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Impacts of Lake Elevation Decline on Tui Chub, A Critical Forage Species for Lahontan Cutthroat Trout in Pyramid Lake, Nevada, USA

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IMPACTS OF LAKE ELEVATION DECLINE ON TUI CHUB, A CRITICAL FORAGE SPECIES FOR LAHONTAN CUTTHROAT TROUT IN PYRAMID LAKE, NEVADA, USA

by

Sarah Barnes

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

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ABSTRACT

Impacts of Lake Elevation Decline on Tui Chub, a Critical Forage Species for Lahontan Cutthroat Trout in Pyramid Lake, Nevada, USA.

by

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Utah State University, 2024

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Lake elevation decline is a global phenomenon with numerous consequences for lake ecosystems, including altering nearshore habitat used by lacustrine spawners, and increasing total dissolved solids (TDS). Changes to nearshore habitat resulting from lake elevation decline are dependent on many factors, although generally nearshore habitat is simplified and reduced in spatial extent as lake elevation declines. Effects of TDS on sensitive early fish life stages has received less attention than adult stages, presumably because of the need for artificial propagation, which can be both difficult and expensive. We investigated the relative threat of both consequences of lake elevation decline on Tui Chub *Siphateles bicolor*, a lacustrine spawner and critical forage species for a valuable native sportfish, Lahontan Cutthroat Trout (LCT), in Pyramid Lake, Nevada. Pyramid Lake has declined 30 meters from 1891 to 1967 as a result of human water extraction and has remained depleted since. To understand the relationship between lake elevation and Tui Chub spawning potential, we investigated Tui Chub use of nearshore habitat during spawning, and the quantity of nearshore habitat available at numerous lake elevations using an elevation-explicit model of the Pyramid Lake basin. To investigate the effects of TDS concentration on Tui Chub early life, we developed a small-scale culture technique to test five TDS concentrations. In our field surveys we observed a significant ($\alpha = 0.05$) increase in Tui Chub spawning activity from 17.5-23 °C and in habitats with larger sediment grain size. Based on our elevation explicit model, we determined that if Pyramid Lake elevation declines by an additional 8 meters, the lake will contain the minimum quantity of nearshore habitat out of all lake elevations tested, 40% less than a realistic theoretical maximum. Larvae did not hatch above present-day TDS concentrations, implying Tui Chub larvae would be negatively impacted by increased TDS. However, we were unable to control the presence of artificially high concentrations of ammonia in most of our aquaria, such that all egg mortality cannot be attributed to TDS alone. Our results suggest further lake elevation decline would have multiple negative consequences for Tui Chub and consequently LCT.

(105 Pages)

PUBLIC ABSTRACT

Impacts of Lake Level Decline on Tui Chub, a Critical Forage Species for Lahontan Cutthroat Trout in Pyramid Lake, Nevada, USA.

Sarah Barnes

Lake level decline affects lakes worldwide, changing the availability and character of nearshore habitat used by fish to spawn, and increasing total dissolved solids (TDS), similar to salinity, a factor that negatively impacts fish health. Lake level decline can affect different lakes in different ways, but typically when lake level declines significantly, there is less nearshore habitat overall, and what nearshore habitat remains has less diverse habitat for fish. We investigated whether both impacts of lake level decline may be causing declines of Tui Chub *Siphateles bicolor,* a large minnow native to Pyramid Lake that spawns in nearshore habitat. Tui Chub are the main food source for Lahontan Cutthroat Trout, a sought after, and vulnerable, sportfish also native to the lake. Pyramid Lake declined 98 feet from 1891 to 1967 because of human water use and remains low today. We used nets to capture Tui Chub during their spawning season to determine their preferred spawning habitat. We then used topographic data of the Pyramid Lake basin to understand the amount of spawning habitat at historical, and potentially future, lake levels if lake levels continue to decline in Pyramid Lake. We tested the response of Tui Chub eggs and larvae to TDS by spawning Tui Chub at a range of TDS levels. Based on our results, Tui Chub spawn in some of the warmest water found in Pyramid Lake during the summer and seek rocky areas to deposit their eggs, habitat features that may be reduced in Pyramid Lake with further lake level decline. With an additional 26 feet of lake level decline, Pyramid Lake will have less nearshore habitat than all other historical and contemporary lake elevations we investigated, potentially seriously restricting habitat available for Tui Chub spawning. Tui Chub eggs and larvae in our experiment were unable to hatch at TDS levels greater than those already found in Pyramid Lake. However, we experienced artificially high levels of toxic ammonia in most replicates such that all egg deaths could not be attributed to the TDS treatments. Our results have important implications for water demand for Pyramid Lake to make sure there are enough Tui Chub to support the population of Lahontan Cutthroat Trout in the lake.

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Sarah Barnes

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CHAPTER 1

INTRODUCTION

Freshwater habitats are biodiversity hotspots making up only 2.3% of Earth's surface (Revenga and Kura 2003, Lehner and Döll 2004), but containing roughly 10% of all species (Dudgeon et al. 2006, Helfman 2007, Balian et al. 2008). Human alterations to the biotic and abiotic environment, including climate change, have led to an extinction crisis in freshwater systems (Duncan and Lockwood 2001, Jelks et al. 2008, Reid et al 2019), through changes to thermal and hydrologic regimes (Cayan et al. 2016, Arthington et al. 2018, Pennock et al. 2022), pollution (Moss 2008, Carpenter et al. 2011, Eerkes-Medrano et al. 2015), and non-native species introductions (Moorhouse and MacDonald 2015, Gallardo et al. 2016, Kiruba-Sankar et al. 2018). These alterations have led to widespread habitat loss for aquatic species (Duncan and Lockwood 2001, Liermann et al. 2012, Davidson 2014) through dewatering (Nagrodski et al. 2012, Rodell et al. 2018), temperatures that exceed species thermal niches (Caissie 2006, Ficke et al. 2007), and intolerable chemical conditions (USEPA 2009, Reid et al. 2019). With climate change and human development only projected to intensify, a better understanding of the impacts of anthropogenic alteration on freshwater species will aid in developing mitigation and adaptation plans for conservation (Rosegrant and Ringler 2000, Dai 2013, IPCC 2023).

Endorheic, or terminal lakes, are relatively unique waterbodies which, due to catchment geography that precludes outflow to the ocean, only lose water through evaporation. Endorheic basins comprise roughly a fifth of the Earth's surface, but also contain half of the water-stressed regions (Wada et al. 2011). Many endorheic lakes in arid regions are also classified as athalassic (i.e., an inland, saline body of water;

Williams 1981) because evaporative loss without sufficient inflow concentrates ionic compounds in these lakes. Saline lakes provide important habitat for aquatic and avian ecosystems in arid regions and support many endemic and endangered species which thrive only in these extreme environments (Zadereev et al. 2020). Shifting precipitation regimes consisting of more precipitation as rain than snow, changes in precipitation magnitude (Trenberth 2011, Cline et al. 2020, Zhang et al. 2021), along with water diversions for agriculture and development (Wan et al. 2017), have decreased water contributions and increased the rate of evaporation in many endorheic lakes, particularly in arid regions (Micklin 2007, Alizadeh-Choobari et al. 2016, Null and Wurtsbaugh 2020).

Persistent lake elevation decline poses numerous threats to lacustrine ecosystems, including altering habitat composition and changing lake chemistry (Jeppesen et al. 2015). Reduction of already restricted nearshore habitat can disrupt the lifecycle of many different fish species (Winfield 2004, Gaeta et al. 2014). In endorheic lakes, total dissolved solid (TDS concentrations can become higher than biota can tolerate (The Nature Conservancy 2013, Larson et al. 2016, Wurtsbaugh et al. 2017). Increasing TDS alters the energy required for osmoregulation in fish (Goss et al. 1992) and ultimately can lead to mortality when physiological limits of compensation are exceeded (Reed and Evans 1981, Wilkie and Wood 1996). Lake elevation decline is particularly concerning in Pyramid Lake, Nevada, an athalassic, endorheic, descendant of historic Lake Lahontan. Pyramid Lake declined 30 meters from 1891 to 1967 due to human water extraction and has remained depleted since (Benson and Thompson 1987, Luck 1991).

Pyramid Lake is located on Pyramid Lake Paiute Tribe (PLPT) land in northeast Nevada (Galat et al. 1981) and is home to native fishes with strong social, economic, and extremely important cultural significance (Bolingbroke 2014). Lahontan Cutthroat Trout (LCT) *Oncorhynchus clarkii henshawi*, a federally Threatened species under the Endangered Species Act, supports a valuable sport fishery in the lake for the PLPT. Naturally-spawning LCT were extirpated from Pyramid Lake in the 1940s because of dewatering that limited fish movement to spawning habitat in the primary river input to Pyramid Lake, the Truckee River (Sigler et al. 1983, Al-Chokhachy et al. 2020). Since then, LCT have primarily been maintained in the lake through hatchery supplementation, but natural spawning and recruitment began roughly a decade ago as a result of conservation efforts (Al-Chokhachy et al. 2020).

Recently, there have been growing concerns about the impacts of lake elevation decline on LCT recovery and the LCT fishery. In simple lacustrine ecosystems such as Pyramid Lake, energy historically transfers directly up trophic levels, with the health of prey and predator populations being tightly coupled (Vadeboncoeur et al. 2002, Heredia and Budy 2018). Despite hatchery supplementation of LCT (Coffin and Cowan 1995) and non-native species introductions (Heredia 2014) which can disrupt ecosystem dynamics (Schröder et al. 2012), the natural food web in Pyramid Lake remains intact. Tui Chub *Siphateles bicolor*, are a large-bodied minnow also native to the lake that remains the main forage species for LCT, helping LCT achieve impressive sizes (Sigler and Sigler 1987, Budy et al. 2021). However, contemporary (1983 to 2023) surveys suggest the Tui Chub population in Pyramid Lake is declining (Budy and Thiede 2022), while the mechanism of decline remains unclear.

A better understanding of the cause of the observed decline in Tui Chub abundance is imperative for LCT management and conservation in Pyramid Lake to avoid decoupling this historic predator-prey relationship (Heredia and Budy 2018). Given recent evidence of the catastrophic impacts of lake elevation decline to fishes in nearby terminal lakes (Dickerson and Vinyard 1999, The Nature Conservancy 2013, USGS 2015), the objective of our study was to examine potential mechanisms of Tui Chub decline in Pyramid Lake from changing lake elevation.

The first potential mechanism we tested was a loss of nearshore spawning habitat. Tui Chub use of nearshore habitat during spawning has been documented (Kimsey 1954, Bird 1975, Sigler and Sigler 1987), but additional habitat characteristics necessary for spawning, such as vegetation or sediment size, are not well understood. Additionally, the relationship between lake elevation and spatial extent of nearshore habitat has not been assessed for Pyramid Lake specifically, or many lakes at all, and will vary with lake morphology and water clarity (Hinch et al. 1991). In Chapter 2, we investigated the impact of lake elevation decline on available nearshore habitat, and whether spawning Tui Chub have specific habitat associations within the available nearshore habitat that might further limit spawning capacity. We predicted nearshore habitat would be positively correlated with lake elevation based on the assumption that less wetted area overall would correlate to less nearshore habitat. We predicted Tui Chub would select areas with higher vegetation cover based on where they have been documented spawning previously (Kimsey 1954, Bird 1975).

In Chapter 3 we investigated a second potential mechanism, the impacts of rising TDS concentrations on survival and growth of sensitive early life stages. We attempted to use an experimental approach to test the effects of increasing TDS concentration on Tui Chub hatch rates, larval growth, and larval survival which might limit recruitment. We tested 5 different TDS concentrations that ranged from freshwater sourced from the Truckee River, to the TDS concentration at which fish were no longer observed in Walker Lake (15,400 mg/L), a nearby endorheic lake that formerly had a similar fish assemblage to Pyramid Lake.

In Chapter 4, we concluded the results from both chapters to inform management actions to mitigate and anticipate Tui Chub population dynamics and maintain a healthy fishery in Pyramid Lake. In this study, we used cutting edge techniques to investigate the impacts of two common stressors affecting desert, terminal lake ecosystems in response to water extraction, habitat change and rising TDS concentrations. Additionally, our research provides basic life history information for a native species and informs conservation of other understudied native cyprinid species which have not received scientific attention in proportion to their importance to aquatic food webs and ecosystem-based fisheries management.

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CHAPTER 2

IMPACTS OF LAKE ELEVATION DECLINE ON SPAWNING HABITAT AVAILABILITY FOR A CRITICAL FORAGE FISH SPECIES IN A TERMINAL DESERT LAKE[1]

Abstract

Objective: Lake elevation decline is a global phenomenon with pronounced effects in arid regions that changes characteristics, and quantity, of nearshore habitat available to lacustrine spawners, potentially impacting recruitment and whole lake food web dynamics. Our objective was to understand the potential effects of lake elevation decline on spawning habitat for Tui Chub *Siphateles bicolor*, a lacustrine spawner and critical forage species for a valuable, native sportfish, Lahontan Cutthroat Trout (LCT), in Pyramid Lake, Nevada.

Methods: We explored Tui Chub nearshore spawning habitat requirements by associating habitat characteristics to fecund Tui Chub catch-per-unit-effort (CPUE) in a custom gill net configuration, analyzed using a generalized linear mixed effects model. We also explored nearshore spawning habitat availability at all potential lake elevations for Pyramid Lake, from a theoretical maximum elevation to desiccation using an elevation-explicit model of the basin we developed using several bathymetric and geospatial datasets.

Results: We observed a significant increase in fecund Tui Chub CPUE from 17.5-23 °C, and in habitats with more larger grain size sediment (> 2 mm). We estimated that with an additional 8 meters of decline Pyramid Lake will contain the minimum quantity of

[1] Co-Authored with Robert Al-Chokhacy and Phaedra Budy

spawning habitat out of all lake elevations considered at a 40% decrease from a realistic theoretical maximum based on morphometry.

Conclusion: A decrease in lake elevation, or an increase in lake temperatures, both probable events based on future climate scenarios and estimates of water extraction upstream of Pyramid Lake, are likely to further restrict large grain size sediment available to Tui Chub for spawning. Our results have important implications for ecological water demand in Pyramid Lake and provide managers information facilitating a science-based, and pre-cautionary approach to managing hatchery LCT to the prey base.

Keywords: Water management, desert lake, fisheries, spawning habitat

Introduction

Lake elevation decline has been shown to reduce the amount of nearshore habitat available to fish at various stages of their life cycles (Winfield 2004; Gaeta et al. 2014; Gownaris et al. 2017). This decline in habitat potentially includes spawning habitat for lacustrine spawners, who often seek large grain size sediment classes and at specific temperatures most often found in nearshore habitat (Kaufmann et al. 2014; Glassic and Gaeta 2019). Water extraction is the leading cause of lake elevation decline, second to climate change, particularly in arid regions where human demand for water often outpaces supply (Wurtsbaugh et al. 2017; Schulz et al. 2020). Habitat coupling between pelagic and nearshore benthic habitats is well-documented in lake ecosystems (Schindler and Scheuerell 2002; Walseng et al. 2006), such that nearshore habitat loss results in cascading consequences to the entire lake ecosystem, not just for species found predominantly in nearshore habitats. While nearshore habitats often comprise a small proportion of total lake habitat, they provide outsized ecosystem benefits in the form of diverse habitats for aquatic organisms, primary productivity, and thermal heterogeneity (Strayer and Findlay 2010; Vadeboncoeur et al. 2011; Vander Zanden et al. 2011).

Habitat coupling in lacustrine ecosystems is driven by trophic interactions and the reciprocity between the health of predators and prey (Vadeboncoeur et al. 2002; Heredia and Budy 2018). Habitat loss (Mesa et al. 1994), fishing pressure (Link and Garrison 2002), and non-native species introductions (Moyle 1986) all alter natural food webs, which can decrease native and desired sportfish populations (Stewart et al. 1981; Ruzycki et al. 2001). Fisheries managers often attempt to remediate decreases in sportfish through artificial supplementation, which can further disrupt historic trophic relationships (Kitchell and Crowder 1986; Vander Zanden et al. 2003). Lacustrine food webs already stressed by fishing pressure, artificial supplementation, and non-native species, may change or collapse entirely with additional stressors such as nearshore habitat loss (Tunney et al. 2012; Madenjian et al. 2013). While fisheries management has historically focused on managing the first 3 stressors listed, nearshore habitat loss is an increasing threat, particularly in arid regions prone to drought and as water demand increases.

The western United States is notorious for over-allocation of water resources, the consequences of which have been exacerbated under climate induced multi-year droughts (Cooley 2012; Dettinger et al. 2015). The western United States contains a relatively large proportion of the world's endorheic, or terminal lakes (Wurtsbaugh et al. 2017), which host many rare and endemic species (Zadereev et al. 2020). Endorheic lakes are unique waterbodies which, due to catchment geography that precludes outflow to the ocean, lose water solely through evaporation leading to long residence times. Water diversion for agriculture and development in the western United States, along with shifting precipitation regimes consisting of more precipitation as rain than snow and changes in precipitation magnitude (Trenberth 2011; Cline et al. 2020; Zhang et al. 2021), have decreased lake elevation in many endorheic lakes (Alizadeh-Choobari et al. 2016; Wang et al. 2018; Null and Wurtsbaugh 2020) likely leading to nearshore habitat loss.

The Pyramid Lake ecosystem exemplifies the tension between human water demand and conservation of irreplaceable ecosystem services (Bolingbroke 2014). Pyramid Lake is an athalassic, endorheic, descendant of historic Lake Lahontan and is home to native fishes with strong social, economic, and cultural importance. Pyramid Lake is located on Pyramid Lake Paiute Tribe (PLPT) land in northeast Nevada (Galat et al. 1981) and has declined 30 meters from 1891 to 1967 as a consequence of human water extraction, remaining depleted since (Benson and Thompson 1987; Luck 1991). Lahontan Cutthroat Trout *Oncorhynchus clarkii henshawi* is a federally Threatened species under the Endangered Species Act native to Pyramid lake that supports a valuable sport fishery for the PLPT. Naturally spawning LCT were once extirpated from Pyramid Lake as a result of dewatering that limited fish movement to spawning habitat in the Truckee River, the primary river input to Pyramid Lake (Sigler et al. 1983; Al-Chokhachy et al. 2020). Lahontan Cutthroat Trout have primarily been maintained in the lake through hatchery supplementation since the 1970s, and conservation efforts have led to natural spawning and recruitment occurring for nearly a decade (Al-Chokhachy et al. 2020).

Despite hatchery supplementation of LCT (Coffin and Cowan 1995) and non-native species introductions (Heredia 2014) which can disrupt ecosystem dynamics

(Schröder et al. 2012), the natural food web in Pyramid Lake remains intact. The Tui Chub *Siphateles bicolor* is a large-bodied minnow also native to the lake (Appendix A for species description) that remains the main forage species for LCT, contributing to the impressive sizes achieved by the trout (Sigler and Sigler 1987; Budy et al. 2021). However, contemporary (1983 to 2023) surveys suggest the Tui Chub population in Pyramid Lake is declining (Budy and Thiede 2022), but the mechanism of decline is not well understood. Tui Chub use of nearshore habitat during spawning has been documented (Kimsey 1954; Bird 1975; Sigler and Sigler 1987), but habitat association within nearshore habitats, and the impacts of lake elevation decline on the quantity of nearshore habitat in Pyramid Lake, has not been studied.

Given our understanding of this important ecosystem and recent evidence of the catastrophic impacts of lave elevation decline to fishes in nearby terminal lakes where Tui Chub once were present (Lopes and LaRue Smith 2007; The Nature Conservancy 2013), our overall goal was to determine if spawning habitat loss due to lake elevation decline may be limiting recruitment and contributing to the observed decline in Tui Chub. Our objectives were to: 1) investigate Tui Chub spawning habitat associations to understand use of specific habitat characteristics that might restrict Tui Chub spawning capacity within nearshore habitats, and 2) quantify the relationship between lake elevation and the amount of likely Tui Chub spawning habitat available using an elevation-explicit model (EEM) of the Pyramid Lake basin and the spawning habitat association model from Objective 1. We predicted Tui Chub would select areas with higher vegetation cover based on documented spawning in other systems (Kimsey 1954; Bird 1975). We predicted that nearshore habitat (defined herein as < 15 m) would decline directly with lake elevation based on the assumption that less wetted area overall will correlate to less nearshore habitat (Kaufmann et al. 2014).

Methods

Study Area

Pyramid Lake is the largest remnant of pluvial Lake Lahontan which, at its maximum, covered northwestern Nevada, southeastern Oregon, and northeastern California (Hamilton-Galat and Galat 1983). Pyramid Lake is currently the deepest athalassic (i.e., inland saline) lake in the western hemisphere with a maximum depth of 106 m (PLPT, unpublished data). The Truckee River, which originates in Lake Tahoe and spans 169 river km to terminate in Pyramid Lake, provides an estimated 80% of the inflow, with precipitation and intermittent streams comprising the rest (Kramer 1988; Galat 1990). The Pyramid Lake fish community consists of five documented species, four native species (Tui Chub; Tahoe Sucker *Catostomus tahoensis*; LCT; Cui-ui *Chasmistes cujus*), two federally threatened or endangered species (LCT and Cui-ui), and one non-native species (Sacramento Perch *Archoplites interruptus*) (Vigg 1981).

The lake is classified as alkaline at a pH around 9.1, moderately saline at 4.79 PSU and an average 5,647 mg/L of TDS as of January 2019 (PLPT, unpublished data). Pyramid Lake productivity is classified as mesotrophic with low productivity for a warm, saline lake, but high productivity compared to freshwater lakes of similar size (Galat et al. 1981). The lake is monomictic with one stratification event typically lasting from May to November and mixing in December (Galat et al. 1981).

Diversion of the Truckee River for irrigation and development began in 1905 with the completion of the Derby Diversion Dam, and diversions have only intensified with prolonged drought and increasing irrigation and development demands in the area (Luck 1991; Fockler 2007). Diversion of the primary water source to Pyramid Lake, and drought, have decreased lake elevation by 30 m from 1,178 to 1,159 masl (Benson and Thompson 1987; USGS 10336500 Pyramid Lake, Nixon, NV) as evaporative loss exceeds water input (Luck 1991). Low lake elevation in Pyramid Lake is believed to already limit LCT growth but the mechanism of limitation is not well understood (Budy and Thiede 2022).

Spawning Habitat Association Model

We assessed habitat associated with fecund Tui Chub CPUE, used as a proxy for Tui Chub spawning activity, in 2023 from May through August, the suspected peak Tui Chub spawning window (Kucera 1978), using a study design based on a pilot study conducted in 2022 (Appendix B; Figure A-1; Figure A-2).

Site Selection

We sampled 21 unique sites from May through July (Figure 2-1). We chose sites that provided systematic coverage of the nearshore area in an attempt to capture the range of habitat types available without *a priori* knowledge of habitat distribution. We attempted to spread effort evenly across the sampling period, but often the timing of sampling was dictated by weather.

Fish Sampling

We deployed a gill net sampling configuration at each sampling event of 12 custom gill nets each composed of 2 panels of the same length as AFS standard core mesh gill net panels (Miranda and Boxrucker 2009), where each panel is composed of 1 of the 6 smallest mesh sizes out of the 8 mesh sizes used in AFS standard core mesh gill nets. We chose to use the 6 smallest mesh sizes based on observations from 2022 that the smaller mesh sizes alone capture the spectrum of fecund Tui Chub sizes. We set 3 of the custom gill nets per depth range out of a series of 4 depth ranges, 0-5 m, 5-10 m, 10-15 m, and 15-20 m, for 12 total. Within each depth range, all 6 mesh sizes were represented across the 3 nets to reduce sampling bias between the depth ranges based on capture efficiency of a particular mesh size. We rotated the set order of the nets within each depth range between sampling events, for a total of 3 possible set order configurations, to eliminate a confounding effect of depth on mesh capture efficiency in our model. We set nets perpendicular to shore attempting to maintain a straight line (Figure 2-2). The custom gill net configuration confers several advantages for studying habitat of smaller bodied fish in a lacustrine system, principally, it reduces bycatch of larger, often limited take species, focuses effort on the species of interest, and allows finer resolution of data at a larger spatial scale. All nets were ordered from Duluth Nets (Duluth Nets Inc., Duluth, MN, USA).

We enumerated and assessed captured Tui Chub for total length, fecundity, and sex. We enumerated fish at the panel level, as opposed to the net level, to capture CPUE by mesh size. We expressed gametes for every fish to assign a fecundity score (fecund/non-fecund) and assigned a sex of male, female, or unknown based on the gametes expressed. We confirmed our field methods to determine fecundity and sex on retained fish in 2022. We also assigned morph type, *pectinifer* or *obesa*, based on a field method developed in 2022 (Appendix C; Figure A-3; Figure A-4).

Habitat Sampling

We assessed sediment size class percent composition, vegetation height, and percent vegetation cover by SCUBA survey when possible, or hydroacoustic data collected with a BioSonics DT-X echosounder (BioSonics Inc., Seattle, WA, USA) otherwise. We collected temperature data with Onset HOBO Waterproof 64K Pendant Temperature Loggers (Onset Inc., Bourne, MA, USA) and compatible Onset accessories and software.

We aligned diving transects as close as possible to the position of our net sets based on GPS locations recorded on a Garmin GPSMap 943 Fishfinder (Garmin Ltd. Olathe, KS, USA) during net deployment. We began our dives at the deepest net in a given transect and followed a compass heading towards shore that provided the best overlap of the gill net GPS locations on the fishfinder, covering as many nets as possible based on a combination of time and diver safety constraints. Divers visually estimated sediment size class percent composition, percent vegetation cover, and 5 vegetation height measurements every 1.5 m of depth change in proportion to the prevalence observed for that depth range (*sensu* Beauchamp et al. 1994). We used a modified Wentworth scale to classify sediment size class composition in all SCUBA surveys (Wentworth 1922).

We aligned hydroacoustic transects over the location of our gill nets based on the same fishfinder GPS locations, up to 5 meters, the minimum depth to safely operate the echosounder equipment when deployed at 1 m below the surface. We collected our data based on manufacturer recommendation (BioSonics Inc., personal communication) for sediment, bathymetry, and vegetation surveys, -130 dB threshold and a ping rate of 2 pings/s.

We set temperature loggers directly on the shallow end of every net, logging hourly. We also recorded the shallow and deep end of each net to calculate average benthic slope.

Data Processing

We converted hydroacoustic data from pings to bathymetry, vegetation cover, vegetation height, and sediment size class values using BioSonics Visual Aquatic software. To determine bathymetry, we used the bottom detection analysis with a rising edge threshold of -35 dB. In areas where the bottom was too soft to be detected, we performed manual edits that most logically interpolated the gaps based on visual assessment of the entire transect file. To determine vegetation cover and height, first we completed a feature extraction analysis and then a plant detection analysis with a -60 dB threshold setting, a .1 m minimum detection height, and a 14.6 m maximum detection depth. We chose a -60 dB threshold and .1 m minimum detection height as conservative settings for plant detection to reduce overestimation of vegetation cover and height, a common problem in systems with soft sediments (BioSonics Inc., personal communication). The maximum detection depth corresponds to the maximum depth we observed macrophyte growth during our dive surveys.

We performed a bottom type principal component analysis (PCA) starting with a k-means cluster value of 8, corresponding to the number of sediment size classes from the modified Wentworth scale that we used during SCUBA surveys. We then performed iterative PCAs, dropping a single cluster each time, until we were able to reliably assign sediment size class to each cluster based on our SCUBA surveys. We assigned sediment size class from the SCUBA surveys by first using the map view in Visual Aquatic to visualize the distribution of each cluster. We then targeted areas on the map where a single sediment size class made up > 50% of the composition in our SCUBA surveys. If a single cluster did not compose >50% in 3 or more of these areas in the hydroacoustic data, or a cluster number could be classified as more than 1 sediment size class based on this method, we reduced the k-means cluster value by 1 and observed the new PCA cluster distribution. Once an analysis passed these initial checks, we plotted clusters by depth to examine depth distributions and find a correlation to the depth distributions observed during our SCUBA surveys. Through this process, we were able to reliably discern the 3 most prevalent sediment size classes from our SCUBA surveys, sand, mud, and silt, in our hydroacoustic data.

We assigned fecund Tui Chub CPUE at the panel level (3 m), and habitat metrics at the net level (6 m). Our habitat metrics included sediment size class percent composition, vegetation cover, vegetation height, average temperature, and average benthic slope. We calculated values for nets that were classified with SCUBA data, by averaging over all estimates for every SCUBA survey depth range within the nearest SCUBA transect that intersected the net depth range. Each diver recorded data for the width of their wingspan on every dive, such that for every recorded depth range there were two independent estimates. For nets that we classified using hydroacoustic data, we calculated the average sediment size class percent composition, vegetation height, and vegetation cover from all pings within the depth range for the transect overlapping the net, or within 0.2 m depth for nets that had no pings fall within range. We converted average sediment size class percent composition estimated using either method into sediment groups based on the Coastal and Marine Ecological Classification Standard (CMECS) (NOAA 2012), first into subgroup, then group, and finally into modified groups specific to this study to reduce the number of model parameters (Table 2-1). For all nets, we calculated benthic slope as the change in depth from minimum to maximum depth of the net over the length of the net. We included benthic slope as a proxy for “cove-like” areas formed by shoreline outcroppings that served as windbreaks, which we hypothesized Tui Chub might use for spawning to protect eggs from wave action. We assigned average temperature to a net as the average temperature recorded in the temperature logger placed on the net for the duration of time the net was set.

We classified the majority, 65%, of our nets using SCUBA, and the other 35% with hydroacoustic data. Most of the habitats we were unable to survey by SCUBA were deep with low gradient benthic slopes, which are typically habitats with minimal vegetation and small grain size sediment that could be reasonably characterized by hydroacoustic data. Of the nets surveyed by hydroacoustic technology, 95% had a median net depth between 9.35-19.15 m, an average median net depth of 15.16 m, and a minimum median net depth of 6.55 m. Of the SCUBA surveys we conducted in other habitats at these depths (n=332), the overall sediment size class percent composition was 93% small grain size sediment classes (<2 mm), silt, clay, or sand , 7% large grain size sediment classes (>2 mm), sediment larger than small gravel, and an average percent vegetation cover of 16.6% overall.

Statistical Analysis

We used a truncated Poisson generalized linear mixed effects model (David and Johnson 1952), with a hurdle model for zero-inflation (Feng 2021), to model fecund Tui Chub habitat association. The truncated Poisson distribution only models non-zero data, while the accompanying hurdle model estimates the probability of zero data. We chose to use a hurdle model to control zero-inflation in this model based on an observation of zero-inflation in the residual pattern of the same model using only a Poisson distribution. We used count of fecund Tui Chub by panel (n=504) as our response with an offset of log transformed effort, functionally turning our response into CPUE (Parry 2018). We included CMECS modified group, percent vegetation cover, temperature, mesh size, and slope as fixed effects. We log-transformed, centered, and scaled percent vegetation cover and slope before including them in the model, adding 0.9 to all values to allow log-transformation of zero values. Based on a plot of the fecund Tui Chub CPUE versus temperature and mesh size, we chose to include both as polynomials in the model. We included site, and net nested within site, as random effects. We used package DHARMa (Hartig 2022) to examine the residual patterns for normality and heteroskedasticity and found no clear deviations.

We used likelihood ratio tests from the package lmtest (Achim Zeileis 2002) to test for statistical significance ($\alpha = 0.05$) of each model subset to determine if a reduced model would be more appropriate. We checked for collinearity before including each input variable with ggpairs from package GGally (Schloerke et al. 2021). We decided not to include vegetation height in the final models based on high correlation with percent vegetation cover (Pearson correlation coefficient = 0.583), and temperature (Pearson correlation coefficient = 0.447). We assessed multicollinearity with package performance (Lüdecke et al. 2021) and found low correlation for all parameters.

Elevation Explicit Model (EEM)

Data Acquisition

We acquired data to build an EEM of the Pyramid Lake basin from three sources. We supplemented bathymetric data provided courtesy of the PLPT and the Pyramid Lake Bathymetric Mapping and Cultural Debris Survey, with hydroacoustic surveys conducted in the summer of 2022, to achieve full bathymetric coverage of present-day Pyramid Lake. The map has a 2-meter resolution and covers the majority of present-day Pyramid Lake, with a small gap in coverage at the northernmost extent of the lake.

To supplement the bathymetric map provided by PLPT, we used a BioSonics DT-X echosounder (BioSonics Inc., Seattle, WA, USA) to survey the perimeter of the lake from 5-30 m of depth along transects perpendicular to shore, spacing transects a maximum of 500 meters apart. We chose the maximum survey depth to align with the maximum extent of our nets in 2022, and the minimum survey depth again based on safe operation of the echosounder equipment. We used the triangulated linear interpolating approach from the built-in gridding function in BioSonics Visual Aquatic software to interpolate between collected pings to generate a bathymetric map solely based on our data, we then eliminated all areas of our bathymetric map that overlapped with the bathymetric map provided by the PLPT and mosaiced the two datasets together. We converted the depth data to elevation in meters above sea level (masl) by subtracting bathymetric values from the surface elevation of the lake at the time bathymetric data was collected (*sensu* Glassic and Gaeta 2019) to create a bathymetric map in units of elevation (masl) with full coverage of the present-day extent of the lake, hereafter referred to as the bathymetric map.

We acquired 1/3rd arc-second Digital Elevation Models (DEM) through the USGS 3D Elevation Program that covered Pyramid Lake, and a minimum of 23 km around Pyramid Lake, at a 10 m resolution, to model the elevation profile of currently exposed, former lakebed.

Model Construction

We eliminated all flat water, and areas that overlapped with the bathymetric map from the DEMs, and then mosaiced the DEMs to the bathymetric map. The raster that resulted from the mosaic was converted to point data that stored elevation as an attribute. We performed inverse distance weighting on the point dataset to populate any areas with missing data and then converted the dataset back to raster format. We then reduced the raster dataset to elevations ≤ 1,202 masl, the elevation at which Emerson Pass north of Pyramid Lake would overflow into the Smoke Creek Desert Basin, a phenomenon that has not been observed by modern humans, and an elevation at which Pyramid Lake would be subsumed by Lake Lahontan (Adams et al. 2008). The reduced raster dataset is the final EEM (Figure 2-3) and describes the bathymetry of the lake from a theoretical maximum elevation within the Pyramid Lake basin, to desiccation. Winnemucca Lake, a dry lakebed directly east of Pyramid Lake, was connected intermittently to Pyramid Lake until 1939 when it completely desiccated due to diversion of the Truckee River (Hardman and Venstrom 1941; Williams 2001). Winnemucca Lake has historically been connected to Pyramid Lake at lake elevations >1,178.5 masl, and accordingly it is included in the EEM from 1,178.5 to 1,202 masl. When connected, the surface elevations of

Winnemucca Lake and Pyramid Lake were not necessarily equal. Discrepancies between the elevation of the two lakes are believed to stem largely from shifts in sediment in the Mud Lake Slough sill through which water passes from Pyramid Lake into Winnemucca Lake (Adams and Rhodes 2019). For simplicity in our analyses, we have assumed that at any elevation where the two lakes could be connected their surface elevations are equivalent. The EEM has a 10 m resolution commensurate with the lowest resolution of input data.

We manipulated and constructed all spatial datasets and models in software ArcGIS Pro (v 3.1.1).

Analyses

We analyzed the relationship between elevation and core Tui Chub spawning habitat, and the percent of the total lake habitat functioning as core Tui Chub spawning habitat. We used the depth at which 95% of the fecund Tui Chub were caught for both years of fish sampling, <15 m ($n_{\text{fecund Tui Chub}}$=4,075), to delineate core Tui Chub spawning habitat in our analyses. We evaluated elevations that ranged from the highest elevation in the EEM (1,202 masl), to an elevation when the lake begins to completely desiccate (1,085 masl), every meter for a total of 118 elevations evaluated. We have not included elevations from 1,085 to 1,055 masl in our analysis because we assumed there would no longer be any native fish populations due to extremely high TDS concentrations and disconnection from river spawning habitat.

To calculate habitat area, we converted the EEM to an integer raster to generate an attribute table with the number of raster cells per meter of elevation. We generated one hundred and eighteen new integer rasters from the converted EEM using the Con geoprocessing tool to eliminate 1 m of elevation for each evaluated elevation. In each new raster dataset, we summed and multiplied the number of cells within the core Tui Chub spawning habitat by 10 m^2 to acquire the area of core Tui Chub spawning habitat. All cells in the new integer raster dataset were summed and multiplied by 10 m^2 to acquire total lake area.

We calculated the percent of the total lake habitat functioning as core Tui Chub spawning habitat at each evaluated elevation using the following equation, where E is the evaluated elevation of interest:

$$\frac{(area\ of\ core\ Tui\ Chub\ spawning\ habitat)_E}{(area\ of\ total\ lake)_E} X\ 100$$

We manipulated and analyzed summary statistics of each raster dataset in ArcGIS Pro (v 3.1.1) and performed calculations in Microsoft Excel.

Results

Spawning Habitat Association Model

We caught 3,984 Tui Chub total, 1,470 male, 934 female, and 1,580 which did not express gametes and were classified as non-fecund. Female fecund Tui Chub were less numerous but achieved larger sizes than males, and non-fecund fish were present at all size classes (Figure 2-4). Our top model of spawning habitat was the most complex model and included CMECS modified group, temperature, percent vegetation cover, benthic slope, and mesh size as fixed effects (Table 2-2).

In the conditional component of our truncated Poisson generalized linear model, we estimated an increase of fecund Tui Chub CPUE with increasing percent of large grain size sediment, from a CMECS modified group that is composed of >90% mud sediment size class, to one that is composed of >30% gravel sediment size class (Table 2-3). Our β coefficients for the CMECS modified groups can be interpreted as relative changes in fecund Tui Chub CPUE when compared to the reference group, or intercept, Gravel Mixes. For instance, we estimated fecund Tui Chub CPUE is 0.17 less on average in habitats classified in the Gravelly CMECS modified group, when compared to those classified in the Gravel Mixes group, not -0.17 in habitats classified as Gravelly. The test statistics for each modified group, other than Gravel Mixes, are computed relative to the distribution of data in the Gravel Mixes reference group. While all CMECS modified groups displayed a decrease in CPUE in relation to the reference Gravel Mixes group, only Mud demonstrated a significant decrease ($\alpha = 0.05$).

We estimated a significant increase of fecund Tui Chub CPUE with increasing temperature until ~ 21.5 °C when we estimated Tui Chub CPUE would decline with increasing temperature (Figure 2-5). The pattern we observed suggests spawning Tui Chub prefer temperatures from 17.5-23 °C, but tolerate temperatures spanning ~15 – 25 °C. We also estimated a significant positive relationship of 0.38 CPUE with percent vegetation cover and a significant negative relationship with slope of -0.17 (Figure 2-5). We estimated a net decrease in fecund Tui Chub CPUE from the smallest mesh size to the largest mesh size, with a maximum between them (Figure 2-5). In the case of mesh size, the magnitude of the estimate does not translate to a real mesh size, because the mesh size input variable was coded as integers that only correspond to mesh size.

We used a hurdle model to model the probability of a fecund Tui Chub CPUE outcome of zero at all parameter conditions using a logit distribution. Only temperature and mesh size were significant in our hurdle model suggesting these parameters are the key drivers of fecund Tui Chub presence or absence (Table 2-3).

Elevation Explicit Model

We modelled a general increase in core Tui Chub spawning habitat from 1,202 to 1,167 masl, with the maximum increase for all evaluated elevations within this range at 1,183 masl and 167% of historical core Tui Chub spawning habitat (Figure 2-6). We defined historical core Tui Chub spawning habitat as the core Tui Chub spawning habitat at the maximum evaluated elevation. From 1,166 to 1,120 masl in our model, core Tui Chub spawning habitat declined from historical, with the minimum core Tui Chub spawning habitat for all elevations at 1,152 masl, a decrease of 40% from historical. From 1,119 to 1,113 masl, we predicted a slight increase in core Tui Chub spawning habitat at 104% of historical, before returning to a deficit from 1,112 to 1,088 masl at 21% less than historical. At elevations below 1,088 masl, we estimated a steady increase in core Tui Chub spawning habitat, but only because at these elevations the entire lake becomes shallow habitat unsuitable for other fish species (e.g., LCT) before reaching desiccation at 1,055 masl. The percent core Tui Chub spawning habitat as a percent of historical core Tui Chub spawning habitat is estimated at 77% for the current lake elevation of 1,160 masl.

The percent of the lake functioning as core Tui Chub spawning habitat out of the total lake area, remains below 20% until 1,120 masl (Figure 2-6). The percent core Tui Chub spawning habitat remains close to 20% until 1,098 masl when the percent core Tui Chub spawning habitat begins to rapidly increase, again because the entire lake becomes shallow unsuitable habitat. The percent core Tui Chub spawning habitat of total lake area is estimated at 11.37% currently.

We manipulated and analyzed all data for our habitat association model and generated all figures for both the habitat association model and EEM, in program R (v4.2.3).

Discussion

To our knowledge, we have conducted the most rigorous investigation of Tui Chub spawning habitat association to date (Kimsey 1954; Bird 1975; Cooper 1982,), enhancing scientific understanding of the life history and habitat needs of a species that serves as a critical component of ecosystems throughout the Intermountain West (Sigler and Sigler 1987), including Pyramid Lake, NV (Budy et al. 2021). Based on our spawning habitat association model it appears Tui Chub spawn in nearshore habitats at some of the warmest temperatures observed in the lake. Tui Chub spawning was also associated with any type of structure, be it larger grain size sediment or vegetation, which supports previous research. We did not observe the relationship we predicted with benthic slope, but the significant negative relationship we did observe could be a response to predator pressure. We also produced an EEM of the Pyramid Lake basin which, when combined with our spawning habitat association model, predicts consequences of lake elevation decline on spawning habitat available to Tui Chub within the Pyramid Lake basin.

Based on long-term temperature monitoring data from Pyramid Lake, we know the temperature range we associated with fecund Tui Chub CPUE in our model only exists at specific times and depths, a factor likely dictating the timing and duration of spawning. Thus far long-term temperature data indicates temperature regimes in Pyramid Lake are stable, although there is missing data over the sampled timeframe, and notably none from the last 5 years. Given the importance of temperature for Tui Chub spawning, consistent monitoring of the Pyramid Lake thermal regime is essential to record annual shifts in nearshore lake temperatures and predict consequences for Tui Chub recruitment. If average lake temperatures begin to rise, as we expect under future climate scenarios (van Vliet et al. 2012), the time of year, duration of spawning, and/or depth range at which spawning occurs may change.

We observed a significant positive relationship between larger grain size sediment and fecund Tui Chub not previously documented in the literature. The association of spawning Tui Chub with structure, presumably for egg attachment, is the most common reproductive strategy documented for freshwater fish with demersal, adhesive eggs (Patzner 2008) and complements accounts of eggs attached to both gravel and vegetation believed to be from Tui Chub (Kimsey 1954; Cooper 1982). Ostensibly, this reproductive strategy aims to prevent burial in small grain size sediments where conditions can become anoxic (Patzner 2008). Indeed, a small-scale experiment investigating the relative success of Tui Chub eggs attached to vegetation, submerged in small sediment, or in an empty jar, documented hatch only in treatments where eggs were not submerged in small sediment (Kimsey 1954). Recruitment could decline if Tui Chub are forced to migrate to deeper habitats with even less large grain size sediment to find suitable spawning temperatures.

While we did observe a positive significant relationship between fecund Tui Chub and vegetation cover, the relationship was not as strong as we anticipated based on the literature, and our confidence intervals nearly overlapped zero. Previous investigation of Tui Chub spawning habitat was not conducted at Pyramid Lake, and the discrepancy between our data and previous work could stem from a difference in Tui Chub spawning strategies in response to available structure types, or simply a potential overestimation of the importance of vegetation cover in previous research based on sampling methods that were qualitative and opportunistic (Kimsey 1954; Bird 1975). In addition, we did not differentiate between different species of macrophytes and periphyton, which could be important defining preferred spawning vegetation (Snickars et al. 2010).

We hypothesized eggs would have lower mortality behind wind breaking structures associated with steeply graded habitat, as documented in other lacustrine spawners (Eshenroder et al. 1995). The negative relationship we observed between fecund Tui Chub and benthic slopes suggests Tui Chub are responding to a different aspect of slope in the environment, potentially predation pressure. Evidence exists that prey species alter spawning habitat selection in response to perceived predation risk (Thomson et al. 2006), and adult LCT in Pyramid Lake have been empirically associated with areas of high benthic slope (Heredia 2014). In fact, the iconic Pyramid Lake ladder fishery is born of the idea that an angler needs to launch bait just past where the shallow areas drop off to where LCT are presumably foraging (Santella 2021). Larger grain size sediment is more exposed in high benthic slope habitats, discussed below, thus if Tui Chub are avoiding these habitats due to predation, access to large grain size sediment would be further limited.

Based on the results of our EEM, with an additional 8 meters of lake elevation decline, Pyramid Lake would reach the minimum quantity of core Tui Chub spawning habitat of all elevations we evaluated at 40% less than the theoretical maximum based on morphometry. In our EEM we defined core Tui Chub spawning habitat based on the relatively coarse description of the depth range where we caught 95% of fecund Tui Chub in our study. Given the correlation between depth and temperature, and the importance of temperature in our habitat association model, the depth range provides a useful beginning metric of Tui Chub spawning habitat quantity. Based on our EEM alone, it is reasonable to assume further lake elevation decline past 8 meters would be equally as effective at producing more Tui Chub spawning habitat as increasing lake elevation, but this assumption would fail to consider the negative effects of lake elevation on TDS concentrations and LCT spawning migration success. Considering these consequences, our EEM strongly suggests that if managers wish to increase the quantity of Tui Chub spawning habitat through water management, lake elevation would need increase.

Increasing sediment grain size also predicted fecund Tui Chub in our habitat association model, but the factors determining the temporal and spatial distribution of sediment grain size in the nearshore are more complex than for temperature. Overall deposition of sediment in lakes is a function of lake volume, retention time, and external loading. Pyramid Lake is a large, deep, endorheic lake, with high retention time and therefore retention of sediments. External loading refers to sediment input from the watershed which can be altered by reservoir and land management practices (Walling 2009). The spatial distribution of sediment grain sizes within lakes is predominantly dictated by the interplay between river currents, wave action, and benthic slope. River currents create a fan of deposited allochthonous sediment where larger grain size sediments are deposited closest to the river inlet and smaller grain size sediments further

(Håkanson and Jansson 1983). Wave action resuspends and erodes sediment to the depth of the wave base, with smaller grain-size sediments deposited deeper than larger grain-size sediments due to the complementary processes of sediment winnowing and focusing (Vincent et al. 2023). Wave velocities, and therefore the wave base, increase with increased fetch and increased wind speed. Increasing percent benthic slope decreases the likelihood of smaller sediment deposition, with no small grain size sediments typically found at slopes >4% (Håkanson and Jansson 1983). Accordingly, larger sediment is more exposed in shallow and/or steep areas where smaller sediment has been eroded and resuspended by wave action. Smaller sediment is then redeposited in deeper and/or flatter areas, where wave action is not present, concentrating smaller sediment and burying larger sediment.

In our EEM analyses for Pyramid Lake, fetch decreases directly with lake area and elevation in Pyramid Lake, such that at constant wind velocity, decreasing lake elevation will decrease wave velocity and the exposure of larger grain size sediments in the nearshore area. Based on our SCUBA surveys, large grain-size sediment (>0.2 mm) is already in low abundance in the nearshore, comprising only 14.71% of all sediment, and potentially limiting spawning habitat available to Tui Chub. Lower wave velocities at lower elevations would only exacerbate the limitation. Additionally, if external loading of smaller grain size sediments increases from different watershed management practices (Walling 2009), exposed larger sediment in the Pyramid Lake nearshore would decrease further. While we cannot quantify future overall sediment quantity and characteristics in Pyramid Lake as a function of retained sediment and external loading, our EEM could be used by managers to estimate exposed larger sediments based on lake bathymetry characteristics and fetch at a particular elevation. Given the probable further limitation of exposed large grain size sediment in the nearshore with decreasing lake elevation, our estimates of core Tui Chub spawning habitat based on our coarse depth range definition are likely overestimated.

While we believe we have provided a robust assessment of Tui Chub spawning habitat association, we acknowledge there are several limitations to our study. For example, we use fecund Tui Chub catch as a proxy for Tui Chub spawning activity. The assumption that the presence of a fecund fish equates to spawning activity could be the source of some of the variability in our results. A fecund fish may be caught by our gear in one habitat, while migrating to, or from, a different habitat where spawning occurred. We chose catch of fecund fish, over methods like SCUBA or snorkel where we might actually observe spawning activity, because we believed these approaches would produce few observations, if any, given the large size and low visibility of Pyramid Lake. To date, there is no direct documentation of Tui Chub spawning activity, which continues to partially limit our understanding of their spawning habitat needs. In general, our conclusions are tempered by the fact that our study does not prove the mechanistic motivation of habitat selection by spawning Tui Chub, and rather meets the requirements for a habitat association model (Diamond 1986; Rosenfeld 2003). Nonetheless, our results suggest Tui Chub are using a habitat type in low abundance throughout Pyramid Lake that would be negatively impacted by lake elevation decline, which likely limits recruitment and is a phenomenon demonstrated by other species in other systems (Glassic and Gaeta 2019).

Our study provides a better understanding of factors driving Tui Chub abundance that can inform LCT hatchery supplementation decision, potential habitat restoration actions, and water management to ensure a healthy Pyramid Lake ecosystem. Using our models and results to anticipate Tui Chub abundance, managers can take a pre-cautionary approach when supplementing LCT to avoid a potential Tui Chub population collapse. Our results also suggest there is a need to monitor water temperature regimes to anticipate the effects of future environmental change on Tui Chub recruitment. Additionally, our results suggest habitat restoration that adds large grain size sediment in the nearshore, could provide more suitable spawning habitat for Tui Chub, and potentially increase recruitment. Finally, the finding that the lake is nearly at the minimum possible quantity of Tui Chub spawning habitat, before likely toxic concentrations of TDS, provides justification for water management that does not lead to further lake elevation decline in order to sustain or enhance the unique Pyramid Lake ecosystem as a whole. Finally, our research provides basic life history information for a native species and informs conservation of other understudied native cyprinid species which have not received scientific attention in proportion to their importance to aquatic food webs and ecosystem-based fisheries management.

Tables & Figures

Table 2-1. Coastal and Marine Ecological Classification Standard (CMECS) modified groups developed to classify sediment size class percent composition for Tui Chub spawning habitat association model in Pyramid Lake. SCUBA Sediment Size Class Percent Composition represents the criteria for each CMECS modified group based on SCUBA data collected from May-August in 2023.

CMECS Modified Group	CMECS Sediment Size Class Group	CMECS Sediment Size Class Subgroup	SCUBA Sediment Size Class Percent Composition
Gravel Mixes	Gravel Gravel-mixes		>30% Gravel
Gravelly	Gravelly		5% to <30% Gravel
Sand	Sand	Slightly-gravelly-muddy-sand Slightly-gravelly-sand	<5% Gravel >50% Sand
Sand/Mud	Muddy-sand Sandy-mud		>10% Silt/Clay <90% Silt/Clay >10% Sand <90% Sand
Mud	Mud	Slightly-gravelly-mud Slightly-gravelly-sandy-mud	>90% Silt/Clay <5% Gravel

Table 2-2. Likelihood ratio test output of model subsets used predict count of fecund Tui Chub in response to different habitat metrics in Pyramid Lake (LRT, $P \leq 0.05$). Model subsets are compared to the model subset in the preceding row with the final model (“Slope”) representing the full or most complex model. Additional Parameter is the new parameter added to the model subset in the preceding row, and Df_{LR} the difference in degrees of freedom between the model subset and the model subset in the preceding row.

Additional Parameter	Df_{model}	LogLik	Df_{LR}	χ^2	$Pr(>\chi^2)$
Null	6	-1,420.13			
Effort	6	-1,416.05	0.00	8.16	0.00*
CMECS Modified Groups	14	-1,386.13	8.00	59.83	0.00*
ln(Percent Vegetation Cover)	16	-1,374.03	2.00	24.21	0.00*
Temperature	20	-1,324.24	4.00	99.58	0.00*
Mesh Size	24	-941.18	4.00	766.13	0.00*
ln(Slope)	26	-937.19	2.00	7.98	0.02*

Table 2-3. Parameter estimates for a truncated Poisson generalized linear model using a hurdle model for zero-inflation with an offset of log effort hours to predict count of fecund Tui Chub in a custom gill net panel in Pyramid Lake (t-test, $P \leq 0.05$).

Conditional Model

Parameter	Estimate	Lower 95% CI	Upper 95% CI	p-value
(Intercept)	-2.06	-2.84	-1.28	0.00*
CMECS: Gravelly	-0.17	-0.66	0.32	0.50
CMECS: Sand	-0.52	-1.10	0.05	0.07
CMECS: Sand/Mud	-0.51	-1.06	0.04	0.07
CMECS: Mud	-0.57	-1.12	-0.01	0.04*
ln(Percent Vegetation Cover)	0.25	0.04	0.46	0.02*
Temperature	30.51	17.03	43.99	0.00*
Temperature^2	-18.44	-25.74	-11.14	0.00*
Mesh Size	-7.96	-9.82	-6.10	0.00*
Mesh Size^2	-22.15	-24.22	-20.08	0.00*
ln(Slope)	-0.32	-0.56	-0.08	0.01*

Hurdle Model

Parameter	Estimate	Lower 95% CI	Upper 95% CI	p-value
(Intercept)	-0.38	-1.97	1.21	0.64
CMECS: Gravelly	1.23	-0.40	2.86	0.14
CMECS: Sand	0.30	-1.50	2.10	0.74
CMECS: Sand/Mud	1.79	0.00	3.58	0.05*
CMECS: Mud	0.72	-0.94	2.39	0.39
ln(Percent Vegetation Cover)	-0.04	-0.5	0.43	0.87
Temperature	-54.07	-73.00	-35.14	0.00*
Temperature^2	12.26	2.34	22.17	0.02*
Mesh Size	2.71	-3.70	9.12	0.41
Mesh Size^2	24.30	15.75	32.86	0.00*
ln(Slope)	0.27	-0.23	0.77	0.29

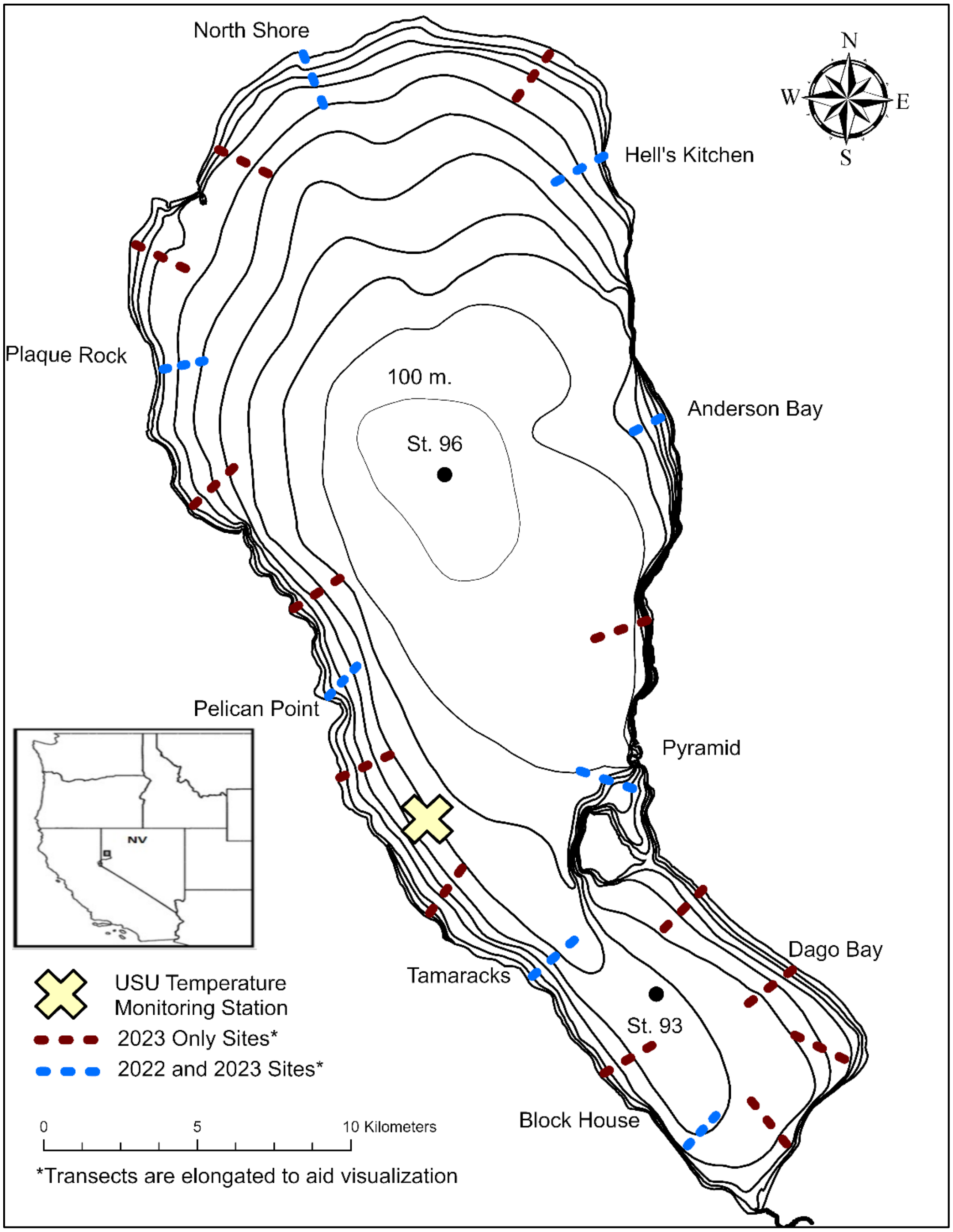

Figure 2-1. Study area map of Pyramid Lake with sites used to assess Tui Chub spawning habitat association identified. Black dots denote long-term water quality monitoring stations 93 and 96. Contour lines are every10 meters of depth. Colloquial names of fishing areas and beaches are also displayed.

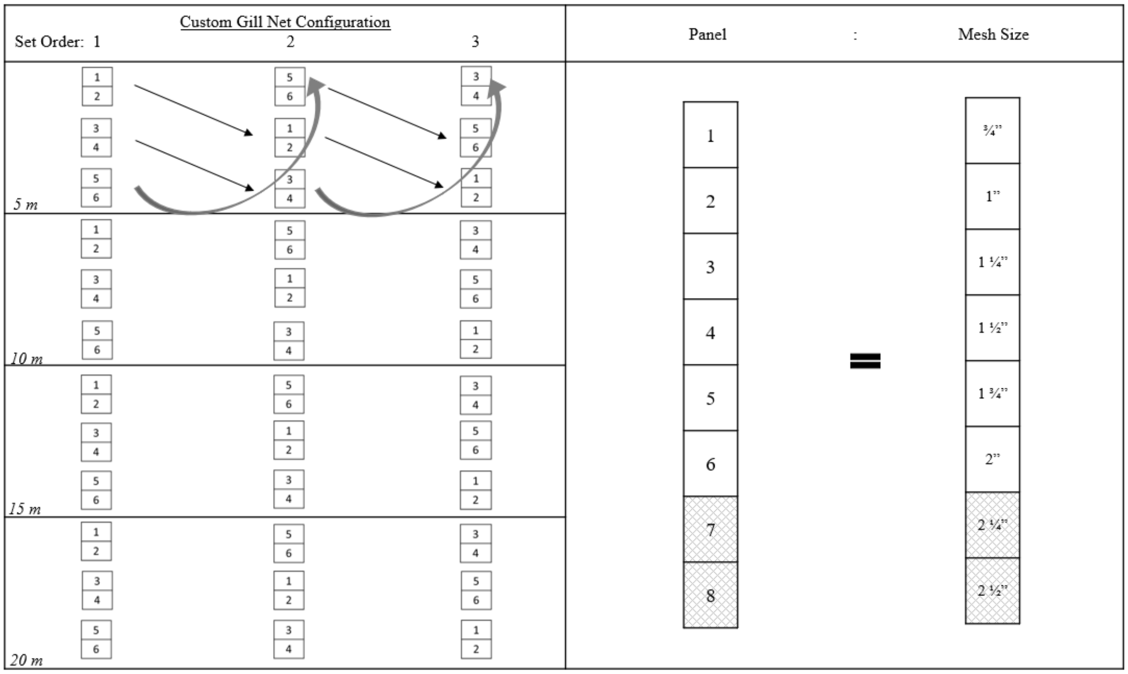

Figure 2-2. Diagram illustrating custom gill net set orders and mesh sizes used to assess fecund Tui Chub spawning habitat association from May-August 2023 in Pyramid Lake. Cross-hatched panels indicate panels from AFS standard core gill nets not used. Columns in the custom gill net configuration demonstrate 3 set orders used to vary depths sampled by each mesh size within a depth range. Arrows demonstrate the order of rotation of nets from one sampling event to the next and apply to all depth ranges below.

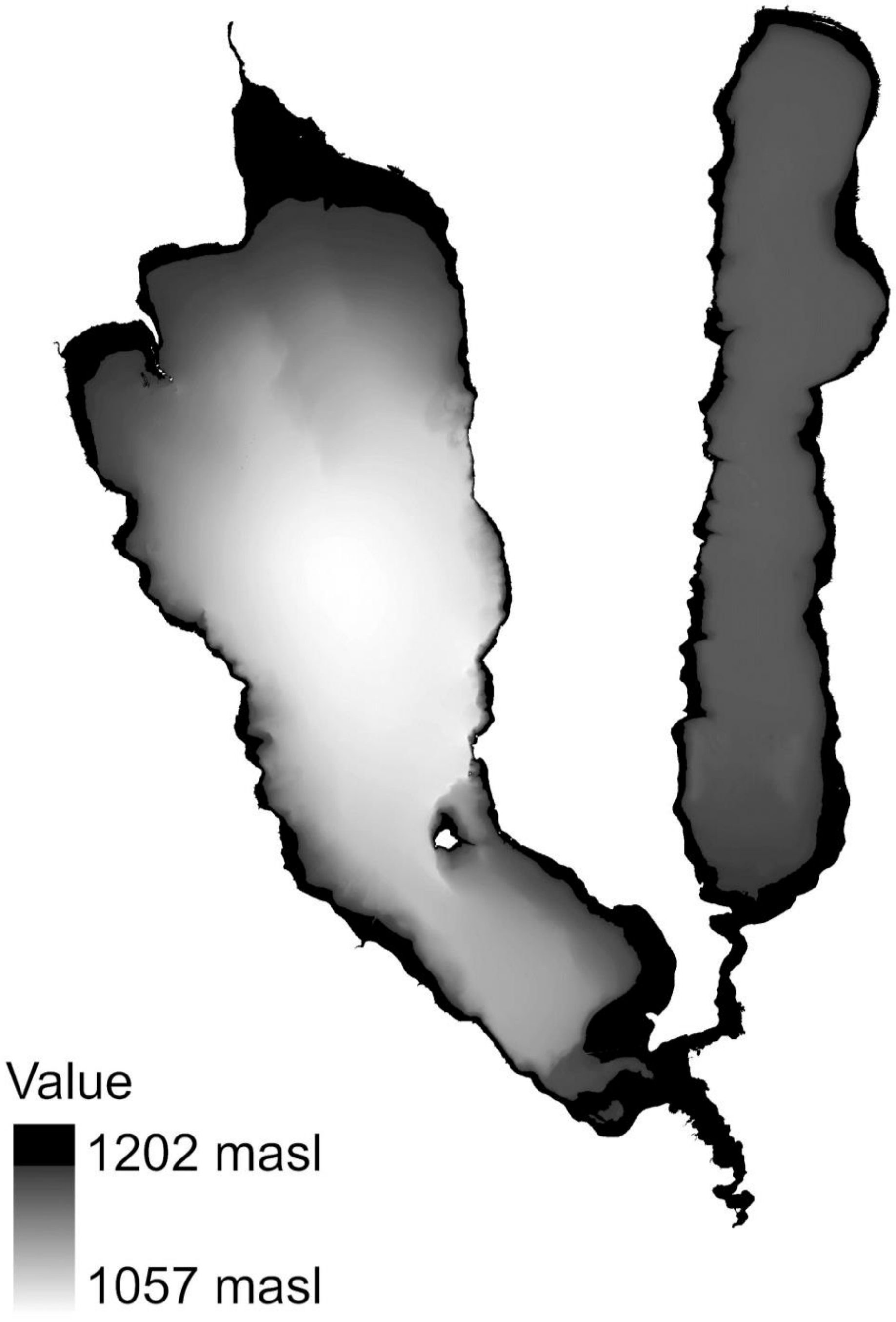

Figure 2-3. Elevation explicit model of the Pyramid Lake basin at a theoretical maximum lake elevation of 1,202 masl. The basin on the right is currently dry Winnemucca Lake and the basin on the left is present-day Pyramid Lake.

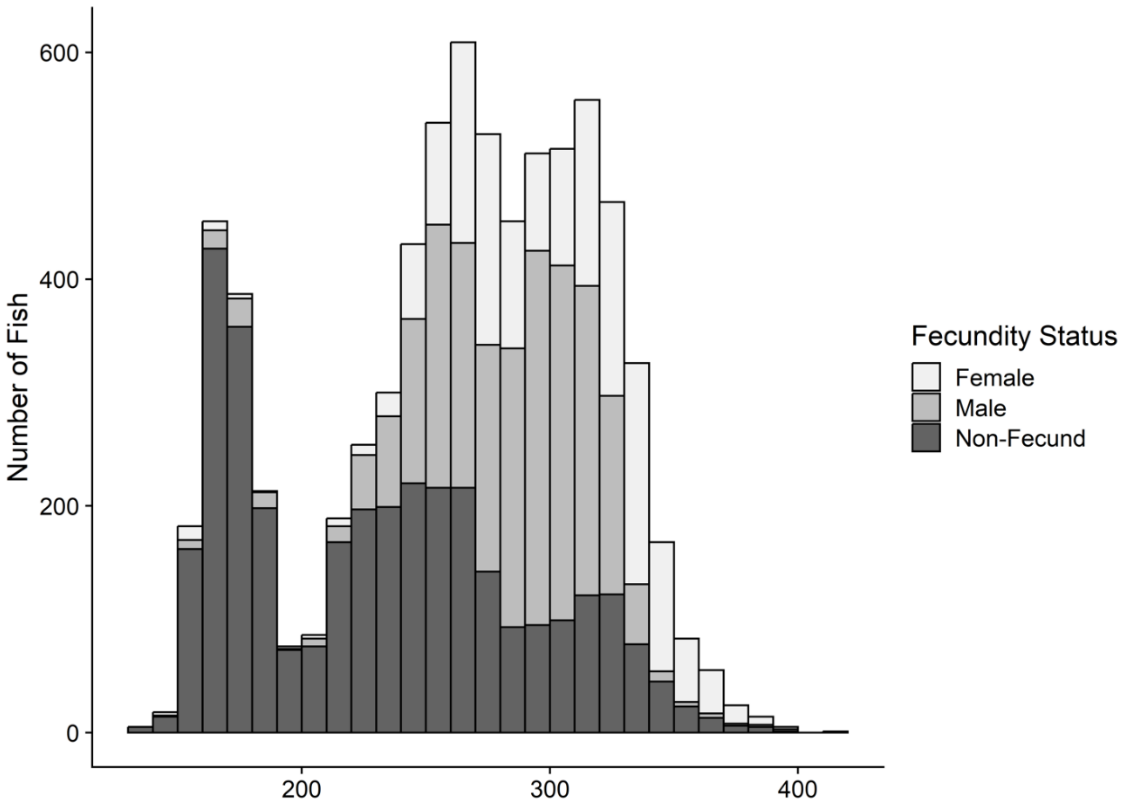

Figure 2-4. Length frequency histogram grouped by sex for all Tui Chub caught by gill net (n=7,449) from May-August in 2022 and 2023 in Pyramid Lake, NV.

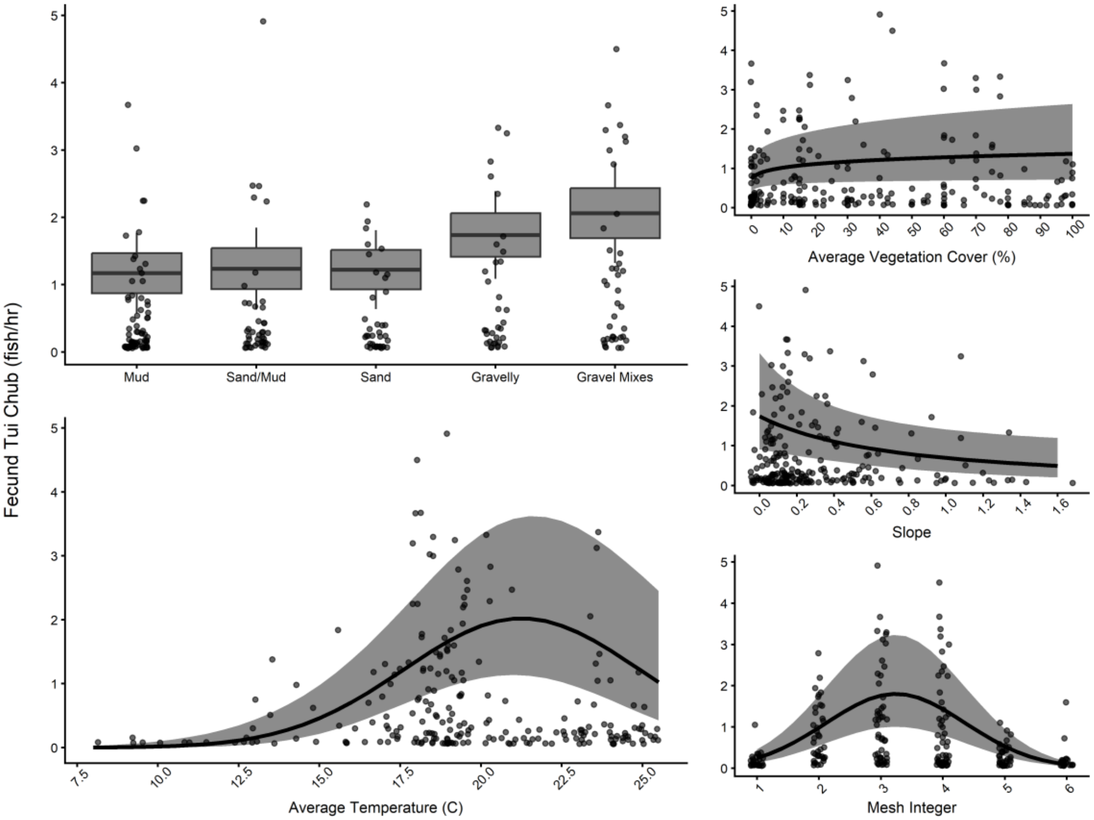

Figure 2-5. Predicted effect of conditional fixed-effect habitat parameters on fecund Tui Chub CPUE in Pyramid Lake, NV from a GLMM (conditional component generalized linear mixed-effects model: LR = -937.19, P = 0.02). The black line represents the marginal mean estimate of fecund Tui Chub CPUE for each parameter (gray shading represents a 95% confidence interval) from a model including random effects of site and net nested within site. Points represent non-zero fecund Tui Chub CPUE observed in a panel (n = 504) with a small amount of jitter added to reduce overlap. The model response was catch with an offset for effort hours, not CPUE, but points and estimated marginal means are plotted on the CPUE scale. Estimated marginal mean CPUE was predicted using 2 effort conditions.

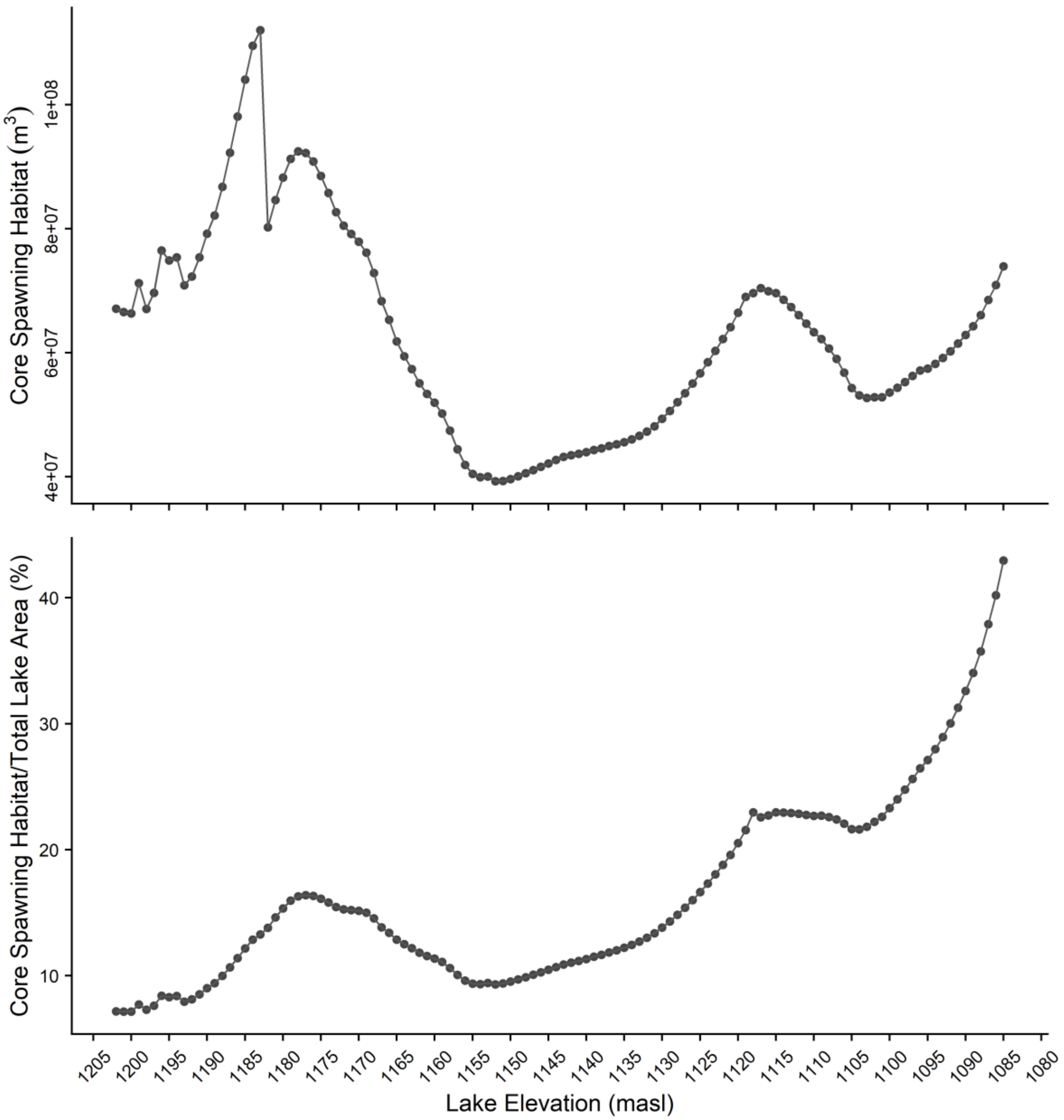

Figure 2-6. Core Tui Chub spawning habitat area (m^3) and percent of total lake area (m^3) functioning as core Tui Chub spawning habitat area (m^3) for each evaluated elevation of an elevation explicit model of the Pyramid Lake basin.

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CHAPTER 3

SMALL SCALE CULTURE TO STUDY IMPACTS OF TOTAL DISSOLVED SOLIDS ON EARLY LIFE STAGES OF TUI CHUB IN PYRAMID LAKE, NV, USA[1]

Abstract

Objective: Fish culture to study impacts of various stressors on early life success of fish is a useful technique that is not implemented widely in native cyprinid species, presumably because these species are not commonly cultured. Further, even when culture techniques have been developed, they are designed for production and not necessarily suited for experimentation. Our objective was to develop a culture technique suitable for experimentation for an understudied native cyprinid, Tui Chub *Siphateles bicolor*, and use the technique to investigate the impacts of a common environmental stressor, total dissolved solids (TDS), on early life stages.

Methods: We strip-spawned Tui Chub harvested from Pyramid Lake, NV, USA, and raised larvae in small plastic storage containers at 5 relevant TDS concentrations using sponge filters for biofiltration.

Results: We only observed larvae in the 2 lowest concentrations tested; however, we observed elevated total ammonia in most of our aquaria due to egg mortality which overwhelmed biofiltration and confounded our ability to attribute differences in hatch to TDS alone. Larvae in the highest TDS concentration where hatch was observed (the current TDS concentration of Pyramid Lake, NV) did not survive for as many days relative to the lowest concentration (freshwater from the Truckee River, NV).

[1] Co-Authored with David Ward, Robert Al-Chokhachy, and Phaedra Budy

Conclusion: The differences in larval success across treatments, despite the presence of artificially elevated total ammonia, imply Tui Chub early life stages may be currently stressed by TDS in Pyramid Lake, NV and would not be as successful at elevated TDS. We document a small-scale culture technique for Tui Chub and provide modifications to our technique which would allow better control of total ammonia in future studies. These efforts will allow experimental evaluation of the effects of environmental stressors on early life stages, or the investigation of early life requirements, of a native cyprinid species, and related species.

Keywords: experimental aquaculture, water quality, Tui Chub, water management, desert lake

Introduction

Assessing the effects of environmental stressors, or egg development needs, requires experimental fish culture that is rarely conducted, likely due to the perceived cost of implementation and lack of well-developed culture techniques for many fish species (Buynak and Mohr 1981; Rakes et al. 1999). Fish culture is typically used to bolster population declines of imperiled or desired sport fishes and necessarily aims to produce large quantities of fish. The techniques used for large scale production require large infrastructure that can be cost prohibitive, or not appropriate for experimentation (Piper et al. 1986; Bonar et al. 2011; i.e., difficult to independently replicate). Native cyprinid species present a particular challenge because documented culture techniques for these fishes are less available (Johnston 1999), and culture techniques often cannot be broadly applied across different members of this taxonomic group because of variable reproductive strategies (Balon 1975; Platania and Altenbach 1998; Kline and Bonar 2009).

Here, we present a small-scale fish culture technique for Tui Chub *Siphateles bicolor*, a native cyprinid lacustrine spawner with demersal, adhesive eggs, to investigate a common environmental stressor, total dissolved solids (TDS), for fishes in arid regions (Vigg 1981; Pimental and Bulkley 1983; Mueller et al. 2017). Large-scale culture of the Mohave Tui Chub *Siphateles bicolor mohavensis*, another sub-species of Tui Chub, has been achieved using captive breeding in a recirculating system (Archdeacon and Bonar 2009), but use of this technique would have been cost and space prohibitive for our on-site, experimental goals. There are reports of successful hatch of Tui Chub from other systems (Harry 1951; Bird 1975; Cooper 1982), but the techniques are not adequately documented to reproduce.

Tui Chub are the primary forage species for Lahontan Cutthroat Trout *Oncorhynchus clarkii henshawi* (LCT) which support a valuable sport fishery in their last lacustrine stronghold, Pyramid Lake, NV (Heredia and Budy 2018). Pyramid Lake is an athalassic, endorheic descendant of Lake Lahontan located on Pyramid Lake Paiute Tribe land in northeast Nevada (Galat et al. 1981) which has experienced significant increases in TDS concentrations since losing ~30m of lake elevation (and thus decreased volume) under human water management (Luck 1991; Jellison and Sevon 2005). The outcome of Walker Lake, another remnant of Lake Lahontan, provides warning of the potential impacts of TDS on the Pyramid Lake fish community. Until 2010, Walker Lake supported a similar fish assemblage to Pyramid Lake, including Tui Chub and LCT. By 2010 Walker Lake was deemed devoid of fish (The Nature Conservancy 2013) from a

~13,500 mg/L increase in TDS after losing 48 m of lake elevation (Lopes and LaRue Smith 2007).

The objective of our study was to (1) develop a small-scale culture technique for Tui Chub, and other species with similar reproductive strategies, that does not require large-scale captive breeding or recirculation techniques, and to use the technique to (2) experimentally determine impacts of TDS on survival and growth of early life stages of Tui Chub. For the latter, we used observations from Walker Lake to inform our treatment selection.

Methods

Water and Aquaria Preparation

We tested a gradient of TDS concentrations from a Low TDS treatment, water sourced from the main freshwater input to Pyramid Lake, the Truckee River, a Control treatment sourced directly from Pyramid Lake, and 3 artificially derived treatments, T1, T2, and T3, representing a gradient up to 15,400 mg/L, the TDS concentration at which adult Tui Chub were no longer observed in Walker Lake (The Nature Conservancy 2013). We attempted 5 replicates for each treatment with a goal of 25 total aquaria (Figure 3-1).

To acquire water with TDS concentrations above the control treatment, we filled 8, 80-gallon troughs with Pyramid Lake water, hereafter lake water, and placed them outside to evaporate to higher TDS concentrations with the same chemical composition as Pyramid Lake. We checked the troughs a minimum of every 3rd day with an Oakton 6+ TDS meter (Eutech Instruments Pte Ltd./Oakton Instruments, Vernon Hills, IL). We harvested water out of the troughs and placed it indoors to slow evaporation once a TDS concentration for one of the treatments was achieved. We used Truckee River water, hereafter river water, to dilute water on the initial aquaria set-up and throughout the experiment to account for evaporative losses. Throughout the experiment, we calibrated the meter weekly using Oakton conductivity standards and the auto-calibration function for each range we tested. We strained all water through 64 µm mesh zooplankton nets (Wildco Inc., Yulee, FL) and added ¾ tsp. of bleach for a full 5-gallon bucket to remove as much biota and detritus as possible. We did not add water to aquaria until 3 days post-bleaching. Our intention in sanitizing the water was to control for any advantages or disadvantages that could be conferred from biota existing in the water, particularly as a food source.

Given the increased conversion of ammonium to unionized ammonia, the form of ammonia toxic to fish in alkaline waters such as Pyramid Lake (Trussell 1972; Hargreaves and Tucker 2004), we began preparing AQUANEAT 10-gallon sponge filters with in-line aeration (Pet Supplies, LLC) as bio-filters for aquaria 2 months in advance of when we anticipated hatching fish in an attempt to ensure adequate denitrification. Herein, we use the term total ammonia to refer to the combined concentration of ammonium and unionized ammonia and the specific form name otherwise. We used a combination of tolerant pet store goldfish and excessive feeding of ground Skretting trout food (Skretting USA Inc., Tooele, UT) to begin nitrogen cycling. We placed enough filters for all replicates in 3 large muck buckets with a minimum of 10 goldfish per muck bucket for initial set-up. After a month, we transferred an individual filter to each 5.7-liter plastic storage container filled with tap water treated with Seachem prime water conditioner which served as our aquaria (Seachem Laboratories, Inc. Madison, GA).

Once filters were added, we began to dose the aquaria with ammonium chloride (Dr. Tim's Aquatics, LLC., Moorpark, CA) routinely according to manufacturer guidelines, and check for total ammonia concentrations with over-the-counter freshwater test kits (API, Mars, Inc.) to ensure performance of the bio-filters. We considered a filter to be cycling adequately for use in the experiment if total ammonia was reduced to 0 ppm within 48 hours. We continued dosing and checking a filter after it achieved this benchmark to maintain cycling, ceasing 3 days prior to adding eggs to aquaria.

We set up aquaria in an insulated room at the Pyramid Lake Fisheries Dunn Hatchery in Sutcliffe, NV, USA small enough to use a Toshiba 8,000 BTU portable A/C unit (Toshiba, Inc.) to cool aquaria to 15-22°C, but still providing adequate space for all experiment infrastructure and for personnel to conduct experiment duties. We began air conditioning the room 3 days prior to capturing mature Tui Chub to spawn to ensure our set-up could sufficiently cool the aquaria.

Adult Fish Capture and Strip-Spawn Preparation

We set 3 knotted mesh hoop nets overnight, each with a 25-foot leader (Duluth Nets Inc., Duluth, MN, USA), between 0 and 10 meters of depth. We injected fish that were expressing gametes with the gonadotropin Ovaprim intraperitoneally (*sensu* Ball and Bacon 1954) at the dosage recommended by the manufacturer (Syndel USA, Inc., Ferndale, WA). We ensured Ovaprim was close to the internal temperature of the fish to ensure maximum absorption. We transferred fish to small off-shore net pens immediately after injection to minimize handling time. Fish were held in the net pens for a minimum of 24 hours post-injection to allow the Ovaprim to absorb.

Strip-Spawn

After a minimum of 24 hours, we checked if the fish were ripe. All fish were ripe, but if not, we would have re-injected them and left them for an additional 12 hours before checking again. We transferred ripe fish in coolers with aerated, chilled, lake water to the PLF Dunn Hatchery where aquaria were set up. Our original goal was to use gametes from a single male and female to produce fertilized eggs for the entire experiment at 4 mL of eggs per replicate, 100 mL total, to minimize genetic diversity across treatments, but a single female did not produce enough eggs, so we used gametes from all 12 fish captured, 6 of each sex.

We sedated fish one at a time with tricaine methanesulfonate (MS-222; Tricaine-S, Syndel USA, Inc., Ferndale, WA) with the concentration recommended for *Cyprinidae* (150-200 mg/l), immediately prior to strip spawning (*sensu* Urbanczyk et al. 2019). We removed fish from the MS-222 once they displayed signs of full sedation and rinsed them in non-contaminated lake water. We strip-spawned all fish of the same sex into a single stainless-steel container, starting with females. Adhesive cyprinid eggs become adhesive upon contact with water which can cause anoxic clumps of eggs (Woynarovich and Woynarovich 1980). Therefore, to decrease the amount of clumping, we dried the fish, the spawners’ hands, and the stainless-steel bowl thoroughly before expressing gametes. We kept all ripe fish, as well as the bowls of gametes, in water chilled to 20 °C to prevent temperature shock, based on a median temperature where successful Tui Chub hatch has been documented (Chapter 2; Cooper 1982).

Once all fish were spawned, we combined milt and eggs, again with dry hands, before measuring a 4 mL sample of fertilized eggs per replicate with a graduated cylinder. We poured eggs onto a 130 mL petri dish filled with treatment water, spacing them as much as possible to avoid anoxic egg clumps, initializing the water hardening process and egg adhesion to the petri dish. We let the eggs rest for 10 minutes to reduce perturbation during water hardening, we then transferred the petri dish to the appropriate replicate tank. We counted every 6th egg sample to estimate the average number of initial eggs per replicate. We intended to have 5 replicates per treatment and 5 egg count samples, but ultimately, we only had enough eggs for 3 of each.

Rearing

We bathed each petri dish daily in a solution of methylene blue for fungus prevention until we observed larvae. To bathe eggs, we removed the petri dish from the aquarium and filled it to the brim with treatment water with 3 ppm methylene blue added. After 10 minutes, we poured out the methylene blue treated water and rinsed the eggs 3 times with just treatment water before returning the petri dish to the aquarium. Once we observed motile larvae (i.e., tail movement) in an aquarium, we began feeding GP 200-300 Micron Larval Diet (Brine Shrimp Direct, Ogden, UT) at 3-4% percent body weight over 4-6 feedings (more feedings once all larvae were swimming) as recommended for other chub species (E. Wagner, retired Utah Division of Wildlife Resources, *unpublished data*). Given the extremely small overall body weight of all fish in a single replicate, we fed an amount that would stick to a finger lightly dabbed on the top of the feed at each feeding. We were more concerned with over-feeding than under-feeding out of a fear of increased total ammonia and unionized ammonia accumulation. To modify total ammonia before larvae were observed, we changed the water in the aquaria.

Data Collection

We recorded dissolved oxygen (DO; %) and temperature (°C) measured using a YSI ProSolo Digital Series handheld meter equipped with an optical DO probe and temperature probe. We recorded total ammonia (ppm) and TDS (mg/L) using the methods described in aquaria set-up. We visually-estimated the number of larvae present twice daily. We made modifications if DO fell below 80%, temperature fell outside 15-22 °C (Cooper 1982), total ammonia was above 0 ppm (Meade 1985), or TDS concentration fell outside 2 standard deviations of the meter accuracy for the appropriate range.

Results

Based on the average of our count samples (n=3) for 4 mL of eggs, each replicate initially contained ~4,229 eggs. We observed a dissolved oxygen range of 78.6-88.6%, a temperature range of 18.3-22.5 °C for all aquaria, and < 1,000 mg/L of TDS fluctuation, with an exception in T2 (Table 3-1). We were unable to maintain total ammonia at 0 ppm in all replicates (Figure 3-2) preventing the attribution of all egg mortalities to TDS along. We observed total ammonia in all aquaria except for replicate 3 in the Low TDS treatment, but no hatch in any TDS treatment higher than the Control.

We first observed non-motile larvae i.e., hatch, on Day 4 (fertilization=Day 0) in the Low TDS treatment, and Day 5 in the Control. We did not observe any hatch in T1, T2, or T3. We observed at least one motile larva, the day after we observed non-motile larvae for each treatment, Day 5 and Day 6, respectively. We observed mostly motile larvae by Day 8 for both treatments. We ultimately ended our experiment early on Day 16; we observed mostly live, highly motile larvae on the final day of the experiment in the Low TDS treatment but complete mortality in the Control treatment.

We began providing exogenous feed as soon as motile larvae were observed in an aquarium, although it is possible these fish were still reliant on endogenous food sources (i.e., yolk sac). We did observe what appeared to be feeding behavior, although only for a few larvae, and usually once food landed on the bottom.

Discussion

After considerable trial and error, we successfully developed a culture technique for Tui Chub, similar to a culture technique described for Mohave Tui Chub (Archdeacon and Bonar 2009), with notable differences that make it less resource intensive and easier to implement for research purposes. Our culture technique also builds significantly on previous culture efforts for Tui Chub (Harry 1951; Bird 1975; Cooper 1982). Even though we were unable to control for total ammonia, the relationship we observed between total ammonia concentration and TDS does indicate some broad negative effects of elevated TDS concentrations that are informative. Given the catastrophic impacts of increasing TDS concentrations on similar ecosystems, attempts to repeat our study taking into consideration knowledge gained from here would be worthwhile.

Pyramid Lake is highly alkaline (pH 9-9.8, PLPT WQMT, *unpublished data*) causing deprotonation of ammonium to unionized ammonia when ammonium is not removed from the system quickly (Trussell 1972; Hargreaves and Tucker 2004). In natural lacustrine systems ammonium is generally rapidly assimilated by autotrophs, or microbially-denitrified at the sediment surface, except in anoxic conditions or highly eutrophic systems, such that even in natural alkaline environments unionized ammonia does not accumulate to toxic levels (Wetzel 2001). In an artificial environment, such as the aquaria used in this study, biofilters consisting of denitrifying bacteria are used to remove total ammonia to avoid toxicity, but these filters can become overwhelmed by total ammonia due to artificially high decaying organic matter to bacteria ratios. Even when Walker Lake reached ~ 13,500 mg/L TDS, unionized ammonia only accumulated in the summer when the hypolimnion became anoxic preventing assimilation and denitrification (Beutel 2001). When the sediment was experimentally-oxygenated, total ammonia was quickly taken up (Beutel 2001), indicating our higher TDS treatments would only naturally accumulate unionized ammonia under extreme conditions.

The ratio of unionized ammonia to ammonium in total ammonia increases non-linearly with pH and is further increased by warmer temperatures (Piper et al. 1986; Hargreaves and Tucker 2004). Total dissolved solid increases can increase pH in systems like Pyramid Lake where the TDS composition is predominantly alkaline compounds (Galat and Jacobsen 1985), making it possible our higher TDS treatments were also higher in pH. We did not directly measure pH, but if true higher TDS treatments would contain a higher ratio of unionized ammonia to ammonium. Still, at ~13,500 mg/L Walker Lake demonstrated a pH of 9.3 (Beutel 2001; USGS 2015) which is within range of Pyramid Lake current pH (PLPT WQMT, *unpublished data*), suggesting that any increases were likely modest. However, the Low TDS treatment sourced from Truckee River water would have much lower pH than that sourced from Pyramid Lake, with a likely pH between 7.5 and 8.2 based on Truckee River water quality monitoring (e.g., California Department of Water Resources 2017). Lower rates of deprotonation in the freshwater treatment may have contributed to the longer lifespan of larvae in the Low TDS treatment when compared with the Control treatment, where larvae may have exhibited delayed impacts of unionized ammonia toxicity although both had motile larvae. Because of the alkalinity, in all replicates where total ammonia was detected there was undoubtedly some presence of unionized ammonia.

The presence of total ammonia in our aquaria at all indicates high levels of decaying organic matter, which prior to exogenous feeding could only result from decaying eggs. Unionized ammonia is known to have detrimental effects, particularly in early life stages, although the exact effect can vary widely based on a multitude of factors (McCormick et al. 1984; Solbé and Shurben 1989). Thus, while the higher TDS treatments overall accumulated more total ammonia indicating higher egg mortality, the positive feedback loop between egg mortality and unionized ammonia precludes TDS as the sole explanation for all egg mortality. The unionized ammonia likely compounded the stress of the higher TDS treatments to increase egg mortality. The observation of hatch in replicates in the Low TDS and Control treatments, despite the presence of total ammonia, suggests with less stress from TDS eggs were more likely to survive exposure to unionized ammonia. The unnaturally high unionized ammonia in our aquaria prevent the direct extrapolation of our results to a natural environment; however, we can conclude that increasing the TDS concentration in Pyramid Lake further would lower Tui Chub egg survival.

Our methods provide a cost and space-effective strategy for culture of fish with similar reproductive strategies, principally native cyprinid, lacustrine spawners with demersal, adhesive eggs. This growing methodology can be used to answer all manner of early life history questions or scaled up for production. We successfully used a strip-spawning method (Urbanczyk et al. 2019), as opposed to a captive breeding approach (Kaya 1991; Archdeacon and Bonar 2009; Kline and Bonar 2009), which dramatically reduced necessary resources. We also did not use a flow through or recirculating system common in fish culture (Piper et al. 1986), because it would have been cost and space-prohibitive to do so while maintaining 25 independent replicates. We believe minor adjustments to our design would allow adequate total ammonia control in future studies. Although we attempted to spread eggs as much as possible on the petri dishes, we still experienced considerable clumping, and in hindsight we would reduce the volume of eggs in each replicate or increase biofiltration to decrease the potential decaying organic matter to denitrifying bacteria ratio. We also recommend checking ammonia levels intensely for the first 24 hours and changing the water at the first indication of ammonia to immediately clear ammonia from initial egg mortalities.

Despite these complications, we observed negative effects of increasing TDS concentration above current concentrations in Pyramid Lake on hatch success. Scientific attention towards native cyprinid species in arid regions is lacking, but growing, as their intrinsic and ecological value is appreciated, and populations decline (Minckley 1991). Our study provides a less resource-intensive culture technique for native cyprinid species with demersal, adhesive egg behavior that can be used to investigate impacts of environmental stressors on sensitive early life stages (Hutchinson et al. 1998).

Tables & Figures

Table 3-1. Range and maximum change of TDS concentrations observed for all replicates (n=3) within a treatment group for an experiment testing the effects of TDS concentration on early life stages of Tui Chub in Pyramid Lake.

Treatment	Observed Range	Maximum Difference
Low TDS: 130 mg/L	88-162	74
Control: 5,888 mg/L	5,470-6,410	940
T1: 9,044 mg/L	8,660-9,600	940
T2: 12,222 mg/L	11,900-13,830	1,930
T3: 15,400 mg/L	15,040-15,920	880

Figure 3-1. Photographs of experimental set-up and strip-spawning of Tui Chub from Pyramid Lake used to test effects of increasing TDS concentrations. Top photo depicts plastic storage containers with sponge filters for biofiltration. Bottom left photo depicts stripping a male Tui Chub. Bottom right photo depicts petri dishes with water hardening eggs, the top right petri dish demonstrates egg clumps that can become anoxic, and the lower right petri dish demonstrates well-spaced eggs.

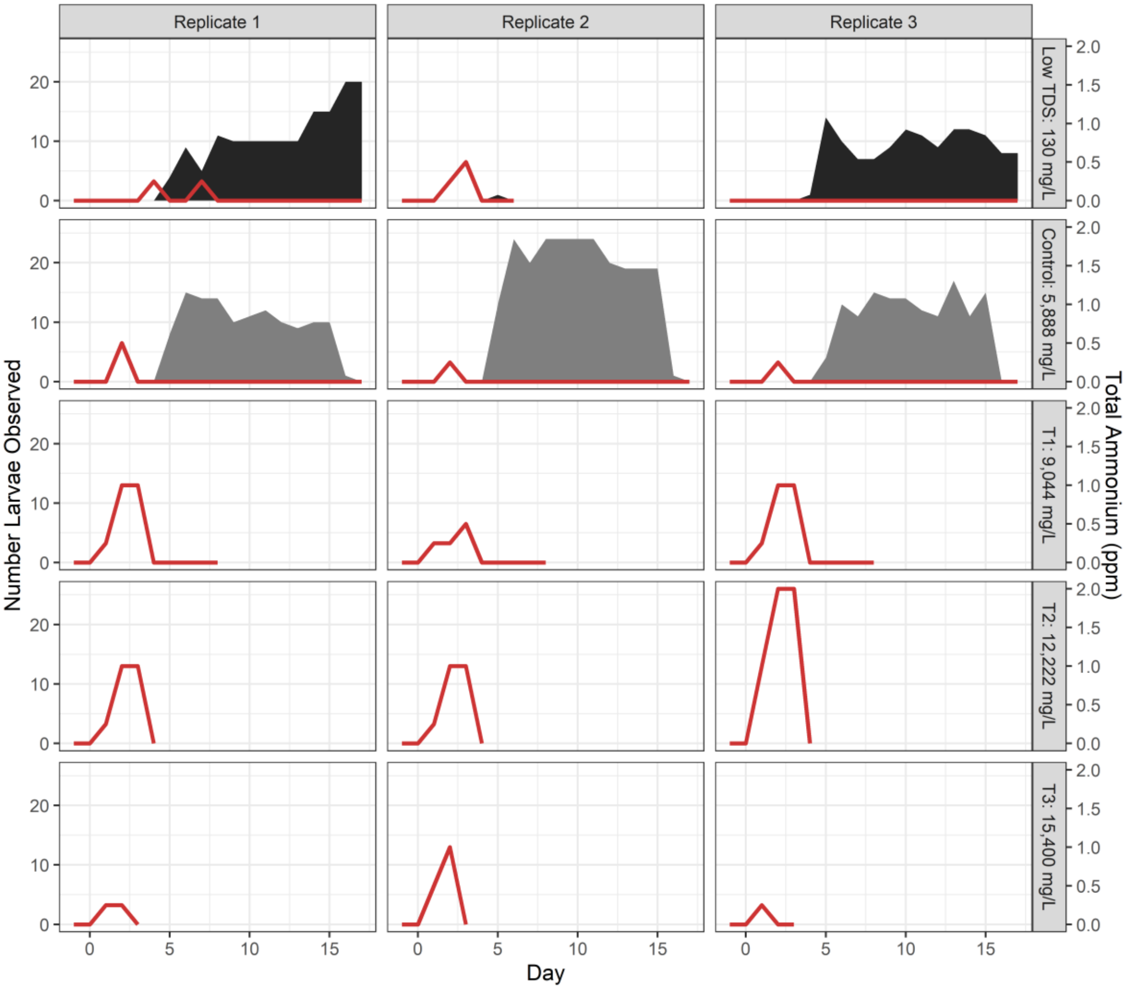

Figure 3-2. Tui Chub larvae were only observed in Low TDS (130 mg/L) and Control (5,888 mg/L) treatments, but results were confounded by the presence of ammonia, in an experiment testing effects of TDS concentration on Tui Chub early life stages from Pyramid Lake. Shaded area represents the number of larvae observed for each replicate by day, left y-axis. Red lines represent ammonia observed by day, right y-axis.

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CHAPTER 4

CONCLUSIONS

We investigated two potential consequences of lake elevation decline, nearshore habitat loss (Gownaris et al. 2017, Carmignani and Roy 2017, Glassic and Gaeta 2019), and rising TDS concentrations (Larson et al. 2016, Wurtsbaugh et al. 2017), on Tui Chub, a lacustrine spawner and native cyprinid species that serves as a critical forage species for a native predator, and valued sportfish, LCT, in Pyramid Lake, NV (Heredia and Budy 2018). We developed techniques that can be used by other researchers to investigate the impacts of this intensifying stressor, or other similar stressors, for native cyprinid species particularly in arid regions, with the goal of increased conservation of biodiversity.

In Chapter 2, we investigated impacts of lake elevation on nearshore habitat available to a lacustrine spawner, and key member of the food web, by connecting basic life history traits to an elevation explicit model of the Pyramid Lake basin, which estimates nearshore habitat quantity at different lake elevations. The techniques we used to construct an elevation explicit model for the Pyramid Lake basin can be used in other systems to quantify effects of lake elevation change on species requiring nearshore habitat for any aspect of their life history. Our findings add to recent work highlighting the impact of lake elevation decline on littoral-pelagic habitat coupling (Jones et al. 2006, Gaeta et al. 2014). We also quantified the importance of critical nearshore habitat in Pyramid Lake highlighting the need for adequate water delivery if the goal is to sustain or enhance LCT recovery. Fisheries managers can also use the findings from this chapter to precautionarily alter LCT hatchery supplementation in response to changing lake elevations and avoid a collapse in the critical Tui Chub forage base, thus sustaining LCT recovery under environmental change.

In Chapter 3, we attempted to investigate the effects of rising TDS concentrations on Tui Chub early life stages, the life stages we assumed would be most sensitive to variation in TDS concentration and therefore have the greatest impact on overall Tui Chub recruitment. The effects of rising TDS on fish populations are well documented (Pimentel and Bulkley 1983, Scannell and Jacobs 2001), but the exact relative effect varies by species and ecosystem, such that understanding specific impacts requires direct study. After considerable trial and error, we successfully developed a technique to study TDS and other environmental stressors on sensitive early life stages of native cyprinid species (Vigg 1982, Pimental and Bulkley 1983, Mueller et al. 2017). Through our application of this culture technique, we found that Tui Chub early life stages are likely already experiencing decreased survival and growth in response to TDS concentrations in Pyramid Lake, supporting our findings in Chapter 2 that adequate water delivery to Pyramid Lake is essential if the goal is to sustain or enhance LCT recovery.

Native cyprinid species are essential for ecosystem-based management practices of fisheries, and the conservation of global freshwater biodiversity (Langhans et al. 2019). Our research provides better understanding of the impacts of a major environmental stressor on the completion of life history characteristics of a native cyprinid that supports a relatively thriving endorheic lake ecosystem. Our findings can be used to manage critical components of the Pyramid Lake ecosystem, enabling a valuable fishery for an ESA threatened species and also sustaining global biodiversity. The results from our research provides further evidence of the grave impacts of water extraction and prolonged drought, particularly on endorheic ecosystems like Pyramid Lake (Wurtsbaugh et al. 2017, Zadereev et al. 2020), and highlights the need for water management that prioritizes ecologically-relevant flows to maintain the plethora of unique species that reside within these basins.

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Appendices

Appendix A: Study Species Description: Tui Chub *Siphateles bicolor*

Distribution

Tui Chub have been found throughout Washington, Oregon, California, Nevada, and parts of Idaho. They are abundant in the Columbia River basin, Klamath basin, Pyramid Lake, Tahoe Lake, and Eagle Lake. Due to their vast range and adaptability to many habitats, they were originally described as several species (Harper 1998), and later reduced to several sub-species. There are reports of up to 16 sub-species, many of which have been declared threatened, endangered, or fully extinct, and conclusive reports of the currently accepted number of sub-species are difficult to find (Center for Biological Diversity 2021). Tui Chub are a main forage item for piscivorous fish and birds across their range (Sigler and Sigler 1987). The main factors impacting imperiled Tui Chub populations are water diversions and pollutants (Sigler and Sigler 1987).

The Lahontan Creek sub-species which is found throughout the Lahontan Basin is currently listed as Least Concern, is commonly referred to as just Tui Chub, and has been described as two distinct morphs, *S.b. obesa* and *S.b. pectinifer,* which are distinguished by morphometry, diet, and habitat, although there is frequent overlap (LaRivers 1952, Galat and Vucinich 1983).

Habitat

Tui Chub can reside in small streams but are primarily found in natural lakes and reservoirs (Sigler and Sigler 1987). They utilize both benthic and pelagic environments for different stages of their life history (Sigler and Sigler 1987). In the Lahontan Creek population, the *S.b. pectinifer* morph is more commonly found schooling in the pelagic zone and the *S.b. obesa* morph is more commonly found in the benthos. The *S.b.*

pectinifer morph appears more plastic in its' habitat association and is found more frequently in the benthos than the *S.b. obesa* is found in the pelagic zone (Vigg 1981).

Life History

Tui Chub are believed to spawn in nearshore habitats and have been found near vegetation (Kimsey 1954, Bird 1975) in 15-22 °C water during spawning (Kucera 1978). Males arrive at the spawning ground in late April to early May before females, who move to the littoral zone to spawn in late May, early June (Kucera 1978). Spawning in Pyramid Lake may happen as early as late April and occurs until late summer, with shorter spawning seasons from June to July in cooler lakes such as Lake Tahoe (Sigler and Sigler 1987). Females produce around 20,000 eggs which are demersal and adhesive (Bird 1975). In Pyramid Lake, some male and female Tui Chub become sexually mature at two years of age, and all are sexually mature by three years of age (Kucera 1978). Accounts of Tui Chub age range vary widely, from a maximum age of 4 (Kucera 1978) to 32 (Scoppettone 1988), and there is no consensus on the best method to age Tui Chub (Scoppettone 1988). Discrepancy over the age range of Tui Chub in Pyramid Lake likely stems from the relatively mild winter conditions in Pyramid Lake that do not produce a clear winter growth check (Whitledge 2017). There is no observed parental care, recently emerged larvae are associated with vegetation until the fall when most Tui Chub are suspected to migrate to deeper water for the winter (Kimsey 1954). Some may remain in thick vegetation for the winter or in schools in the water column above deeper water (Kimsey 1954, Sigler and Sigler 1987).

Diet

In Pyramid Lake the two morphs must be considered when discussing diet preferences, although they are described generally as opportunistic omnivores (Kimsey 1954). In general, the *S.b. pectinifer* morph feeds more heavily on zooplankton, and the *S.b. obesa* morph feeds more heavily on benthic invertebrates. In one study in Pyramid Lake, the cladoceran *Diaphanosoma leuchtenbergianum* was found most frequently in diet analysis of the *S.b. pectinifer* morph, and the copepod *Cyclops vernalis* was found most frequently in diet analysis of the *S.b. obesa* morph (Galat and Vucinich 1983). The cladoceran *Moina hutchinsoni* has been found in stomach analysis of both morphs in Pyramid Lake regardless of location in the water column (Galat and Vucinich 1983). Both morphs have been found to adapt their food preferences to available feed but have diet preferences that grow more distinct as they age, potentially due to gill raker differences adapting them to different food types (Galat and McConnell 1981, Galat and Vucinich 1983). *S.b. pectinifer* gill rakers are relatively thin, and *S.b. obesa* gill rakers are thicker and less numerous, presumably to capture their respective preferred prey (Galat and Vucinich 1983). Feeding occurs primarily at dawn and dusk with large schools of Tui Chub coming to the surface to feed on zooplankton (Vigg 1981).

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Appendix B: 2022 Pilot Study

Methods

Site Selection

We sampled fish at 8 sites, noted in maroon in the study area map in the main text, in May, June, and July, repeating sampling at each site once a month. We chose sites that provided systematic coverage of the nearshore area from sites that have historically been sampled by Utah State University and other researchers for fish composition (Monda 1999, Budy and Thiede 2022). We used systematic sampling in an attempt to capture the range of habitat types available without a priori knowledge of habitat distribution. Notably, we did not sample the south-easternmost bay of the lake, colloquially known as Dago Bay, to avoid capturing endangered Cui-ui during spawning.

Fish sampling

We set three AFS standard core gill nets (Miranda and Boxrucker 2009) at each sampling event, one net set perpendicular to shore at each of three depth ranges from 0-10 m, 10-20 m, and 20-30 m. We chose these depth ranges based on a conservative estimate of the maximum depth spawning Tui Chub would be observed (Vigg 1981). In July, we ceased setting a net from 20-30 m after 4 sampling events due to high undesired LCT catch with no fecund Tui Chub catch at this range.

We enumerated and assessed captured Tui Chub for total length, fecundity, and sex. We used the same field methods to assess fecundity as in 2023, but in 2022 we retained a subset of the Tui Chub captured to determine the accuracy of our field methods for classifying fecundity. We retained every 10th Tui Chub mortality, up to 10 mortalities, per sampling event. For retained fish, we first attempted to express gametes to give the fish a field fecundity score, and then confirmed sex based on an examination of internal organs and classified fish as undeveloped, male, or female regardless of fecundity status. We then assessed the proportion of retained fish that did not express gametes, but had developed gametes upon internal examination, to determine our capacity to detect fecund fish in the field.

Habitat

To characterize bathymetry, sediment size class, and vegetation of the entire Pyramid Lake nearshore area, and define habitat of our nets, we surveyed from 5-30 m of depth with a BioSonics DT-X echosounder (BioSonics Inc., Seattle, WA, USA) along transects perpendicular to shore, a maximum of 500 m apart. We chose the maximum survey depth to align with the maximum extent of our nets, and the minimum survey depth based on the minimum depth for safe operation of the echosounder equipment which was deployed approximately 1 m below the surface. To verify hydroacoustic date, we dove 2, 100 m transects parallel to shore at each site at both 5 and 10 m of depth where we recorded sediment size class percent composition, percent vegetation cover, and presence or absence of 3 categories of vegetation heights, < .75 m, .75 – 1 m, and >1m for the transect based on visual estimate. We processed the hydroacoustic data using the same methods as described in the main text.

We assigned temperature to each net based on data collected by an existing series of loggers maintained and deployed by USU lake monitoring efforts near the Pyramid Lake Fisheries office, as depicted in the study area map in the main text. The loggers are set to log temperature hourly and are deployed at 3, 5, 13, 15, 25, 27, and 30 m to capture the epilimnetic, metalimnetic, and hypolimnetic temperatures. We assigned temperature to a given net as the average temperature recorded at the logger closest to the median depth of the net over the duration of time the net was set. We also deployed temperature loggers at 3, 15, and 30 m depth at each site from May through August to support the assumption of homogenous temperature at depth throughout the lake.

Results

We caught 1,926 total Tui Chub, 445 male, 348 female, 986 non-fecund, and 147 confirmed undeveloped. Based on the fish we retained (n=327), 0% of fish that did not express gametes using our field method actually had developed gametes, giving us high confidence in our sex and maturity estimates. We observed a strong correlation between fecund Tui Chub CPUE and depth, with the majority of our catch at < 20 m (Figure 3-1). Based on this finding, in 2023 we focused our effort from 0-20 m. Our data did not support our earlier assumption that Julian day, within the peak spawning window, would significantly affect fecund Tui Chub CPUE (Figure 3-2), so in 2023 we sampled at unique sites each sampling event to capture spatial variability, instead of repeated sampling to capture temporal variability.

To reduce costs, we initially planned to solely use hydroacoustic data for sediment size class and vegetation classification and only conduct a single series of dives in July 2022 to verify the hydroacoustic data. However, we were unable to reliably detect larger grain size sediment from the combination of hydroacoustic and SCUBA data in 2022, or survey at <5 m where we planned to consistently set nets in 2023, so in 2023 we increased our SCUBA effort, surveying in June, July, and August. Our inability to reliably detect complex larger grain size sediment may be a result of the low overall prevalence of larger grain size sediment from 5-30 m which made it difficult to detect in the PCA used by BioSonics Visual Aquatic software to classify sediment size class. We also decided to set temperature loggers directly on nets in 2023 because the methods used in 2022 would not provide temperature data at the necessary depth resolution without large overlap between nets.

We manipulated and analyzed all data in R software (v 4.2.3).

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Figures

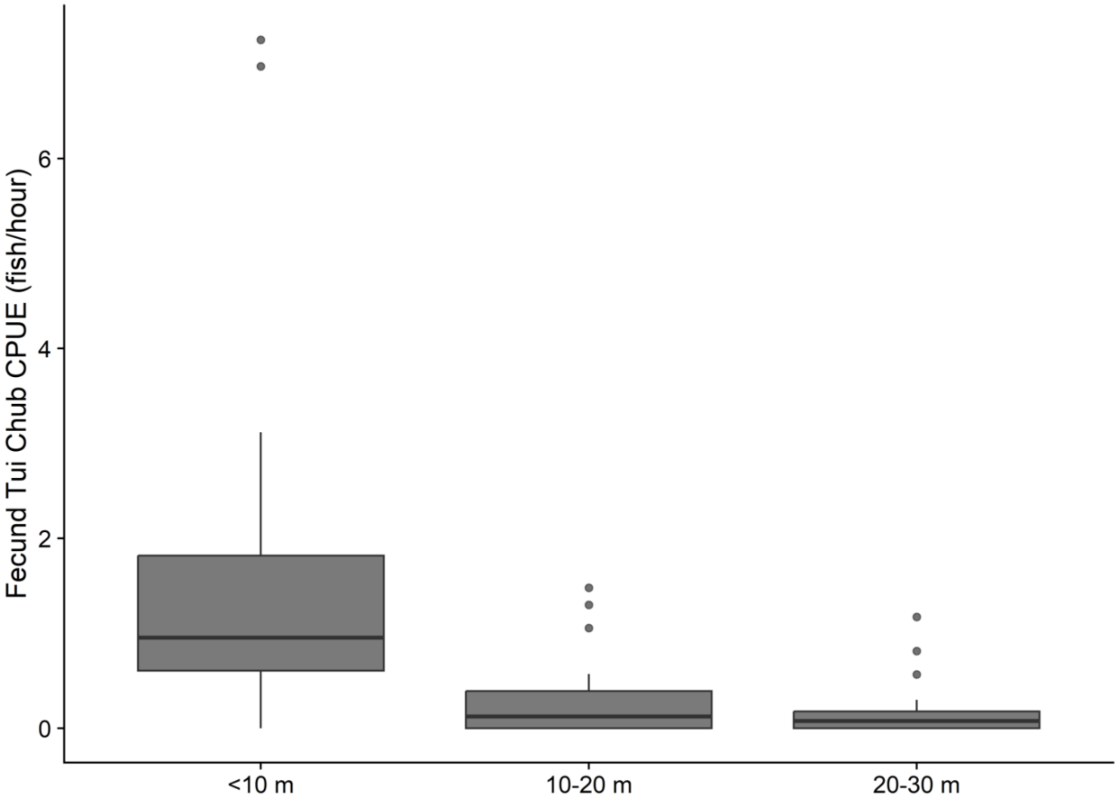

Figure A-1. Fecund Tui Chub CPUE in Pyramid Lake significantly decreases with increased depth and is largely absent past 20 m of depth. Box denotes quartiles, center line represents mean, whiskers represent the full distribution, and dots represent outliers.

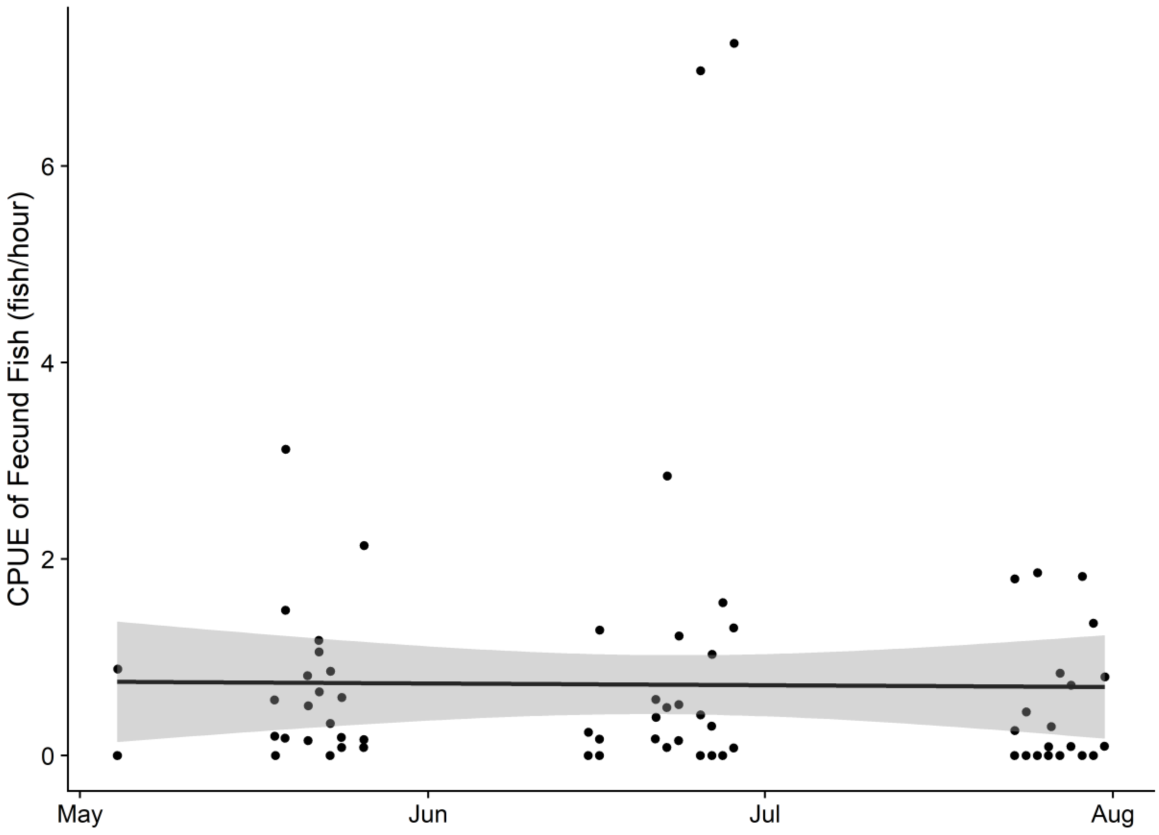

Figure A-2. Fecund Tui Chub CPUE in Pyramid Lake, NV does not change significantly (α = 0.05, p=0.92) during peak Tui Chub spawning from May to August. Black center line represents a linear model. Grey shading represents a 95% CI.

Appendix C: Tui Chub Morph Visual Classification Technique

Methods

In 2022 we developed a method to identify Tui Chub morph in the field based on gill raker characteristics (sensu Galat and Vucinich 1983). We classified gill rakers as *pectinifer*, *obesa*, potential intermediate, or unknown, based on a visual inspection of the first left gill arch. We classified Tui Chub with thin gill rakers and no visible gap as the *pectinifer* morph, and Tui Chub with thick gill rakers and a visible gap as the *obesa* morph (Figure A-3). We classified fish that exhibited characteristics of both morphs as potential intermediate. We classified fish that were caught before we developed our method, too small to visually inspect in the field, or missing the first left gill arch from netting injuries, as unknown. We determined the true classification by counting fill rakers of a subset (n=22) of the fish retained in 2022 that were classified as potential intermediated based on field methods, where ≤ 21 rakers is *obesa*, 22-26 rakers is intermediate, and ≥ 27 rakers is *pectinifer*.

Results

In 2022, we caught 727 *pectinifer* morph Tui Chub, 386 *obesa* morph, 337 potential intermediate, and 476 fish of unknown morph classification. In 2023, we caught 2,420 *pectinifer* morph, 2,573 *obesa* morph, 425 potential intermediate, and 105 fish of unknown morph classification. Tui Chub classified as *obesa* tended to be larger than those classified as *pectinifer* (Figure A-4), but the morphs were caught in roughly the same proportion. Of the subset of potential intermediate fish that we counted gill rakers for, 1 was intermediate (Galat and Vucinich 1983), and 21 were *obesa* morph, suggesting that a high proportion of the Tui Chub we classified as potential intermediate in the field may actually have been *obesa* morph.

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Figures

Figure A-3. Photos demonstrating differences used to identify Tui Chub morphs in Pyramid Lake, NV. Top left photo illustrates the left first gill arch, the gill arch used for classification in Tui Chub, on a fish that was classified as *obesa* morph. Top right photo also illustrates the thicker, shorter, and wider spaced gill rakers of the *obesa* morph. Bottom left photo illustrates a gill raker that would be classified as potentially intermediate morph based on field methods. Bottom right photo illustrates the thinner, longer, and less spaced gill rakers of the *pectinifer* morph.

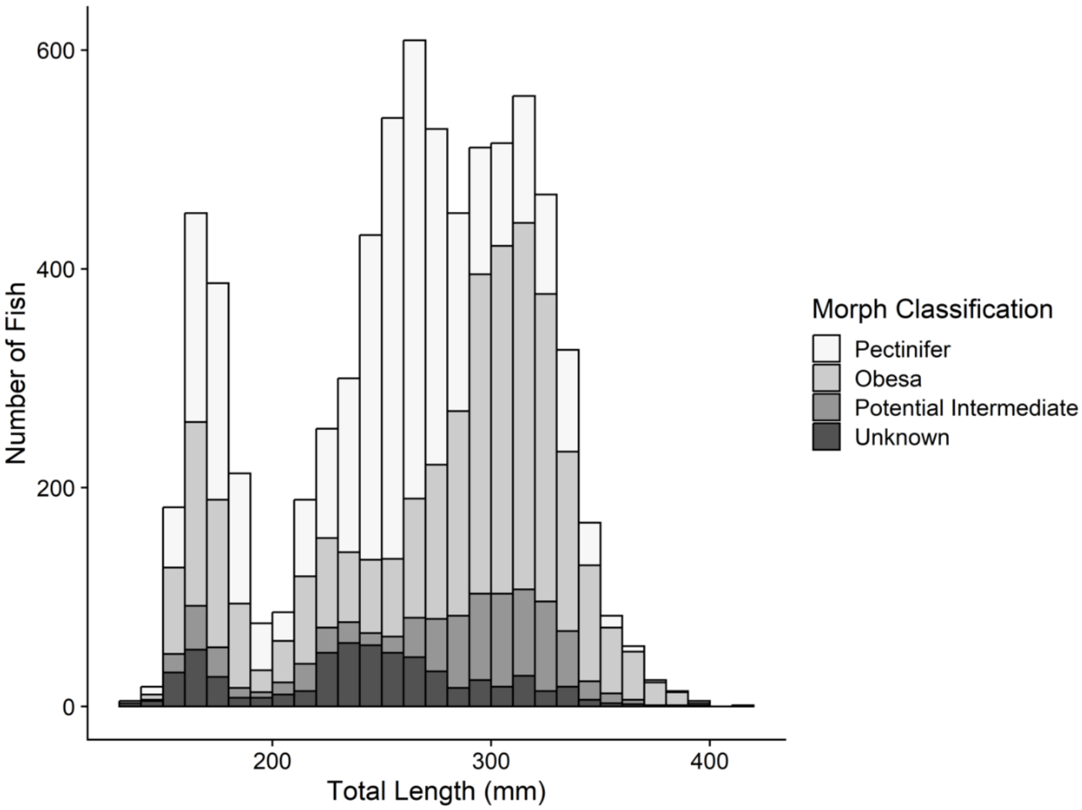

Figure A-4. Length frequency histogram for all Tui Chub caught by gill net (n=7,449) May-August 2022 and 2023 in Pyramid Lake, NV.

Appendix D: Co-author Permission Letter

United States Department of the Interior

FISH AND WILDLIFE SERVICE
Arizona Fish and Wildlife Conservation Office
2500 S. Pine Knoll Dr
Flagstaff, Arizona 86001

Dec 8, 2023

To whom it may concern,

I have read and agree to be a co-author on Chapter 3 of the thesis written by Sarah Barnes related to the Impacts of Total Dissolved Solids on Early Life Stages of Tui Chub *Siphateles bicolor* in Pyramid Lake, NV, USA.

Sincerely,

David Ward

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