet composition of large LCT was made up of a minimum of 70% fish, mostly tui chub, for all three seasons (Fig. 2-3B). Percent diet composition made up of fish prey, peaked in summer for large LCT, and was lowest during spring, but the difference was only 12%.

Sacramento perch were highly piscivorous during spring and summer, and shifted to consuming more benthic invertebrates during winter (Fig. 2-3C).

Dietary overlap between large LCT and non-native Sacramento perch was significant across all seasons and highest during summer (Table 2-1). Overlap between small LCT and Sacramento perch was also significant during summer, but biologically insignificant during spring and winter (Table 2-1). Intraspecific dietary overlap between small and large LCT was insignificant during spring (Table 2-1), when small LCT were not yet highly piscivorous, but was significant during summer and winter, as small LCT transitioned to higher rates of piscivory.

Trophic position, benthic reliance, and niche space overlap

The trophic positions of small LCT, large LCT, and Sacramento perch were indicative of high rates of piscivory. Large LCT (TP = 4.30 ± 0.04 [mean ± 1.96·SE]) and Sacramento perch (TP = 4.38 ± 0.11) had similar trophic positions (t-test $P = 0.19$, $t$-value = 2.13) and similar carbon signatures ($P = 0.44$, $t$-value = 2.1; Fig. 2-4) as represented by percent benthic reliance. Small LCT (TP = 4.13 ± 0.17) had a marginally
lower trophic position than large LCT ($P = 0.086$, $t$-value = 2.10) and a significantly lower trophic position than Sacramento perch ($P = 0.026$, $t$-value = 2.06; Fig. 2-4). Carbon signatures were not significantly different between groups (all $t$-tests $P > 0.16$). Tui chub (TP = 3.40 ± 0.17) and suckers (Tahoe; TP = 3.01 ± 0.22) had significantly different trophic positions ($P = 0.016$, $t$-value = 2.11; Fig. 2-4) but similar carbon signatures ($P = 0.48$, $t$-test = 2.07). Benthic reliance values for small LCT (BR = 41.7% ± 3.7 [mean ± 1.96*SE]), 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 $P = 0.65$, $F$-value = 2.47; Fig. 2-4).

Percent dietary niche space overlap was high between piscivore groups, specifically for large LCT. Large LCT niche space was 89% overlapped by Sacramento perch and 100% of large LCT niche space was overlapped by both Sacramento perch and small LCT (Fig. 2-5). In comparison, only 32% of small LCT space was overlapped by Sacramento perch (36% by a combination of Sacramento perch and large LCT). A combination of large LCT (50%) and small LCT (50%) overlapped 62% of Sacramento perch niche space (Fig. 2-5). Tui chub niche space overlapped 48% of sucker niche space, and sucker niche space overlapped 28% of tui chub niche space (Fig. 2-5).

**Prey-to-predator contribution mixing model**

Similar to the diet data, the SIAR mixing model suggests that all three groups (small LCT, large LCT, and Sacramento perch) are highly piscivorous and that tui chub are the most important contributors to small and large LCT (Fig. 2-6). Large LCT consumed mostly tui chub (95% credibility interval: 45-73%; Figure 2-6) and a smaller amount of suckers (12-42%; Fig. 2-6). Six of the remaining 7 diet items included in the
analysis returned lower bound 95% credibility intervals of 0 (0-2.5% Amphipoda, 0-1.8% Diptera, 0-1.4% Ephemeroptera, 0-1.4% Hemiptera, 0-2.6% Odonata, and 0-4.5% Tricoptera), suggesting that invertebrate prey contribute relatively little to the energetics of large LCT. Pelagic zooplankton made up a small, but significant contribution to large LCT diets (4.4-13% Cladocera; Fig. 2-6).

Small LCT exhibited similar trends to large LCT, with a slightly lower emphasis on fish prey and a slightly higher emphasis on invertebrate prey and consumed mostly tui chub and suckers (95% credibility intervals: 16-66% and 1.2-45%, respectively; Fig. 2-6). Consistent with large LCT, 6 of the 7 remaining taxa included in the analysis produced credibility intervals which included 0 (0-13% Amphipoda, 0-10% Diptera, 0-7.4% Ephemeroptera, 0-7.8% Hemiptera, 0-14% Odonata, and 0-20% Tricoptera; Fig. 2-6). However, all of these taxa consistently resulted in upper bound credibility intervals larger than those produced for the same prey items of large LCT. Pelagic prey made up a relatively small portion of prey consumed by small LCT (0.8-17% Cladocera; Fig. 2-6).

The SIAR mixing model for Sacramento perch demonstrated diet contributions similar to both large and small LCT. Sacramento perch fed mostly on tui chub and suckers (95% credibility intervals: 13-69% and 1.5-49%, respectively; Fig. 2-6) and all of the remaining diet items exhibited 95% credibility intervals that included zero. These modeled diet proportions indicate that Sacramento perch, similar to LCT, consume primarily fish.

Discussion

Despite the current status of LCT throughout their native range (Coffin & Cowan 1995) and the established population of Sacramento perch in Pyramid Lake (Crain &
Moyle 2011), LCT remain an apex predator. In this study, I demonstrate how the Pyramid Lake fish community supports the predator-prey interaction most valuable to LCT. While LCT in Pyramid Lake now depend entirely on stocking programs, potentially de-coupling them from their historical predator-prey relationship with tui chub, both diet and isotope analyses indicate that LCT rely more heavily on tui chub for food than any other prey type. This dependence on tui chub persists despite potential for competition with Sacramento perch, and seasonal shifts in species depth distributions. Additionally, as indicated by isotope analysis, LCT remain an upper trophic-level fish predator within this unique desert lake. The energetically-rich and historically-abundant tui chub was the most abundant species caught and was the most commonly found diet item in LCT, resulting in a high trophic position for LCT. These trends, in combination with bioenergetic simulations (Ch. 3), suggest that LCT still strongly rely on tui chub as a primary food source throughout the year, and are not likely limited by food availability.

Seasonal depth distributions 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 30m, where temperatures ranged from 8 - 15°C. In Pyramid Lake, spring marks the transition from isothermal to stratified temperatures in the lake (Galat et al. 1981; Chandra & Lawrence 2005), and when surface temperatures approach those more suitable for LCT (Dickerson & 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 reflect suitable temperature optimums for the various species.
August sampling took place when the lake was stratified and trends in species distribution corroborated temperature preferenda previously described for each species. Tui chub catch rates decreased with depth, and 79.1% of the catch was in the epilimnion where temperatures are more suitable for both metabolic processes (Castleberry & Cech 1986; McClanahan et al. 1986) and spawning (Kucera 1978), which generally occurs in late July. Conversely, both small and large LCT were more commonly caught below the epilimnion, spatially separating predator from prey. All Sacramento perch were caught in the warmer epilimnion, closer to their preferred temperature range. Additionally, as my nets were set to rest on the bottom of the lake, shallow nets were always in littoral regions, where tui chub spawning occurs during midsummer (Kucera 1978).

Winter sampling efforts marked a period when the lake was transitioning to an isothermal state (Galat et al. 1981; Chandra & Lawrence 2005). During which point, total tui chub catch was reduced and consistent across depths. Additionally, cooling water temperatures reduce metabolism and maximum swimming speeds of tui chub (McClanahan et al. 1986), likely contributing to the reduction of catch rates, when compared to spring and summer. Differences in species distribution could have significant impacts on dietary make up, specifically during the stratified season; however, laboratory studies of LCT demonstrate that they can maintain reduced, yet positive growth rates while subject to temperature fluctuations similar to those in the epilimnion of Pyramid Lake (Dickerson & Vinyard 1999). These shifts in distribution likely have important implications for foraging behavior and success.

The large dietary overlap between native LCT and non-native Sacramento perch, most notably during summer, indicates potential for competitive interactions between the
two species. However, the high amount of overlap, indicative of little to no resource partitioning, suggests that food resources are likely not limiting (Grossman 1986). Moreover, isotopic niche space data reflect little to no trophic separation among piscivores, with the strongest overlap occurring between large LCT and Sacramento perch. Nevertheless, both LCT and Sacramento perch in Pyramid Lake obtain the largest sizes observed throughout their respective geographic ranges (Trotter 2008; Crain & Moyle 2011). Conversely, in other systems where upper trophic level piscivores are introduced, competitive interactions commonly result in altered foraging habits of native counterparts (Vander Zanden et al. 1999; Vander Zanden et al. 2003), a phenomenon that does not appear to be true for LCT in Pyramid Lake.

The comparatively small amount of dietary overlap and trophic niche space between small LCT and Sacramento perch might suggest resource partitioning due to a negative influence of Sacramento perch on LCT; however, previous studies of lacustrine cutthroat trout populations (Ruzycki et al. 2001; Nowak et al. 2004) suggest that LCT undergo an ontogenetic shift within this size range, likely explaining the low proportion of fish in the diets of small LCT during spring. Prior to the many anthropogenic alterations to the Lake Tahoe fish community, LCT up to 406 mm TL were reported to have diets consisting only of benthic invertebrates and zooplankton (Juday 1907). At the time of that study, Lake Tahoe contained a relatively similar fish community to that of Pyramid Lake’s current fish community. The LCT populations of these two lakes may have regularly mixed, as LCT from Pyramid Lake reportedly migrated up to and throughout the tributaries of Lake Tahoe, prior to the construction of water diversions on the Truckee River (Sigler et al. 1983). During winter, small-LCT and Sacramento perch
exhibited weak dietary overlap, potentially indicating resource partitioning or competitive exclusion. However, this overlap is likely due to the reduction in percent fish consumption by Sacramento perch, while small LCT continued to feed on the more energetically rich fish prey. This difference in diet is likely a result of Sacramento perch and tui chub not occupying common habitat during this period. This trend reflects the propensity of Sacramento perch to occupy benthic habitat high in structure (Crain & Moyle 2011), while total tui chub catch was less than half of that produced during spring or summer, indicating a transition away from benthic habitat, high in structure. Additionally, while both LCT and Sacramento perch are highly piscivorous in Pyramid Lake, I found no indication of predation on one piscivore by the other. Lastly, only one trout was found in an LCT diet and no perch were found in perch diets, indicating little to no cannibalism; yet another indication that food resources are not limiting (Hecht & Pienaar 2007).

This continued persistence of highly piscivorous feeding behavior by LCT is indicative of high encounter rates of large prey, as predicted by optimal foraging theory (Werner & Hall 1974; Maszczyk & Gliwicz 2014). While few empirical comparisons between current and historical fish communities of Pyramid Lake exist, the trophic position of LCT in Pyramid Lake is currently higher than any LCT trophic position observed in Lake Tahoe, even when the native fish community was still intact (Vander Zanden et al. 2003). Over the last century LCT have exhibited lower trophic position, leading up to their eventual extirpation, as the number of invasive piscivores entered the lake (Vander Zanden et al. 2003). While Pyramid Lake and Lake Tahoe differ in many lake characteristics, prior to human disturbance, the LCT populations of these two lakes
likely intermixed (Juday 1907). Prior to their extirpation, LCT occupied the highest trophic position observed in Lake Tahoe (Vander Zanden et al. 2003). However, in comparison, the current LCT population in Pyramid Lake occupies a higher trophic position than any observed in Lake Tahoe, and the current Pyramid Lake LCT population bears a carbon signature indicative of more benthic resource reliance than any point in Lake Tahoe. Additionally, the LCT population in Cascade Lake near Lake Tahoe, CA exhibited a lower trophic position than both historical Lake Tahoe and current Pyramid Lake populations, a trend attributed to competitive displacement by non-native brown trout (Vander Zanden et al. 2003).

My study provides evidence that LCT are not likely food limited and that competition for food with non-native Sacramento perch is minimal. However, there were still limitations to the study. For example, prey source contributions, developed using the SIAR mixing model, only include the major prey items previously found in the diets of LCT and Sacramento perch. $\delta^{15}$N values for some Calanoida and Copepoda zooplankton were extremely high and variable, likely due to high rates of nitrogen turnover (Toda & Wada 1990; Yoshioka et al. 1994; Cabana & Rasmussen 1996), and were therefore left out of this analysis. Additionally, past research has indicated that seasonal variation in $\delta^{15}$N values for *Daphnia* can lead to inaccurate depictions of trophic position (Matthews & Mazumder 2005) and that averaging values over time can reduce this discrepancy, which was not able to be done during my study. Using CPUE as a measure of species distribution can 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 will vary with light intensity, which in turn varies with depth. Additionally, as my nets were always set
on benthic substrate, they do not sample the pelagic regions of the lake. Given these limitations, the combination of robust analyses presented herein and bioenergetics modeling described elsewhere (Ch. 3), all of which converge on a similar trend, indicate that LCT in Pyramid Lake are not currently limited by food resources.

Although my results for the different groups of fishes indicate similarities in diet and resource use, I found evidence that piscivores in the lake share very high trophic positions, indicating successful foraging on high trophic-level prey. The distribution and diet of LCT in Pyramid Lake is characterized by a clear reliance on tui chub as the main source of food during both stratified and non-stratified times of the year. While the vertical distribution and temperature preferences of LCT and tui chub appear to vary by season, tui chub still remain the primary diet item of LCT throughout the year, allowing this native piscivore to maintain a trophic position atop the food-web. These trends underscore the complex behaviors exhibited by fish that have adapted to the unique environment of Pyramid Lake, and how foraging on prey is a key component of the continued success of LCT.

References


Table 2-1. Seasonal estimates of Schoener’s Index (\(\alpha\)) of diet overlap. Symbols Small, Large, and SAP refer to Lahontan cutthroat trout \(\leq 400\) mm TL, Lahontan cutthroat trout \(> 400\) mm TL, and Sacramento perch \(> 100\) mm TL, respectively. Values \(\geq 0.6\) are marked bold.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Spring</th>
<th>Summer</th>
<th>Winter</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small LCT x SAP</td>
<td>0.41</td>
<td>0.72</td>
<td>0.53</td>
<td>0.55</td>
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<tr>
<td>Large LCT x SAP</td>
<td>0.73</td>
<td>0.79</td>
<td>0.63</td>
<td>0.72</td>
</tr>
<tr>
<td>Small LCT x Large LCT</td>
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<td>0.76</td>
<td>0.69</td>
<td>0.64</td>
</tr>
<tr>
<td>Mean</td>
<td>0.54</td>
<td>0.75</td>
<td>0.62</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 2-1. Map depicting Pyramid Lake, Nevada, U.S.A. The labels around the perimeter of the lake indicate routine sample sites for, gill, and trap netting, and the dotted lines indicate the transects that were used.
Figure 2-2. Catch-per-unit-effort (fish/net/hour) by season for small LCT, large LCT Sacramento perch, and tui cub. Data are from gill net catches in Pyramid Lake, NV, from June 2011 through December 2012. Note: tui chub x-axis is scaled differently than the 3 other groups and error bars represent 2 standard errors.
Figure 2-3. Seasonal diet composition as proportion by wet weight of small LCT (panel A; 200-400 mm TL), large LCT (panel B; TL > 400 mm), and Sacramento perch (panel C), in Pyramid Lake, NV. “Suckers” represent a mix of Tahoe and cui-ui suckers, “Fish” represent fish that were too digested to be identified to species, “Invertebrates” represents both terrestrial and aquatic macroinvertebrates, and “Other” represents a mixture of unidentifiable organic matter.
Figure 2-4. Trophic position and percent benthic reliance (mean ± 1.96SE) for fishes in Pyramid Lake, NV. Values were calculated as described in Vander Zanden et al. 1999.
Figure 2-5. Trophic niche spaces occupied by fish species of Pyramid Lake, NV. Points represent empirical $\delta^{13}C$ and $\delta^{15}N$ values. Ellipses encompass ±1 S.D. around the centroid as produced through bivariate Bayesian inference using the SIBER package in R. Large LCT (>400 mm TL) are shown in black, small LCT (200 – 400 mm TL) are shown in red, Sacramento perch (SAP) are represented by green, Tahoe suckers are represented by blue, and tui chub are in cian.
Figure 2-6. Results of the SIAR mixing model (95, 75 and 50% credibility intervals) showing the estimated prey contributions to small LCT (panel A; 200-400 mm TL), large LCT (panel B; TL > 400 mm), and Sacramento perch (panel C) in Pyramid Lake, NV. Results were calculated from δ¹³C and δ¹⁵N isotope signatures and elemental concentrations of consumer and prey sources alike. Amph = Amphipoda, Moin = Daphnia moina, Dip = Diptera, Ephe = Ephemeroptera, Hemi = Hemiptera, Odo = Odonata, Tri = Trichoptera, Chub = Tui chub, and Sucker = Tahoe and cui-ui suckers.
CHAPTER 3

QUANTIFYING ENERGETIC DEMANDS, AND IDENTIFYING FACTORS POTENTIALLY INFLUENCING LAHONTAN CUTTHROAT TROUT

ONCORHYNCHUS CLARKII HENSHAWI ABUNDANCE AND DISTRIBUTION IN PYRAMID LAKE, NV

Abstract

Lahontan cutthroat trout (LCT) *Oncorhynchus clarkii henshawi* have seen marked reductions in population size and distribution throughout their native range. Effective management and conservation of this important sport fish relies on understanding the relationships between LCT and the biotic and abiotic influences in their remaining habitats. I used a set of thermal history scenarios with bioenergetics modeling to estimate the effect of LCT consumption on the tui chub *Gila bicolor* population, the most important prey source for LCT, and compared these results to hydroacoustic estimates of predator and prey abundances. Additionally, I used random forest regression to determine the influence of biotic and abiotic factors on the distribution of LCT in Pyramid Lake, NV. Bioenergetic simulations indicate that LCT consume somewhere between 24% and 32% of the biomass of tui chub annually. Large LCT (>400 mm TL) distribution was best explained by water transparency, sample location, and depth. For large LCT water transparency had a positive effect, while depth had a negative effect on catch rates. The model for small LCT (200 – 400 mm TL) only explained a marginal amount of the variation in catch. Temperature exhibited a positive effect, while depth exhibited a negative effect on small LCT catch. Results from this study suggest abiotic and not biotic factors generally have more effect on the distribution of LCT.

1Coauthored by Nicholas Heredia, Phaedra Budy, and Gary Thiede.
throughout the lake. Additionally, bioenergetics simulations suggest that variation in thermal history has little influence on the effect of LCT predation on the tui chub population. Collectively, these results suggest that LCT are not limited by food in Pyramid Lake.
Introduction

Throughout western North America cutthroat trout *Oncorhynchus clarkii* have experienced dramatic declines in both population size and geographic distribution, resulting from habitat alterations and non-native species invasions. Of the 14 documented subspecies of cutthroat trout, two are now extinct, and five are listed as threatened (Trotter 2008). Among those listed as threatened, Lahontan cutthroat trout (LCT) *O. clarkii henshawi* have experienced some of the most marked reductions in size and distribution over the last century throughout much of their native range in the Western Great Basin (Williams et al. 1989). The Lahontan cutthroat trout is a federally listed threatened subspecies (Office of the Federal Register 40[1975]:29864, Coffin and Cowan 1995), of cultural significance to the Pyramid Lake Paiute Tribe, and an important game fish throughout its range. Population reductions reflect anthropogenic habitat alterations in the forms of altered flow regimes, restricted habitat, and overfishing (Sigler 1983). Additionally, interactions with nonnative species have altered LCT distributions and population densities via competition (Vander Zanden et al. 2003), predation (Al-Chokhachy et al. 2009; Vander Zanden et al. 2003), and hybridization with other salmonids (Peacock and Kirchoff 2007). Given the imperiled status of these endemic fish, understanding threats to remaining populations is vital for effective management and conservation.

LCT currently occupy only 0.4% of their native lacustrine habitat (Coffin and Cowan 1995) and are found in only five of the eleven historically occupied lakes. An important game fish and apex predator in lacustrine habitats, LCT are listed as threatened under the Endangered Species Act (ESA), indicating a need for understanding potential
limitations to the few remaining populations. However, understanding potential threats and determining limitations to fish populations in lake studies is often confounded by within-lake spatiotemporal variation (e.g., Hinch and Collins 1993), latent responses to change (e.g., Werner et al. 1981), lack of replication (e.g., Carpenter 1989), and lack of understanding of historical trends. Nonetheless, strong ecological constructs provide a template for developing testable hypotheses about limiting factors, and relying on ecological theory, can point to possible limitations. When at carrying capacity, species are often thought to be constrained by the amount or extent of available resources. Furthermore, theories that underline density-dependent habitat preference, such as the Ideal Free Distribution (Fretwell and Lucas 1970; Power 1985), and subsequent applications of the theory that followed (e.g., Kennedy and Gray 1993; Shepherd and Litvak 2004; Hedger et al. 2005), suggest that when prey resources are limiting, mobile foraging predators will distribute themselves to optimize use of habitat or resources. However, in anthropogenically-altered ecosystems, manipulated food-webs often alter the nature of interactions between species, and can alter otherwise dependent relationships (e.g., Winder and Schindler 2004; Rodewald et al. 2011). These potentially-altered species interactions may still act in a similar manner to unaltered interactions, yet, if resource or prey-demand is lessened from otherwise natural states, it would follow that the spatial distribution of prey and potential competitors would have little influence on the distribution of a predator of interest.

In Pyramid Lake, NV, the LCT population has been exposed to numerous anthropogenic threats, yet has not shared the same fate as less fortunate lacustrine populations in the Western Great Basin. Lakes Tahoe, Cascade, and Walker have been
influenced by anthropogenic alterations to their respective watersheds, and these changes have had negative effects on their LCT populations. LCT were historically a native apex predator in Lake Tahoe, however, following the introduction of multiple salmonids and other cool and cold water piscivores, LCT were extirpated (Vander Zanden et al. 2003). Similarly, the LCT population in Cascade Lake persisted after the introduction of brown trout *Salmo trutta*, but exhibited a reduced trophic position when compared to LCT populations throughout their native range and prior to non-native species introductions. Additionally, in nearby Walker Lake, a terminal desert lake similar in character to Pyramid Lake, LCT experienced dramatic reduction in population size following rapid water loss and significant increases in total dissolved solids. A change attributed to agricultural demands for water and continued evaporative water loss (Dickerson and Vinyard 1999). Given their imperiled status range-wide and because of the once extirpation of LCT from Pyramid Lake, changes in lake level, and the introduction of a non-native piscivore, the current status and potential limitations to this important population of LCT is of considerable conservation and management interest (Pyramid Lake Fishery Conservation Plan 2004).

Determining the relative strength of abiotic and biotic factors in regulating LCT abundance should aid managers in understanding the mechanistic causes that affect fish abundance and distribution. The overall goal of this study was to understand whether this threatened population of LCT in Pyramid Lake was food limited. Specifically, are LCT limited by their primary food source, tui chub. In light of historic changes to Pyramid Lake, the food-web has likely been altered such that the magnitude of interactions between community members from basal resources to top-level predators is relatively
unknown. Understanding these competitive and predator-prey relationships between community members will aid in managing for improved LCT growth and production. The specific objectives of this study were: 1) to determine if the relative abundance of LCT was best explained by habitat or resource availability or whether fish were constrained by their physiochemical environment; and 2) to determine if LCT were food limited by tui chub biomass and production.

Study Area

Pyramid Lake is a cool monomictic lake with summer stratification generally occurring from July through November. The metalimnion typically forms between 16 and 22 m deep at a temperature of ~16°C. Maximum surface temperatures range from 21 to 24°C, while hypolimnetic temperatures generally remain at or below 10°C throughout the year (Galat et al. 1981; Chandra and Lawrence 2005). Pyramid Lake has maximum depth of 105 m, averages 53 m deep, and covers an area of approximately 488 km².

The Pyramid Lake fish community is dominated by tui chub *Gila bicolor*, which has historically been the primary forage of LCT. The five most abundant species make up more than 99.9% of the fish catch in Pyramid Lake (Vigg 1981). The two other prey fish for LCT are both benthically-oriented suckers, the Tahoe *Catostomus tahoensis* and cui-ui *Chasmistes cujus*. The only potential competitor with LCT is the non-native Sacramento perch *Archoplites interruptus*. While described as being well established in Pyramid Lake following their introduction sometime around 1880 (Crain and Moyle 2011), previous studies have suggested that Sacramento perch appear to have little impact on the native fish community (e.g., Monda 1999; Chandra and Lawrence 2005; See Chapter 2).
Over the last 130 years, Pyramid Lake has undergone multiple alterations which may have reduced the size and condition of LCT. Overfishing, the construction of the Derby Dam on the Truckee River, which reduced water levels and spawning success, and the eventual extirpation of naturally-reproducing LCT in 1942, have all potentially contributed to the current threatened status of this native, game fish. In 1950, the Nevada Fish and Game Department began stocking LCT back into Pyramid Lake, and the program has now grown and is maintained jointly by Pyramid Lake Fisheries (PLF) and the Lahontan National Fish Hatchery (Trelease 1969). Although stocking rates and fish length at the time of stocking have changed throughout the years, approximately 350,000-850,000 LCT, about 120 mm TL have been stocked annually for the last 10 years (PLF stocking records).

Methods

Routine sampling

I sampled the Pyramid Lake food-web during three time periods throughout the year from summer 2011 to spring 2013. As Pyramid Lake is a monomictic system, I focused on sample periods that would best represent the dynamic nature of the temperature regime. I sampled during the last two weeks of late-May/early-June (spring), the first two weeks of August (summer), and late-November/December (winter). Spring sampling was conducted only once during 2012, whereas both summer and winter sampling was conducted twice, in 2011 and 2012. Spring sampling occurred while the lake was transitioning from an isothermal to stratified state, summer sampling occurred while the lake was stratified, and the winter sampling occurred while the lake was
isothermal. I chose sampling locations that were evenly distributed around the lake and likely to represent a range of habitat types (Figure 3-1).

During each sampling period, I conducted overnight gill net sets at 8 locations around the lake. I set nets at dusk and pulled them the following morning after dawn to capture two crepuscular periods. To measure fish activity in both littoral and profundal habitats, I set 6 variable-mesh gill nets on the bottom of the lake, which increased in depth at 10 m intervals, starting at 10 m deep and ending at 60 m deep. To attain representative size distributions of all fishes within Pyramid Lake, I used sinking horizontal gill nets with variable mesh sizes (24 m long × 1.8 m tall with eight monofilament panels of 38, 57, 25, 44, 19, 64, 32, and 51 mm knot-to-knot bar mesh). Starting in August 2012, I attached temperature loggers to each gill net, to record temperatures at which fish were caught.

Indices of fish abundance

*Tui chub* – I used a combination of hydroacoustic estimates of fish abundance, mid-water trawl catch, and stage-based estimates of tui chub survival to produce estimates of biomass and annual production. Hydroacoustic and mid-water trawling were both performed in October 2012. I collected hydroacoustic data using a Biosonics Model DE6000 scientific echosounder with 420 kHz dual-beam transducer (6 X 15°) and towed the transducer on a fin at a 1-m depth while recording data using Biosonics Visual Acquisition processing software. I conducted hydroacoustic surveys to estimate density and abundance information for fish >85 mm TL (-49 dB) and verified targets using mid-water trawling. I conducted hydroacoustic surveys during new moon events, when fish were more likely to be suspended off the bottom of the lake and higher in the water.
column reducing the amount of fish that would be within the hydroacoustic dead zone near the bottom of the lake (Luecke and Wurtsbaugh 1993; Gaudreau and Boisclair 2000). Hydroacoustic surveys were conducted across 12 transects running east and west distributed from north to south covering the length of the lake. To reduce acoustic noise associated with surface wave action and extreme lake depth, I eliminated all acoustic targets within 1 m of surface and 1 meter of bottom, and confined target acceptance requirements for all surveys over deep water to target detections within the stratum of 1–44.2 m. I used transects as samples to calculate mean fish per cubic meter and estimate variance and 95% confidence intervals (CI). I extrapolated density of fish (fish/m³) into lake-wide abundance within the top 44.2 m of the lake only (i.e., volume at average transect depth = 20.0 billion m³). I derived an estimate of age-1 tui chub production (fish smaller than 85 mm TL) from a combination of hydroacoustic estimates of tui chub >85 mm TL, male to female ratio, egg to fish body weight ratios, and survival estimates of egg-to-YOY and YOY-to-age-1 tui chub. Survival estimates were taken from Diamond Lake, OR (Jackson et al. 2003) and fecundity estimates were taken from Kucera (1978) for tui chub in Pyramid Lake. Additionally, confidence interval estimates from hydroacoustics were carried through to the estimates of tui chub production (i.e. variability associated with each of the hydroacoustic size classes was used to explain potential variation in production).

I conducted mid-water trawling concurrently with hydroacoustics to verify targets. I used a mid-water trawl to sample fish in the pelagic zone over bottom depths of 33–70 m to verify prey species targeted during hydroacoustic surveys. At each of the eight index sites, I conducted two mid-water night-time tows, one parallel to shore (10–
22 m depth range) and one perpendicular to shore (21 – 28 m depth range) on October 15 and 16, 2012. The eight sites are the same index sites used for gill netting. I towed a mid-water trawl (3-m wide · 7-m high · 18-m long, with stretch mesh ranging from 10.2 cm near the mouth to 3 mm at the cod end) at an average speed of 4.0 km/h for 10 minutes filtering approximately 14,000 m$^3$ of water. I trawled in two depth strata: 10 – 22 m and 21 – 28 m, enumerated all fish, identified fish to species, and measured (total length and blot-dry wet weight) a subsample of individuals (~40).

*LCT* – Large LCT abundance was estimated from hydroacoustic targets greater than 400 mm TL and verified with trawl catch. However, because no small LCT were caught during mid-water trawling surveys, I used the ratio of small to large LCT caught while gill netting throughout the study to estimate small abundance using large LCT abundance.

*Individual and population-level estimates of LCT consumption*

To estimate individual and population-level consumption of tui chub by small (200 – 400 mm TL) and large (>400 mm TL) LCT in Pyramid Lake, I used the Wisconsin bioenergetics 3.0 model (Hanson et al. 1997). I used laboratory-derived physiological parameters developed for coho salmon *Oncorhynchus kisutch*, and altered the optimum temperature for consumption (CTO) to 14°C and maximum temperature for consumption (CTM) to 16°C to match more appropriate temperatures described for LCT bioenergetic simulations (Dwyer and Kramer 1975; Beauchamp et al. 1995) and other lacustrine populations of cutthroat trout (Ruzycki et al. 2001). Although used in past studies, the parameters used for this model may not reflect the actual temperatures at which LCT grow best. Therefore, I conducted a sensitivity analysis by increasing the
CTO and CTM to 15°C and 18°C, respectively. Results are discussed briefly, but do to minimal changes they are not discussed in detail. I limited my energetic analysis to only include LCT greater than 200 mm TL because LCT smaller than 200 mm TL were caught very infrequently, and are not very piscivorous (Nowak et al. 2004). I calculated population-level LCT consumption of tui chub from a combination of mean annual consumption by an average size LCT for each of the two stage classes. I ran all model simulations for 365 days, starting on 1 January. The Wisconsin bioenergetics modeling approach required estimates of LCT growth (described below), seasonal diet composition (Ch. 2), thermal history (described below), and taxa-specific energy content of prey (Table 3–1).

**LCT Growth** – I used length-at-age data collected by Monda 1999 (provided by PLF) to back-calculate growth rates of LCT. I calculated growth as a function of length (fork length, FL) to age using the von Bertalanffy growth model:

\[ L(t) = L_{\infty} [1 - e^{-k(t-t_0)}] \]

where \( L \) = length (mm), \( L_{\infty} \) = the horizontal asymptote at which growth approaches 0 (Francis 1988), \( k \) = the Brody growth coefficient which represents the rate of change to the growth rate as it approaches the asymptotic size, and \( t_0 \) = the theoretical age at which a fish would be of length 0 (Schnute and Fournier 1980).

To estimate growth for small and large LCT, I developed the following length-at-age equation from data reported in Monda (1999):

\[ FL = 577.19 [1 - e^{-0.26(t+0.93)}] \]
where FL = fork length (mm). I used mean age of small and large LCT, 1.8 years and 6.5 years, respectively, and used the von Bertalanffy growth curve to calculate start and end lengths for the two groups. I used a length-weight regression \( (R^2 = 0.97, n = 705) \) to calculate start and end weights from my pooled data collected 2 August, 2011 to 20 December, 2012, using the following equation:

\[
\ln(wt) = 3.0579(\ln(FL)) - 11.922
\]

where \( wt \) = weight (g) and \( FL \) = fork length (mm). The beginning of each growth year for LCT begins approximately 1 June, when they transition to swim-up fry (N. Vucinich, Pyramid Lake Fisheries, personal communication). Therefore, start and end weights were back calculated for the two size classes to correspond with the weight an average fish (within the two groups) would be on 1 January. Additionally, because large-LCT contribute 8% of their body mass annually to reproduction, and attempt to spawn near 1 May (N. Vucinich, personal communication), I applied an 8% weight loss, on that date, in all large LCT simulations.

**LCT diet composition** – I used diet data collected from the spring, summer, and fall sample periods of 2011 and 2012 (pooled by season) as an input to model simulations (Ch. 2). I identified and separated prey by taxon, blotted them dry, and calculated proportion by wet weight. I calculated diet composition as proportion of the total wet mass (g) of each diet item for each fish. I used linear interpolation between sample periods to reflect changing diet composition throughout the calendar year. I modeled diet composition for small and large-LCT separately, to reflect ontogenetic and seasonal trends that were potentially specific to each stage class.
LCT thermal history – To estimate thermal history of LCT and explore the effects of different potential thermal strategies, I used a combination temperature-at-catch data and reported optimum temperatures (Dwyer and Kramer 1975; Beauchamp et al. 1995; Dickerson and Vinyard 1999) to develop a set of annual temperature scenarios that would likely bracket the range of possible strategies used by LCT (Figure 3-2). I developed four temperature scenarios for small and large-LCT separately (Figure 3-2). For the ‘LOW’ scenario, I calculated the average temperature where LCT were caught (small LCT and large LCT calculated separately) during each time period, and used linear interpolation between sample periods. The “LOW” temperature scenario was named as such because the benthic-set gill nets likely give a biased representation of habitat occupied by LCT. However, I used surface temperature during times of the year when the lake was isothermal. I developed the ‘OPTIMUM’ scenario to mimic LCT that occupied the theoretical optimum (14°C), when available (Julian dates 135 – 288), and occupied the closest temperature to optimum, during all other dates when lake temperatures were below 14°C.

For the four remaining temperature scenarios, I incorporated foraging behavior indicative of LCT spending part of each day at temperatures preferred by tui chub. I added these scenarios, which incorporate the temperature preference of tui chub, to mimic diel vertical migration (DVM) behavior observed in other lentic cutthroat trout populations (Nowak and Quinn 2002) and to create an upper bound to potential temperature regimes. For the tui chub-influenced temperature scenarios, I first modeled, in the same manner as described for LCT, annual temperature regimes for all tui chub caught, and all tui chub caught that were below 200 mm TL. I divided tui chub into these
two groups to reflect available prey of LCT, based on gape limitation calculations. For large LCT, I then combined the ‘LOW’ scenario with the tui chub temperature scenarios at a 3:1 ratio of time spent at the ‘LOW’ scenario temperatures to time spent at the average tui temperature-at-catch, to create the ‘LOW+TUI’ scenario. I chose the 3:1 ratio as it is a conservative upper bound based on past cutthroat trout DVM studies (Vigg 1978; Nowak and Quinn 2002). Similar to the ‘LOW+TUI’ scenario, I combined the ‘OPT’ and tui temperature-at-catch data, at a 3:1 ratio, to calculate the ‘OPT+TUI’ scenario. I then calculated ‘LOW+TUI’ and ‘OPT+TUI’ temperature scenarios for small-LCT using the same steps as used for the large scenarios, except with tui chub temperature data for those below 200 mm TL rather than all tui chub caught. I ran all bioenergetic simulations, with the varying temperature scenarios, from 1 January through 31 December (Figure 3-2).

Although, bioenergetic simulations were performed using parameters commonly used for lake-dwelling cutthroat trout (Beauchamp et al. 1995; Ruzycki et al. 2001), I conducted a sensitivity analysis by adjusting CTO and CTM to warmer temperatures of 15°C and 18°C, respectively. This was done to observe how a change in parameters would affect overall consumption of tui chub. Because changing these parameters had minimal effect on scenarios of the total consumption of tui chub by small and large LCT combined (range: -0.7 to 0.1% change in total annual consumption by LCT) they were left out of further analyses.
Influence of biotic and abiotic factors on LCT catch

I assessed the relationship between site and date specific LCT catch per unit effort (CPUE; fish/net/hour) and a suite of abiotic and biotic predictors using Random Forest (RF) regression (Breiman 2001). RF regressions are useful and widely applied in ecology, in part, because they are able to characterize nonlinear complex relationships, have high classification accuracy, and are simple to interpret (Cutler et al. 2007). I included, dissolved oxygen (DO; mg·L\(^{-1}\)), temperature (°C), depth (m), Secchi depth (m), sampling location within the lake, season (spring, summer, winter), and slope of the benthic habitat as potential abiotic predictors of LCT CPUE. I used CPUE of small (<200 mm TL) and large (≥200 mm TL) tui chub (see Ch. 2), Tahoe suckers, cui-ui suckers, and Sacramento perch as potential biotic predictors. Variable importance in RF regression is assessed using percent change in mean square error. Percent change in the mean square error for a predictor variable is calculated by replacing the variable of interest with a random variable and observing the change in explained variance.

For DO, I used annual depth profile data collected at Station 96 (Figure 3-1) monthly at every meter deep by PLF. Pyramid Lake Fisheries collects DO data monthly at Station 96 using a SeaCAT profiler. I used linear interpolation between sample dates to calculate depth-specific values for each day. For water transparency, I collected Secchi depth data at Station 96 for sites Pelican Point, Plaque Rock, North Shore, Hell’s Kitchen, Anderson Bay, and Pyramid, and collected data at Station 93 for sites Block House and Tamaracks (Figure 3-1). Secchi depth was collected once during each sampling trip at stations 93 and 96, over the shaded side of the boat, using a standard 30 cm Secchi disk. Although there may be discrepancies between the specific sample sites
and the location of Secchi depth recordings, the recorded Secchi depths offer a representation of changes in water clarity through time that would be representative of the whole lake (Swift et al. 2006). I calculated the slope of benthic habitat as rise-over-run using depths at the terminal ends of each net. I used the shallow end of each net for the depth variable. For all temperature data used in regression modeling, I attached temperature loggers to each gill net and used the average temperature observed over the course of the sample period (one overnight set). For the summer of 2011, I calculated temperature in the same manner as described for and DO.

**Results**

*Indices of fish abundance*

Lake-wide abundances of tui chub were estimated at 21.0 million 85-150mm TL fish, 12.3 million 151-225mm TL fish, 5.2 million fish between 226-270mm TL, and 4.2 fish between 271-365mm TL; a total of 42.7 million tui chub. The male to female ratio of tui chub was 0.61 over the course of the study. The average number of eggs per female was, 12,878 eggs per female between 151-225 mm TL, 27,791 eggs per female between 226-270 mm TL, and 63,436 eggs per female between 271-365 mm TL (Kucera 1978). Production of age-1 tui chub was estimated at 2,791 metric tonnes. Standing-stock of tui chub in the lake was 3,481 metric tonnes (95% CI; 1,945 – 5,017) and production was estimated to be 3,643 metric tonnes (95% CI; 2,038 – 5,248). The production:biomass ratio was 1.05. During our acoustic surveys I determined there were 324,000 large LCT. Using the ratio of small to large LCT caught in gill nets over the course of the study, I back-calculated that there were 122,000 small LCT.
Individual and population-level estimates of LCT consumption

Individual consumption of tui chub by both large and small LCT was fairly consistent across the different temperature scenarios (Table 3-3). Based on bioenergetics model estimates, large LCT annually consume 2,388g of tui chub within the constraints of the ‘LOW’ scenario, 3,057g within the ‘OPTIMUM’ scenario, 2,458g within the ‘LOW+TUI’ scenario, and 2,989g of tui chub within the ‘OPT+TUI’ scenario. The proportion of maximum consumption $p(C_{max})$ for large-LCT ranged from 0.35 (‘LOW’ scenario) to 0.41 (‘OPTIMUM’ scenario), indicating that given the thermal regime and estimated allometric, physiological relationships, they consume at less than half their potential maximum rate of consumption. Small LCT annually consumed 830g of tui chub within the constraints of the ‘LOW’ scenario, 992g within the ‘OPTIMUM’ scenario, 667g within the ‘LOW+TUI’ scenario, and 766g of tui chub within the constraints of the ‘OPT+TUI’ scenario. The proportion of maximum consumption $p(C_{max})$ for small LCT ranged from 0.30 (‘LOW+TUI’ scenario) to 0.38 (‘OPTIMUM’ scenario), indicating that similar to large LCT, consumption at the time of this study was less than half the maximum consumption rate.

Based on the four different temperature scenarios for LCT consumption of tui chub, the total grams of tui chub consumed by small and large LCT combined was 874 million for the ‘LOW’ scenario, 1,110 million for the ‘OPTIMUM’ scenario, 877 million for the ‘LOW+TUI’ scenario, and 1,061million for the ‘OPT+TUI’ scenario (Table 3-3). These estimates of tui chub consumption by LCT range from 25% to 32% of tui chub biomass in Pyramid Lake at the time of the study, and 24.0% to 30% of annual production, an estimate which does not include YOY production (Figure 3-4).
Influence of biotic and abiotic factors on LCT catch

The Random Forest model fit reasonably well for large-LCT and explained 36% of the variation in catch data, with the more important predictors generally being abiotic. The most important predictors of large LCT were water transparency (Secchi depth), sample site, and depth of the net set (Figure 3-5). Water transparency demonstrated a positive relationship with large LCT catch, and depth of net set demonstrated a negative relationship with large LCT catch (Figure 3-2). The other strong predictor, sample site, captured the highest catches of large LCT at Anderson Bay and Plaque Rock, and the lowest catches at Tamaracks and North Shore (Figure 3-2). Slope of benthic habitat, season, temperature, and DO were all of moderate importance; however, none of the biotic factors were strong predictors of large LCT CPUE.

The Random Forest model predicting small LCT CPUE only explained 14% of the variation in the data (Figure 3-6). The most important factors used to predict small LCT CPUE were temperature, small tui chub CPUE, and depth of net set (Figure 3-6). Temperature exhibited a positive relationship with small LCT catch, which plateaued at 13°C and above, small tui chub CPUE demonstrated an overall negative relationship, and depth of net set again indicated a negative relationship (Figure 3-6). Other factors included in the model were small and large tui chub, season, slope of benthic habitat, DO, Tahoe sucker CPUE, and water transparency.

Discussion

Understanding the factors that limit fish population abundance and distribution is among the most important challenges facing fisheries managers. As such, potential limitations are made up of a suite of biotic and abiotic factors and understanding which
factors are limiting will aid in understanding mechanistic influences on species interactions. Within the context of the threatened population of LCT in Pyramid Lake, my data suggests that LCT distribution within the lake, particularly large LCT, is more influenced by abiotic rather than biotic factors, indicating little limitation via food availability. The current distribution of LCT and their fish prey suggest that large trout do not distribute themselves proportionately among their food sources, and that physical factors such as temperature, water clarity, and depth play a larger role in predicting LCT catch. While the mechanisms limiting production can vary between systems, the artificial nature of this fishery has potentially disrupted the natural drivers of this predator-prey cycle.

Fish populations are generally restricted by food resources, competition for food, or predation (Ney 1990), and these resource restrictions act to shape food-web structure (Paine 1980; Polis and Strong 1996), which in turn can determine individual species’ abundances. This is not to suggest that biotic, and only biotic factors, act to constrain species abundances, but in Pyramid Lake, the weak to nonexistent correlations between LCT and prey fish, and LCT and their only potential competitors, Sacramento perch, indicates that this hatchery population is likely not limited by biotic interactions. More specifically, this indicates that consumption of prey may be well below annual production of prey, namely tui chub. Tui chub are the most common prey found in LCT diets, throughout the year, and this reliance on tui chub is the likely cause of LCT attaining such high trophic positions (see Ch. 2). The high reliance on tui chub, and the weak relationship between LCT and tui chub distributions indicates that LCT are not restricted by density-dependent food availability, typically observed when resources are limited
(Fretwell and Lucas 1970; Kennedy and Gray 1993; Hedger et al. 2005). These results indicate that tui chub biomass is far greater than the biomass of tui chub consumed by LCT annually.

My bioenergetics assessment of the effect of LCT predation on the current tui chub population in Pyramid Lake also suggests that food is not limiting. While the diet proportion of large-LCT diet made up of tui chub changes little throughout the year (40.7% [+27.2% unidentified fish] - 59.4% [+15.5% unidentified fish]), summer temperatures likely increase both metabolism and total LCT consumption of all prey; not just tui chub. Although LCT in Pyramid Lake do attain large sizes, in comparison to other cutthroat trout throughout Western North America, the cool winter temperatures throughout the water column in winter likely decrease annual growth rates. This reduction is likely reflected, in part, in the moderate $P(C_{\text{max}})$ values associated with these piscivores, an artifact of estimating growth across an entire year. Nonetheless, the net biomass of tui chub, an estimate which doesn’t include YOY fish, is 4-5 times that of what is consumed by large-LCT annually. Additionally, while conducting SCUBA surveys during the summer of 2012, I encountered large schools of tui chub ranging up to several meters in diameter and over 100m in length (personal observation). These large schools of tui chub had to be eliminated from my acoustic analyses of tui chub abundance, as I was unable to discern individual fish. As such, my estimates of tui chub are likely underestimates of the true abundance and production of tui chub in the lake, further confirming that tui chub production likely far exceeds LCT consumption of tui chub.
Abiotic factors produced the strongest relationships with large-LCT catch, and water transparency, site location, and depth of net set were among the best predictors of catch throughout the lake. Increased reaction distances (Vogel and Beauchamp 1999), increased size-selectivity (Rowe et al. 2003), prey species selectivity (Stuart-Smith et al. 2004), and increased predation on pelagic prey (Rowe 1984; Rowe and Taumoepeau 2004) by salmonid predators are all outcomes associated with increased water clarity. Accordingly, large cutthroat trout in Strawberry reservoir were found to have increased reaction distances to prey when in regions of the lake with higher transparency (Baldwin and Beauchamp 2002). Additionally, decreased water clarity leading to reduced predation of fish prey has also been shown to reduce the condition of upper-trophic level piscivores in lotic systems (Craig and Babaluk 1989). However, my findings are opposite those which have found that water clarity generally increases net avoidance (Olin et al. 2004), and suggests an increase in activity during clear water periods. This trend may have been a factor of my nets having been set at night, likely making nets less avoidable by fish, and therefore making gear type less of a factor in determining catch.

My results suggest that site specific trends are likely associated with a variety of physical attributes. Anderson Bay and Plaque Rock consistently produced the highest large LCT catch, a pattern that can likely be attributed to the presence of physical structure in those areas. LCT and other lake dwelling salmonids tend to favor areas associated with structure, such as rocky substrate (Al-Chokachy et al. 2009) and other complex structures (Gorman et al. 2008). The benthic habitat of Anderson Bay, unlike other areas consisting of fine substrates, is characterized as being made up of a combination of calcified tufa formations intermixed with large rocky substrate (personal
SCUBA observations). In contrast, areas such as Hell’s Kitchen and the Pyramid area, similarly rich in course substrate, do not produce the consistently high catches associated with Anderson Bay. The two areas with the lowest large LCT abundances were North Shore and Tamaracks, areas with little course substrate and little benthic slope, a surrogate of physical structure.

For small LCT, higher abundance was associated positively with temperature and negatively with depth. Although the predictive power of the small LCT catch model was weak, temperature was the single best predictor of small LCT CPUE. This result suggests that small LCT are at least marginally influenced by this abiotic factor, which in salmonids can affect feeding activity (Elliot 1976), metabolism (Elliot 1976; Dickerson and Vinyard 1999) and ultimately distribution (e.g., Ferguson 1958; Hayes et al. 2009). Increased temperatures from 12°C to 24°C and increases in diel temperature fluctuations from 15-21°C to 12-24°C have been shown to reduce juvenile LCT growth (Meeuig et al. 2004). Windell et al. (1978) also found that the digestibility of protein and lipids increased with fish size for rainbow trout held at cooler temperatures (7°C) than at warmer temperatures (11°C and 15°C), indicating potential for more efficient digestion. However, contrary to these physiological analyses, my data shows that catch rates were consistently highest at temperatures ranging from 14-24°C. Possibly as a result of small LCT consuming a substantial amount of benthic invertebrate prey, often more abundant in warmer littoral regions.

Compared to large LCT, results from random forest modeling of small LCT are relatively weak and may reflect the lack of sampling for potential food sources for these small fish. This study (Ch. 2) and other studies of lake dwelling cutthroat trout
(Beauchamp et al. 1990; Nowak et al. 2004) suggest that small LCT regularly feed on invertebrates and zooplankton. Although, I sampled both benthic invertebrates and zooplankton, I did not do so in a manner that would allow me to use these data as predictors of small trout catch.

Results from this study indicate that factors limiting LCT growth and survival are more likely to be abiotic rather than biotic. However, a number of possible limitations remain untested. In recent years, management has focused on the genetic strains of LCT used by PLF and the USFWS’s Lahontan National Fish Hatchery Complex. Past genetic work has indicated that the current strain of LCT most commonly stocked in Pyramid Lake is most closely related to a strain of LCT found in Summit Lake, California (Nielsen and Sage 2002). In 2006, the two stocking programs jointly began stocking the Pilot Peak strain of LCT, a strain described as being recent descendants of the otherwise extirpated strain of LCT which historically inhabited the Truckee River Drainage (Peacock and Kirchoff 2007). Preliminary results from growth and condition metrics indicate that the Pilot Peak strain is outperforming the Summit Lake strain of LCT used in Pyramid Lake. However, further study of consumption, growth, and behavioral differences between the two strains may result in a better understanding of current limitations.

My study also assumes that the LCT population has no aquatic predators; however, two forms of predation were not a part of this study. Human anglers and piscivorous birds, American white pelicans and double-crested cormorants, are the primary consumers of LCT at Pyramid Lake. American white pelicans and cormorants have been part of the Pyramid Lake ecosystem prior to the decline in the LCT population,
and are therefore likely not the cause of the current status of LCT. In addition, exploitation of fisheries has proven to have pervasive impacts on fish populations in lakes (e.g., McDonald and Hershey 1989; Rochet 1998; Paukert and Willis 2001), and specifically for LCT (Coffin and Cowen 1995). In Pyramid Lake, however, tight regulations and management, following the extirpation of LCT in the mid-20th century appear to have ensured a future for a healthy population of LCT. In sum, currently neither sport angling nor bird-predation appears to limit the LCT population in Pyramid Lake. Despite these potential limitations, this multifaceted food-web study lays a strong framework upon which to build future management decisions and goals.

Future management decisions should take into account the current relationship between LCT and their prey base. Specifically as observations made in this study indicate that food available to LCT may be able to support a larger population of in the lake. A management plan which monitors and adjusts stocking strategies with an adaptive management framework may give a more comprehensive understanding of Pyramid Lake species interactions and carrying-capacity for LCT. However, complex species interactions often complicate the outcomes of food-web perturbations (Elser et al. 1995), and as such, the effect of increased stocking rates in the future is difficult to predict with certainty, and if undertaken, should be closely monitored through annual analysis of LCT consumption and growth. Long-term monitoring of abiotic environmental factors, LCT distribution, LCT survival, and the production, or recruitment rates of prey fishes can help ensure effective management of this important population and sport fishery.
References


Craig, J.F., and J.A. Babaluk. 1989. Relationship of condition of walleye (Stizostedion vitreum) and northern pike (Esox Lucius) to water clarity, with special reference to Dauphin Lake, Manitoba. Canadian Journal of Fisheries and Aquatic Sciences 46: 1581-1586.


Table 3-1. Prey item energy densities used for bioenergetic modeling scenarios.

<table>
<thead>
<tr>
<th>Prey Item</th>
<th>Energy Density (J/g)</th>
<th>Source</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphipoda</td>
<td>4429</td>
<td>Wissing and Hasler 1968</td>
<td></td>
</tr>
<tr>
<td>Arachnida</td>
<td>3176</td>
<td>Cummins and Wuycheck 1971</td>
<td>Insecta value</td>
</tr>
<tr>
<td>Chironomid</td>
<td>2745</td>
<td>Cummins and Wuycheck 1971</td>
<td></td>
</tr>
<tr>
<td>Coleoptera</td>
<td>2199</td>
<td>Penczak et al. 1999</td>
<td></td>
</tr>
<tr>
<td>Corixidae</td>
<td>2696</td>
<td>Cummins and Wuycheck 1971</td>
<td>Notonectide surrogate</td>
</tr>
<tr>
<td>Cui-ui</td>
<td>5377</td>
<td>Bryan et al. 1996, Cummins and Wuycheck 1971</td>
<td>Average of white sucker, labridae, and clupeidae</td>
</tr>
<tr>
<td>Detritus</td>
<td>1017</td>
<td>Penczak et al. 1999</td>
<td>Unidentified organic matter</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>4703</td>
<td>Cummins and Wuycheck 1971</td>
<td>Baetidae value</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>2696</td>
<td>Cummins and Wuycheck 1971</td>
<td></td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>6688</td>
<td>Cummins and Wuycheck 1971, Penczak 1999</td>
<td>Average of two sources</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>3176</td>
<td>Cummins and Wuycheck 1971</td>
<td>Insecta value</td>
</tr>
<tr>
<td>Macrophyte</td>
<td>2100</td>
<td>Woolhead 1994</td>
<td></td>
</tr>
<tr>
<td>Mollusca</td>
<td>2008</td>
<td>Cummins and Wuycheck 1971</td>
<td></td>
</tr>
<tr>
<td>Nematoda</td>
<td>2699</td>
<td>Cummins and Wuycheck 1971</td>
<td>Annalid as surrogate</td>
</tr>
<tr>
<td>Odonate</td>
<td>5151</td>
<td>Penczak et al. 1999</td>
<td></td>
</tr>
<tr>
<td>Orthoptera</td>
<td>3176</td>
<td>Cummins and Wuycheck 1971</td>
<td>Insecta value</td>
</tr>
<tr>
<td>Sucker</td>
<td>5377</td>
<td>Bryan et al. 1996, Cummins and Wuycheck 1971</td>
<td></td>
</tr>
<tr>
<td>Tahoe sucker</td>
<td>5377</td>
<td>Bryan et al. 1996, Cummins and Wuycheck 1971</td>
<td></td>
</tr>
<tr>
<td>Tui chub</td>
<td>5230</td>
<td>Raymond and Sobel 1990</td>
<td></td>
</tr>
<tr>
<td>Unidentified fish</td>
<td>5304</td>
<td>Bryan et al. 1996, Cummins and Wuycheck 1971, Raymond and Sobel 1990</td>
<td>Average of suckers and tui chub</td>
</tr>
<tr>
<td>Unidentified invertebrate</td>
<td>3639</td>
<td>Cummins and Wuycheck 1971, Penczak et al. 1999, Wissing and Hasler 1968</td>
<td>Average of all other invertebrates</td>
</tr>
<tr>
<td>Zooplankton</td>
<td>2653</td>
<td>Cummins and Wuycheck 1971, Snow 1972</td>
<td>Average reported values</td>
</tr>
</tbody>
</table>
Table 3-2. Age-based tui chub biomass and production for Pyramid Lake, NV. Tui chub age-class data derived from hydroacoustic surveys conducted October 2012. Survival rates were taken from Jackson et al. 2003.

<table>
<thead>
<tr>
<th>Size class</th>
<th>Size (mm)</th>
<th>Number</th>
<th>±1 SE</th>
<th>Survival</th>
<th>Median individual mass (g)</th>
<th>Biomass (metric tonnes)</th>
<th>Production (metric tonnes)</th>
</tr>
</thead>
<tbody>
<tr>
<td>YOY</td>
<td></td>
<td>0.01</td>
<td></td>
<td></td>
<td>20,992,172</td>
<td>4,818,678</td>
<td>2,791</td>
</tr>
<tr>
<td>1</td>
<td>85-150</td>
<td>12,344,116</td>
<td>2,722,064</td>
<td>0.27</td>
<td>151-225</td>
<td>123,441,116</td>
<td>2,722,064</td>
</tr>
<tr>
<td>2</td>
<td>151-225</td>
<td>11,89,094</td>
<td>1,189,094</td>
<td>0.92</td>
<td>226-270</td>
<td>5,224,259</td>
<td>1,189,094</td>
</tr>
<tr>
<td>3</td>
<td>226-270</td>
<td>4,240,380</td>
<td>955,219</td>
<td>*0.12</td>
<td>271-365</td>
<td>4,240,380</td>
<td>955,219</td>
</tr>
<tr>
<td>4+</td>
<td>271-365</td>
<td>4,240,380</td>
<td>955,219</td>
<td>*0.12</td>
<td>271-365</td>
<td>4,240,380</td>
<td>955,219</td>
</tr>
</tbody>
</table>

*indicates average survival rates for age 4 through age 9 fish.
Table 3-3. Individual and population-level annual consumption (g) of tui chub by LCT, in Pyramid Lake, NV. Estimates are based on the various temperature regime scenarios used for bioenergetic modeling, and the abundance estimates of small and large-LCT.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Individual</th>
<th>Total (Millions)</th>
<th>Individual</th>
<th>Total (Millions)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>830</td>
<td>101</td>
<td>2388</td>
<td>773</td>
</tr>
<tr>
<td>Optimum</td>
<td>992</td>
<td>121</td>
<td>3057</td>
<td>989</td>
</tr>
<tr>
<td>Low + Tui</td>
<td>667</td>
<td>81</td>
<td>2458</td>
<td>795</td>
</tr>
<tr>
<td>Opt + Tui</td>
<td>766</td>
<td>93</td>
<td>2989</td>
<td>967</td>
</tr>
</tbody>
</table>
Figure 3-1. Map of Pyramid Lake, Nevada, U.S.A. The labels around the perimeter of the lake indicate routine sample sites for minnow, gill, and trap netting. Sample transects started near to, and ran perpendicular to shore.
Figure 3-2. Water temperature regimes for small (top panel) and large (bottom panel) LCT used in the bioenergetic modeling of prey consumption rates. Four temperature regimes are depicted to represent potential habitat use by LCT. ‘LOW’ = temperatures associated with LCT temperatures at the time of capture, ‘OPTIMUM’ = LCT using their optimum temperature (14°C), ‘LOW+TUI’ = the average temperature wherein LCT spend 75% of the day at the ‘LOW’ temperature scenario and 25% of the day at the average temperature for which tui chub were caught for that given day, and ‘OPT+TUI’ = the average temperature wherein LCT spend 75% of the day at the ‘OPTIMUM’ temperature scenario and 25% of the day at the average temperature for which tui chub were caught for that given day.
Figure 3-3. Individual daily consumption rates of tui chub (g) by small (top panel) and large (bottom panel) LCT that were estimated by the Wisconsin bioenergetics model assuming four different temperature scenarios that the trout utilized.
Figure 3-4. Tui chub biomass, tui chub production, and total estimated annual consumption of tui chub by LCT (black bar). Error bars for tui chub biomass and production were calculated using twelve hydroacoustic transects and represent 95% confidence intervals. Confidence intervals (95%) for tui chub consumed by trout were calculated from four different bioenergetic scenarios.
Figure 3-5. Variable importance plot (top left), and partial dependency plots of water transparency (top right), sample site lake depth (bottom left), and benthic slope (bottom right) for the random forest regression used to predict large LCT (>400mm TL) CPUE for benthic gill nets in Pyramid Lake, NV. Variable importance plots rank the variables as a function of the percent variation explained (as represented by %IncMSE; percent increase in the mean squared error) that would be lost from the model if that variable were replaced with a random variable. Partial dependency plots represent the relationship between a given predictor and the response variable after the variation associated with all other predictors has been accounted for.
Figure 3-6. Variable importance plot (top left), and partial dependency plots of temperature (top right), small tui chub CPUE (bottom left), and depth of the net set (bottom right) for the random forest regression used to predict small LCT (<400mm TL) CPUE for benthic gill nets in Pyramid Lake, NV. Variable importance plots rank the variables as a function of the percent variation explained (as represented by %IncMSE; percent increase in the mean squared error) that would be lost from the model if that variable were replaced with a random variable. Partial dependency plots represent the relationship between a given predictor and the response variable after the variation associated with all other predictors has been accounted for.
CHAPTER 4

SUMMARY

Given numerous changes to the food-web and surrounding environment within Pyramid Lake, the LCT population appears to be healthy and not limited by potentially-altered predator-prey or competitive interactions. Following declines in lake level, reduced access to spawning habitat, heavy fishing pressure, the extirpation of naturally-reproducing fish, and the introduction of an upper trophic-level piscivore, LCT in Pyramid Lake maintain high trophic status and appear not to be limited by biotic interactions. Recent genetic work on the different strains of Lahontan cutthroat trout (Nielson & Sage 2002; Peacock & Kirchoff 2007) suggest that identifying and stocking fish most similar to pre-extirpation LCT may act to maximize production and growth of these unique salmonids. Nonetheless, my thesis work has laid the ground-work for developing and implementing more effective management of LCT in Pyramid Lake, based on species interactions. My thesis research has furthered our understanding of: 1) seasonal and annual trends in LCT and Sacramento perch diets, 2) how diet reflects the current trophic positions of these piscivores, 3) the biotic and abiotic factors that currently influence LCT distribution and abundance, and 4) the impact of LCT consumption on the biomass and annual production of tui chub.

The objectives of Chapter 2 were to compare seasonal depth distributions, seasonal diet trends and dietary overlap between LCT and Sacramento perch, and to understand longer-term time-integrated measures of LCT and Sacramento perch diets. Additionally, another objective was to understand seasonal depth distributions of LCT and tui chub, how they may affect LCT diet, and the current trophic status of LCT. To
address these objectives, I used dietary composition data, catch data, and carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) isotopes in order determine how vertical fish distribution changes throughout the year, how diet reflects those changes, and to determine trophic status and niche-space overlap of upper-trophic level piscivores.

The results detailed in Chapter 2 suggest that despite the current status of LCT throughout their native range (Coffin & Cowin 1995) and the established population of Sacramento perch in Pyramid Lake (Crain & Moyle 2011), LCT remain an apex predator with little competition for food. The Pyramid Lake fish community supports the predator-prey interaction most valuable to LCT, that between LCT and tui chub. While LCT in Pyramid Lake now depend entirely on stocking programs, potentially de-coupling them from their historical predator-prey relationship with tui chub, both diet and isotope analyses indicate that LCT rely more heavily on tui chub for food than any other prey type. Additionally, as indicated by isotope analysis, LCT remain the top fish predator within this unique desert lake. These trends suggest that LCT still strongly rely on tui chub as a primary food source throughout the year, and that competition between LCT and Sacramento perch is limited despite similar resource reliance. These results indicate that LCT still remain highly dependent on tui chub as a primary food source, competition with Sacramento perch is minimal, and that they maintain a high trophic position despite various changes to the surrounding ecosystem and the loss of other nearby lacustrine populations.

The objectives of Chapter 3 were to determine which biotic and abiotic factors most influence LCT distribution and abundance, and to understand the impact of LCT consumption on tui chub production and biomass. I used a suite of biotic and abiotic
variables collected during fish sampling to elucidate which factors most strongly influence the distribution of LCT. Additionally, I used bioenergetic simulations to estimate the biomass of tui chubs consumed by LCT annually.

Results from Chapter 3 analyses indicate that LCT distribution in Pyramid Lake is more influenced by abiotic rather than biotic factors and that LCT consume well below the standing biomass or production of tui chub annually. Transparency, temperature, and depth tended to be more influential on the distribution of LCT than other biotic factors, such as the abundance of prey, or potential competitors. These results, coupled with energetics results indicating little impact on the tui chub population via LCT consumption, suggest that LCT are potentially at or below carrying capacity. However, further investigation of changes to the LCT population size may give more insight to population level responses to food and habitat availability.

In conclusion, LCT do not appear to be limited by biotic interactions or food availability, indicating that density-dependent resource restriction is not a factor potentially limiting the population. These results lay the groundwork for future conservation and management of this imperiled sub-species of cutthroat trout.

References


Appendix
Dear Gary,

I am requesting your permission to include our paper, which you are a coauthor on, to include in Chapter 3 of my thesis.

Please indicate your approval of this request by signing in the space provided below, and by attaching any other form or instruction necessary to confirm permission.

Thank you,

Nicholas A. Heredia

I hereby give permission to Nicholas A. Heredia to print the requested paper as a chapter in his thesis:

______________________________  ____________________
Gary P. Thiede                  Date