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ARTICLE

Spatial and Temporal Distribution and Habitat Selection of Native Yellowstone Cutthroat Trout and Nonnative Utah Chub

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Abstract

Henrys Lake, Idaho, is a renowned trophy trout fishery that faces an uncertain future following the establishment of Utah Chub (UTC) *Gila atraria*. Utah Chub were first documented in the lake in 1993 and have become abundant over the past two decades. Little is known about the ecology of UTC, but they typically have negative effects on salmonids in systems where they have been introduced. We sought to fill knowledge gaps in UTC ecology and provide insight on potential interactions with Yellowstone Cutthroat Trout (YCT) *Oncorhynchus clarkii bouvieri*. Ninety-four YCT and 95 UTC were radio-tagged in spring 2019 and 2020 to better understand potential interactions between YCT and UTC in Henrys Lake. Fish were located via mobile tracking and fixed receivers from June to December 2019 and 2020. In June of both years, YCT and UTC were concentrated in nearshore habitats. As water temperatures increased, UTC were documented in deeper water (mean ± SD = 3.6 ± 1.4 m) and YCT became more concentrated in areas with cold water (e.g., mouths of tributaries, in-lake springs). In July and August, large congregations of UTC were observed. Yellowstone Cutthroat Trout were detected in tributaries from June to August, but no UTC were detected in the tributaries. By late fall (November–December), YCT were located along the shoreline and UTC were detected in the middle of the lake. Both YCT and UTC were observed in areas with dense vegetation. Macrophytes likely provided a food source for UTC and cover from predators for both species. Locations of YCT were negatively related to warm water temperatures, whereas UTC were positively associated with warm water temperatures. Results from this research fill knowledge gaps in UTC and YCT interactions as well as provide valuable insight on the ecology of UTC and adfluvial Cutthroat Trout populations. Furthermore, distribution patterns and habitat selectivity of YCT and UTC in Henrys Lake can be used to inform management decisions for fishery improvement and YCT conservation.

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Yellowstone Cutthroat Trout (YCT) *Oncorhynchus clarkii bouvieri* is a popular sport fish native to Idaho, Montana, Nevada, Utah, and Wyoming (Gresswell 2011). Yellowstone Cutthroat Trout inhabit a wide variety of habitats from large rivers and lakes to small streams and beaver *Castor canadensis* ponds. Historically, YCT were distributed throughout the Snake River, Idaho, and the Yellowstone River system of Montana and Wyoming (Behnke 1992). As of 2011, YCT occupied only 42% of their historical distribution and genetically unaltered populations remained in only 28% of the historical distribution (Gresswell 2011). The current distribution of YCT is limited to the Snake River drainage upstream of Shoshone Falls on the Snake River and the Yellowstone River drainage downstream of the Tongue River and including the Tongue River (Behnke 1992). This truncated distribution is caused by threats from nonnative species and anthropogenic activities that have reduced habitat quality and quantity (Behnke 1992; Campbell et al. 2002; Gresswell 2011).

Rainbow Trout *Oncorhynchus mykiss*, Brown Trout *Salmo trutta*, Brook Trout *Salvelinus fontinalis*, and Lake Trout *Salvelinus namaycush* have all been introduced into waters where YCT are native (Young 1995; Kaeding et al. 1996; Gresswell 2011; Al-Chokhachy et al. 2018). Approximately 70% of YCT populations have been hybridized with Rainbow Trout (Al-Chokhachy et al. 2018). Hybridization is a growing challenge and concern in the Snake River basin (Young 1995; Campbell et al. 2002; Kovach et al. 2011). On the Henrys Fork Snake River, Idaho, hybridization with Rainbow Trout has caused the near-complete disappearance of YCT (Young 1995). Other interactions with nonnative salmonids include competition and predation. In 1994, Lake Trout were discovered in Yellowstone Lake (Kaeding et al. 1996). Lake Trout are highly piscivorous and have caused a decline in the YCT population, with consequent ecosystem-level effects (Koel et al. 2011). Brook Trout and Brown Trout have also been associated with reduced growth and recruitment failure of YCT in multiple systems (Young 1995; Peterson et al. 2004; Al-Chokhachy and Sepulveda 2018). As YCT maintain high ecological, cultural, and economic value, minimizing the negative effects of nonnative species is a top priority for fisheries managers.

The introduction of nonnative Utah Chub (UTC) *Gila atraria* into many YCT waters is a growing concern. Utah Chub are native to the Lake Bonneville basin in Utah, Idaho, and Nevada and to the Snake River drainage upstream of Shoshone Falls and downstream of Mesa Falls in Idaho (Sigler and Sigler 1996). Utah Chub tolerate temperatures up to 31.1°C and are common in systems with dense vegetation. Spawning generally takes place in late spring or early summer when water temperatures are between 11.0°C and 20.0°C. Though UTC are omnivorous and shift their diet to available food resources, the majority of their diet is composed of aquatic vegetation (Graham 1961; Sigler and Sigler 1996). Outside of their native distribution, UTC are generally considered a nuisance and often compete with popular sport fishes (Davis 1940; Graham 1961; Sigler and Sigler 1996; Teuscher and Luecke 1996). Utah Chub have diets similar to those of salmonids, and diet overlap has been documented in many reservoirs and lakes (Hazzard 1935; Davis 1940; Schneidervin and Hubert 1987; Teuscher and Luecke 1996; Winters and Budy 2015). For example, a decline in trout abundance was associated with competition with UTC for prey resources in Fish Lake, Utah (Hazzard 1935; Davis 1940). The majority of prior research has described changes following the establishment of nonnative UTC, but few studies have directly focused on the ecology of UTC (e.g., Hazzard 1935; Davis 1940; Teuscher and Luecke 1996).

In 1993, nonnative UTC were first detected in Henrys Lake (Gamblin et al. 2001). Henrys Lake is a shallow lake (mean depth is 4 m; Flinders et al. 2016a, 2016b) located in eastern Idaho near the Idaho–Montana border. Although Henrys Lake is managed for trophy YCT, Rainbow Trout × YCT hybrids, and Brook Trout, the Idaho Department of Fish and Game (IDFG) has prioritized conservation of native YCT (Campbell et al. 2002). Idaho Department of Fish and Game has reported increasing catch rates of UTC in annual gill-net surveys over the last two decades (High et al. 2015; Flinders et al. 2016a, 2016b; Heckel et al. 2020). For example, catch per unit of effort was 1.6 UTC per net-night in 2002 and 25.5 UTC per net-night in 2018 (Heckel et al. 2020). Beginning in 2011, YCT catch rates declined consistently from 12.4 YCT per net-night to 1.5 YCT per net-night in 2018—the lowest on record (McCarrick et al., in press). The influence of UTC on YCT in the system is unknown, but resource managers are concerned about potential negative interactions and the potential for those interactions to be compounded with environmental stress (i.e., climate change).

Yellowstone Cutthroat Trout are thermally sensitive, so understanding how YCT respond to warm water temperatures in lakes is particularly important. Some climate models predict that trout habitat in North America will decline by 58% with warming air temperatures (Wenger et al. 2011). In 2017, water temperatures throughout Henrys Lake exceeded 25°C (B. High, unpublished data), a temperature shown to result in elevated mortality of other Cutthroat Trout subspecies (e.g., Johnstone and Rahel 2003). Henrys Lake does not stratify; therefore, thermal refuge is limited to springs and tributaries. Climate change, particularly warming temperatures, may compound the negative effects of invasive species (e.g., reduction in suitable habitat and negative interactions with nonnative species; Williams et al. 2009).

Understanding the ecology of YCT and UTC will guide management and conservation decisions. For example, understanding habitat selection can inform restoration efforts in tributaries or decisions to close angling in certain areas or at certain times to protect a particular species. Identifying potential overlap in resource use between native YCT and nonnative UTC is particularly helpful to resource managers as they evaluate threats to species of conservation concern. Distribution information will be beneficial for successful control or suppression efforts where UTC are deemed a problem. Managers can use seasonal information to target efforts for the highest desired effect while minimizing negative effects to YCT.

Insight as to how YCT react to environmental changes and nonnative UTC would be greatly beneficial for their management. The specific objective of this study was to describe spatial and temporal patterns in distribution, habitat use, and habitat selection of YCT and UTC in Henrys Lake. For the purposes of this study, distribution is defined as where fish are located throughout the sampling period, habitat use refers to the habitat characteristics at a fish's location (i.e., what habitat the fish is using), and habitat selection is defined as how habitat use compares to habitat availability lakewide. We hypothesized that YCT and UTC distribution patterns would be related to habitat characteristics, particularly temperature, depth, and macrophyte cover. Specifically, we predicted that YCT and UTC would select cool, oxygen-rich habitats during periods of elevated water temperatures (e.g., summer). We expected UTC to be found in areas with dense macrophyte cover. We further predicted that fish would be broadly distributed throughout the lake in fall and winter because fish would not need to find refuge from warm water temperatures that exist in the summer.

METHODS

Study area.— Henrys Lake is located 1,974 m above sea level in eastern Idaho (Figure 1). The lake is approximately 3.2 km wide and 6.4 km long, and mean depth is 4 m (Flinders et al. 2016a, 2016b). Henrys Lake provides the headwaters for the Henrys Fork Snake River. Several springs are present in the lake (e.g., Staley Springs, Kelly Springs), and some of the largest tributaries are Targhee, Howard, and Duck creeks. In 1922, a dam was constructed on the outlet to increase water storage capacity for downstream irrigation and to maintain the lake and fishery (Irving 1955). Idaho Department of Fish Game began operating an egg-take station on Hatchery Creek to mitigate losses of natural YCT recruitment due to losses in habitat after the creation of the dam (Campbell et al. 2002). Many of the tributaries have also been subjected to water diversion for irrigation. For example, Targhee Creek was dewatered in 1966 and 1973, and the majority of flow from Howard Creek was diverted for irrigation in 1978. This resulted in substantial losses of juvenile YCT migrating into the lake (i.e., 71–95% lost in Howard Creek). In recent years, IDFG has conducted extensive habitat restoration efforts, including the installation of fish screens on irrigation diversions, riparian fencing along tributaries and lake shorelines, and instream habitat improvement on tributaries.

Data collection.— Fish were captured for telemetry tagging via angling and electrofishing and with trap nets from May 28 to June 5, 2019, and from May 24 to June 4, 2020. For electrofishing, a boat was outfitted with a variable voltage pulsator (Infinity control box; Midwest Lake Electrofishing Systems, Inc., Polo, Missouri) and a generator (American Honda Motor Co., Inc., Alpharetta, Georgia). Trap nets had two rectangular frames (0.9 × 1.9 m), five hoops (0.8-m diameter), and a single lead (0.9 × 21.9 m). The nets had a single slit at the mouth, a single throat (30.5-cm stretch measure), and 1.3-cm bar-measure mesh. Two trap nets were set perpendicular to shore each night and pulled after 12 h. Fish were captured throughout the lake to ensure that the radio tags were evenly distributed. After capture, fish were placed in an aerated holding tank

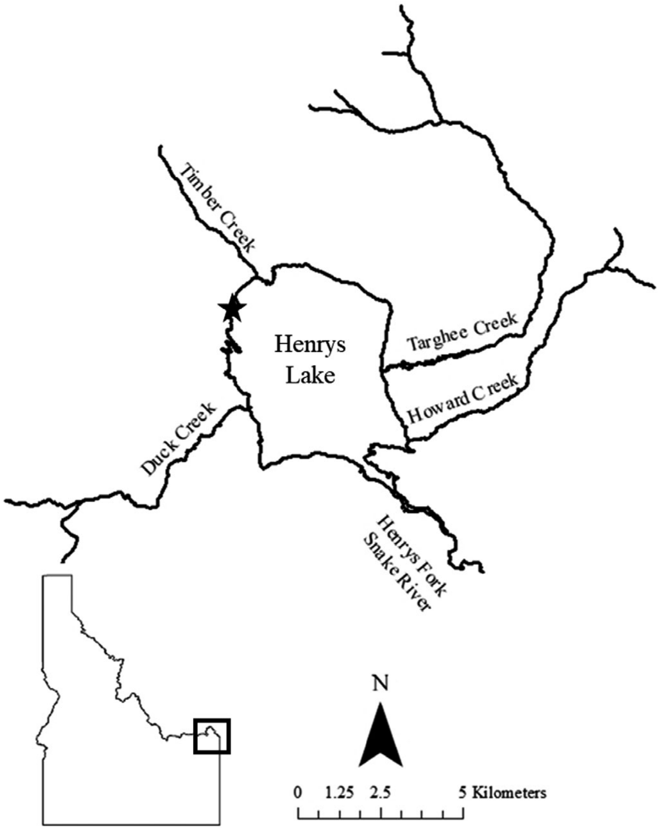

FIGURE 1. Henrys Lake, Idaho, and major tributaries. The star represents the location of Staley Springs.

and pretagging condition was assessed. If a fish was injured during capture, it was not tagged. Total length was measured to the nearest millimeter for fish selected for tagging. Utah Chub had to be at least 205 mm long (total length) and YCT had to be at least 215 mm long to ensure that tag weight did not exceed 2% of the fish's body weight (Zale et al. 2005; Liedtke et al. 2012).

Radio transmitters were one of four models: MST-820 T, MST-930 T, MCFT2-3BM, or MCFT2-3EM (Lotek Wireless, Inc., Newmarket, Ontario). Transmitter models MST-820 T and MST-930 T were used in 2019, and models MCFT2-3BM and MCFT2-3EM were used in 2020. Transmitters included a temperature sensor that transmitted an instantaneous temperature reading. In an effort to increase tag detection, transmitters were programmed on two frequencies (i.e., 149.300 or 149.400 MHz in 2019 and 148.360 or 149.520 MHz in 2020) and were grouped into one of three burst intervals (i.e., transmitting a signal every 6.0, 6.5, or 7.0 s). Transmitter longevity was approximately 120 d (MST-820 T), 320 d (MST-930 T), 444 d (MCFT2-3BM), or 528 d (MCFT2-3EM). Surgeries were conducted at or near the point of capture following Liedtke et al. (2012). Proper operation of transmitters was confirmed prior to tagging (i.e., receiver detected transmitter, and the sensor accurately measured temperature). Transmitters, forceps, hemostats, needles, scalpel blades, surgical scissors, and sutures were disinfected with chlorhexidine solution between fish. Fish selected for tagging were anesthetized, and the radio transmitter was implanted into the body cavity via an incision made with a stainless-steel surgical scalpel blade. The radio antenna was guided through the body cavity to the exit point using the shielded-needle technique (Ross and Kleiner 1982). The incision was closed with interrupted sutures. After completion of the surgery, fish were placed in an aerated holding tank to assess the immediate effects of surgery and allow for recovery. Fish were released at or near the point of capture after they had recovered.

A combination of mobile and fixed receivers was used to monitor fish locations. Four stationary receivers (Model SRX-DL3; Lotek Wireless) were placed near the mouths of Howard, Targhee, Timber, and Duck creeks to evaluate fish use of tributaries for thermal refuge (Figure 1). Three-element Yagi antennas were used on each stationary receiver. Stationary receiver locations were chosen based on flows and predicted fish use from historical data. Data were downloaded every 2 weeks and included transmitter identification number, the date and time of the detection, and the temperature measured by the transmitter. Temperature was monitored continuously in the tributaries with instream thermographs deployed at the mouth of each tributary. Mobile tracking was conducted with an SRX800-M2 mobile tracking receiver (Lotek Wireless); a six-element Yagi antenna was used with a boat, and a three-element Yagi antenna was used with an airplane. Starting locations were randomly selected for mobile tracking. Tracking was conducted along transects, and the entire lake was covered approximately three times by boat each month from June to August. A transmitter was considered to have been shed if maximum signal strength was achieved and the fish could not be disturbed. Only data from active fish were included in subsequent analyses. Aerial surveys were also conducted approximately twice per month from June to September and once per month from October to December. Aerial surveys included Island Park Reservoir and the Henrys Fork Snake River from Henrys Lake Dam to Ashton, Idaho. Tracking did not occur from January to May because ice cover made transmitters difficult to detect.

Detection distance was assessed by lowering a transmitter into the water column at 1, 3, and 6 m deep and maneuvering the boat around the transmitter location to determine the maximum distance at which the receiver could detect and decode the transmitter. Detection distance varied between tag types, but transmitters could be detected at distances up to 50 m at a depth of 6 m. Location error was estimated by comparing the distance between a known location transmitter and the location identified during a typical tracking event of the same transmitter. The GPS point recorded during tracking was approximately 10 m from the known locations when tracking by boat and within 400 m when tracking by airplane. Distribution maps were compared for boat and plane fish locations each month. Patterns in distribution were consistent between tracking methods.

When a transmitter was relocated, a GPS point was recorded with the tag identification number and the transmitted temperature. A habitat assessment was conducted for each fish located by boat (i.e., fish habitat use). Visibility was estimated to the nearest tenth of a meter with a Secchi disk (Reischel and Bjornn 2003). Depth (m) of the water column was estimated to the nearest tenth of a meter. Water temperature (°C) and dissolved oxygen (mg/L) were measured every meter from the surface with a multiparameter water quality meter (Pro2030 Dissolved Oxygen, Conductivity, Salinity Instrument; YSI, Inc., Yellow Springs, Ohio). Macrophyte cover was defined as any living submerged aquatic vegetation visible with the naked eye and was assessed visually (Fisher et al. 2012). An underwater camera (760c Series; Aqua-Vu, Crosslake, Minnesota) was lowered to the lake floor, and percent macrophyte cover was estimated. The camera was oriented in two directions, and the percentage of macrophyte coverage visible in the display monitor was recorded in each direction; the two values were averaged, and the average was recorded. Additional habitat assessments were conducted at 5 and 20 m away from the fish's location in two different randomly selected directions (e.g., north, south, east, or west) for a total of four additional habitat assessments. Habitat availability was evaluated with the same habitat assessment described above at 20 randomly selected sites every 2 weeks from June to August of each year. Because we were particularly interested in the response of fish to warm water temperatures, habitat assessments were only conducted from June to August, the warmest time of the year.

Data analysis: distribution.— ArcMap GIS version 10.5.1 (Esri, Redlands, California) was used to map the spatial distribution of YCT and UTC (e.g., Penne and Pierce 2008). Probability of use was estimated using the kernel density tool in the ArcMap Spatial Analyst toolbox. The density estimate was described by detections of radio-tagged fish in Henrys Lake. Because sampling conditions and distribution patterns were similar between sampling years, 2019 and 2020 data were combined. Fish locations were randomly subsampled for individual fish detected more than four times per month to prevent autocorrelation (Hansteen et al. 1997). The multivariate kernel density estimator was defined as

$$\hat{f}(x) = \frac{1}{nh^d} \sum_{i=1}^{n} K\left[\frac{1}{h}(x - X_i)\right],$$

where K is the Gaussian kernel; $K(x)$ is the kernel function defined for d-dimensional x; h is the bandwidth; and X_i is a random sample of sample size n (Silverman 1986). The kernel was defined as

$$K_2(x) = \begin{cases} 3\pi^{-1}(1 - x^T x)^2 & \text{if } x^T x < 1 \\ 0 & \text{otherwise} \end{cases}.$$

The default bandwidth was calculated in ArcMap as

$$f(x) = 0.9 \times \min\left[D_s, \sqrt{\frac{1}{\ln(2)}} \times D_m\right] \times n^{-0.2},$$

where D_s is the standard distance; D_m is the median distance; and n is the sample size. Kernel density function was estimated for UTC and YCT in Henrys Lake for each month (i.e., June–December; Rogers and White 2007; Penne and Pierce 2008).

Data analysis: habitat selection.— Resource selection functions were used to assess habitat selection (e.g., Long et al. 2014; Merems et al. 2020). Similar to probability of use, data were combined for 2019 and 2020 because no notable differences in sampling conditions or data trends were observed between years. Covariates for models were depth, visibility, percent macrophyte cover, average dissolved oxygen, and water temperature. Habitat values at the fish's location reflected use, and biweekly lakewide habitat assessments were used to reflect available habitat. Water temperature values from the temperature sensor on the radio transmitter represented fish use. Water temperature was averaged across the depth profile at each site to estimate availability. Dissolved oxygen was also averaged across the depth profile at each site. Variation in temperature and dissolved oxygen was minimal in the water column. Probability of YCT or UTC use at a location was extracted from the kernel density estimates. Probability of YCT use was included in regression models for UTC, and probability of UTC use was included in YCT models. Spearman's correlation coefficient was used to evaluate multicollinearity among variables (Sokal and Rohlf 2001). If two covariates were significantly correlated (Spearman's $r \leq |0.70|$), the most ecologically relevant variable was retained for further analysis. For example, visibility and macrophyte cover were highly correlated. Since visibility was primarily a function of aquatic vegetation (e.g., visibility was greatly limited where vegetation was abundant), macrophyte cover was deemed more ecologically relevant and retained for regression analysis. Dissolved oxygen and water temperature were also highly correlated, but both variables were ecologically relevant and retained for further analysis; however, they were not used in the same models.

Habitat selectivity was analyzed at the lakewide scale with a use–availability design (Manly et al. 2002). Locations where individual fish (2019: $n = 50$ YCT, 50 UTC; 2020: $n = 44$ YCT, 45 UTC) were found represented use, and the random habitat sites from the lakewide habitat availability assessments represented availability (up to 80 total random locations per month). Generalized linear models with a logit link function and binomial response variable distribution were used to model habitat selectivity. The response variable in the models was binary for fish presence or absence (i.e., 1 for present, 0 for absent). Separate resource selection functions were fit for each month (i.e., June–August) and species. Models were ranked with Akaike's information criterion adjusted for small sample size (AIC$_c$). The top model had the lowest AIC$_c$ score, and models within 2 AIC$_c$ units were considered top models. McFadden's pseudo-R^2 was used to evaluate model fit and was calculated as 1 minus the ratio of the log likelihood of a model with parameters and the intercept-only model (McFadden 1974). Models with a McFadden's pseudo-R^2 value of 0.20–0.40 are considered excellent models, but models with R^2 values as low as 0.10 have been shown to have good fit (McFadden 1974; Hosmer and Lemeshow 1989; Klein et al. 2015). Multimodel inference was conducted by model averaging with shrinkage (Burnham and Anderson 2002; Lukacs et al. 2010).

RESULTS

Fish Tagging and Detection

In total, 95 UTC (2019: $n = 50$; 2020: $n = 45$) and 94 YCT (2019: $n = 50$; 2020: $n = 44$) were implanted with radio transmitters. Utah Chub varied in length from 222 to 343 mm (mean ± SD = 279.4 ± 34.3 mm) in 2019 and from 245 to 369 mm (294.0 ± 3.3 mm) in 2020. Yellowstone Cutthroat Trout varied in length from 275 to 595 mm (414.4 ± 88.1 mm) in 2019 and from 315 to 562 mm (418.0 ± 49.4 mm) in 2020. Seventy-six UTC (33 in 2019 and 43 in 2020) and 82 YCT (40 in 2019 and 42 in 2020) were located at least once during the study period. The number of relocations per individual fish varied from one to six relocations. No fish tagged in 2019 were detected in 2020. Nineteen UTC (6 in 2019; 13 in 2020) and 25 YCT (9 in 2019; 16 in 2020) died or shed their transmitters during the study period. One UTC transmitter and five YCT transmitters were located on land but could not be recovered because they were located on private property. Two transmitters were recovered during the study period. One recovered transmitter was from a YCT found dead near Hope Creek. The other was from a UTC under a double-crested cormorant *Phalacrocorax auritus* nest. The remaining 36 transmitters were not recovered because they were located on the lake bottom. No fish were detected outside the system (e.g., downstream of the dam during aerial surveys).

Distribution

Distribution patterns varied seasonally and between species (Figures 2, 3). In June, when lakewide water temperatures averaged 14.0°C (SD = 0.9°C), YCT and UTC were located primarily in nearshore habitats (i.e., within 1 km of shore). Utah Chub were congregated in the outlet and the northwest region of Henrys Lake. As water temperatures increased in July (mean ± SD = 17.9 ± 1.1°C) and August (19.9 ± 0.9°C), YCT became more closely associated with coldwater sources (i.e., Staley Springs, Targhee Creek, Gillan Creek). Utah Chub moved into deeper water and became densely congregated at the outlet during July and August. During mobile tracking, congregations of UTC were frequently observed throughout the lake in July and August. In September and October, both species were distributed throughout the lake but were most common in the northwest region of the lake. Ice formed on the lake in November, and UTC were rarely found nearshore in late fall and winter. In contrast, YCT were located throughout the lake in November. In December, YCT were located primarily in nearshore habitats, particularly in the southern half of the lake. Spatial overlap was minimal between the two species (Figure 3). Yellowstone Cutthroat Trout were consistently located near Targhee Creek regardless of season. Sixteen YCT were detected at tributary mouths on fixed receivers during June–August in both years (17% of YCT; Table 1). No UTC were detected on the fixed receivers. Detections of fish in the tributaries increased from 2019 to 2020, which is likely due to the use of larger, more powerful transmitters in 2020. Average June–August water temperatures in the tributaries were cooler than lakewide water temperatures. Water temperatures averaged 10.5°C (SD = 3.1°C) for Duck Creek, 9.0°C (3.2°C) for Howard Creek, 9.5°C (3.1°C) for Targhee Creek, and 13.7°C (2.9°C) for Timber Creek, whereas water temperature for Henrys Lake was 17.7°C (6.0°C).

Habitat Use

Fish locations appeared to be related to habitat characteristics, and fish habitat use differed between species (Figure 4). Visibility averaged 3.9 m (SD = 0.9 m) in June and decreased to 3.2 m (0.8 m) by August. Both species were typically located in areas with low visibility (e.g., ≤2.5 m). Similarly, YCT and UTC were consistently located in association with macrophytes during the study period. Percent macrophyte cover varied greatly across sites throughout the lake. In June, little vegetation was observed in the lake and averaged 22.6% (SD = 39.9%) cover across habitat availability sites. Average macrophyte cover peaked at 51.6% (46.3%) in July at habitat availability sites. Yellowstone Cutthroat Trout were located in water averaging 3.2-m (SD = 1.4 m) depth. Utah Chub were located in shallower water in June (mean ± SD = 2.8 ± 1.3 m) but moved to deeper water in July and August (3.7 ± 1.4 m). Water temperature in 2019 and 2020 increased from an average of 14.0°C (SD = 0.9°C) in June to an average of 19.9°C (0.9°C) in August. On average, YCT and UTC used habitat with water temperatures similar to lakewide water temperatures; however, some YCT were located near coldwater sources that were several degrees cooler than surrounding water temperatures. For example, YCT located near Targhee and Gillan creeks in July were in water that averaged 13.6°C (SD = 1.5°C) when lakewide water temperatures averaged 17.9°C (1.1°C). Dissolved oxygen decreased from June to August. No distinct pattern was identified between fish locations and dissolved oxygen levels based on averages.

Habitat Selectivity

Habitat selection varied by month and between species (Tables 2, 3). Although model fit was relatively poor, relationships between fish presence and habitat characteristics were identified (Table 2). Regression modeling indicated that in June, YCT presence had a negative relationship with depth and dissolved oxygen and a positive relationship with water temperature and probability of UTC. Utah Chub presence in June was positively associated with macrophyte

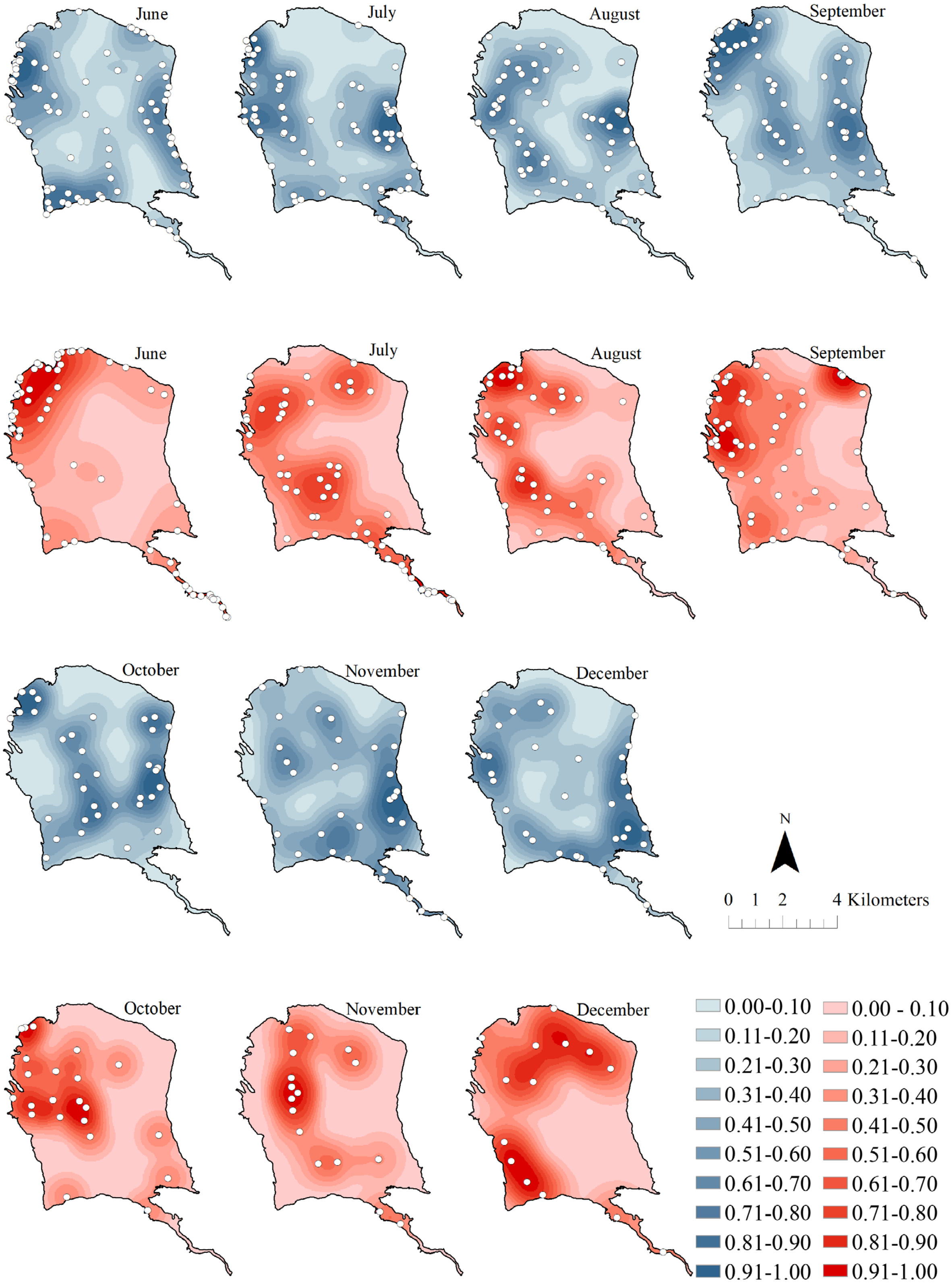

FIGURE 2. Monthly distribution maps of Yellowstone Cutthroat Trout (YCT) and Utah Chub (UTC) in Henrys Lake, Idaho (2019–2020). Fish locations are indicated by white circles; maps in blue depict YCT, and maps in red depict UTC. Shaded contours represent density of use from kernel density estimates. Darker shading indicates higher probability of use, and lighter shading indicates lower probability of use.

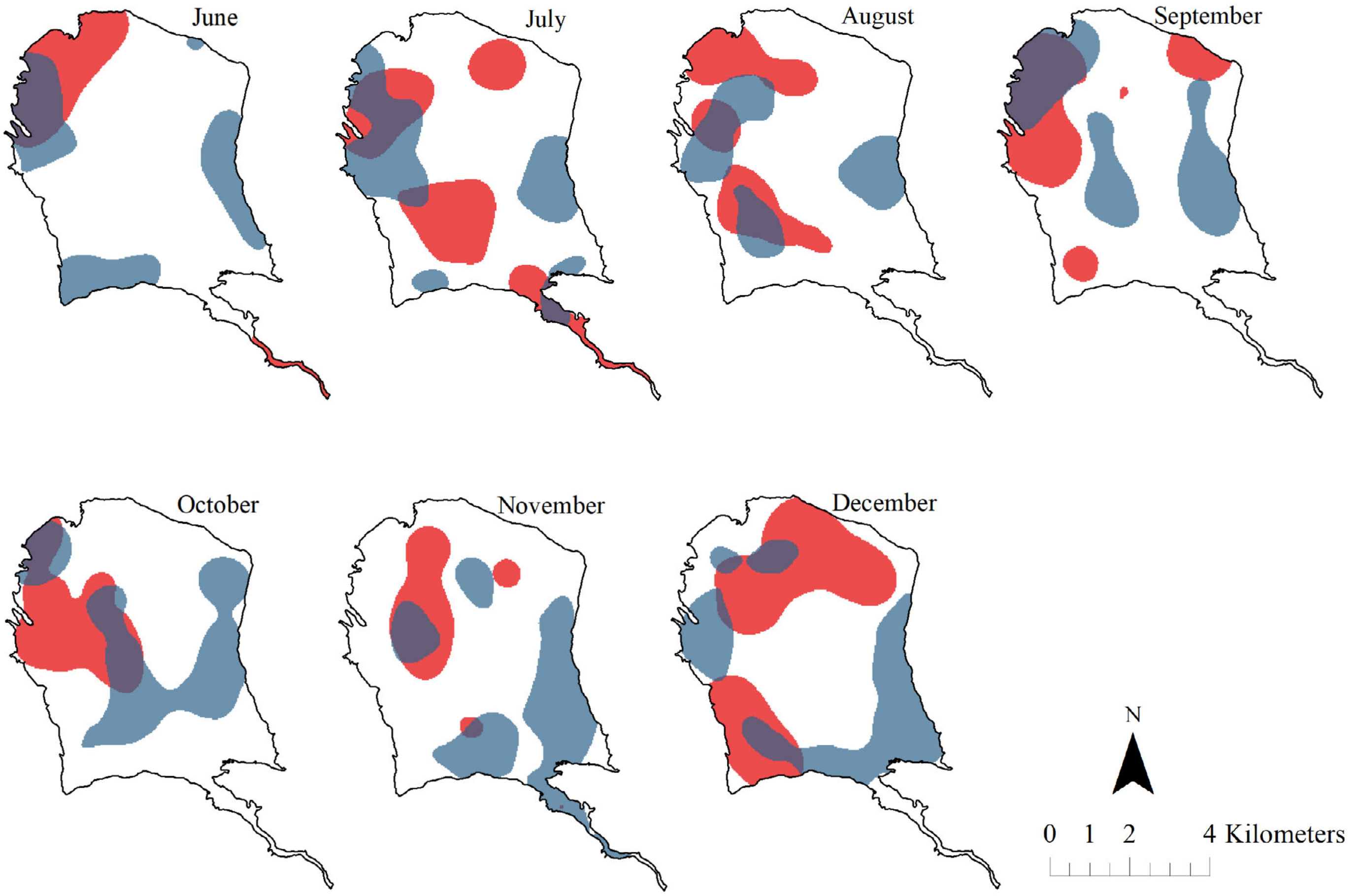

FIGURE 3. Monthly overlap maps of Yellowstone Cutthroat Trout and Utah Chub in Henrys Lake, Idaho (2019–2020). Fifty-percent core use areas are displayed based on kernel density estimates. Yellowstone Cutthroat Trout core use areas are displayed with blue polygons, Utah Chub core use areas are displayed with red polygons, and the overlap between the two species is displayed in purple.

cover, water temperature, and probability of YCT. Regression models for July revealed similar habitat selection between the two species. In July, YCT presence was negatively related to depth and positively related to dissolved oxygen and probability of UTC. Specifically, YCT were common in areas with shallow depths, high dissolved oxygen, and UTC. Utah Chub presence in July was positively associated with water temperature and probability of YCT. Lastly, regression models for presence of YCT in August identified a positive relationship with macrophyte cover and negative relationships with water temperature, dissolved oxygen, and depth. In August, UTC presence was negatively associated with dissolved oxygen and depth and positively associated with macrophyte cover.

TABLE 1. Radio-tagged Yellowstone Cutthroat Trout detected in four tributaries of Henrys Lake, Idaho, during June–August (2019–2020). No Utah Chub were detected in tributaries during the study period.

Stream	Jun	Jul	Aug
	2019		
Duck Creek	1	1	
Howard Creek	1	1	
Targhee Creek			1
Timber Creek			
	2020		
Duck Creek	1		
Howard Creek	1		
Targhee Creek	4	3	1
Timber Creek	1		

DISCUSSION

Management and conservation decisions benefit from understanding distribution and habitat selection of fishes. In Henrys Lake, species distribution patterns were related to habitat characteristics and appeared to be influenced by temperature and macrophyte cover. Yellowstone Cutthroat Trout congregated near coldwater sources during

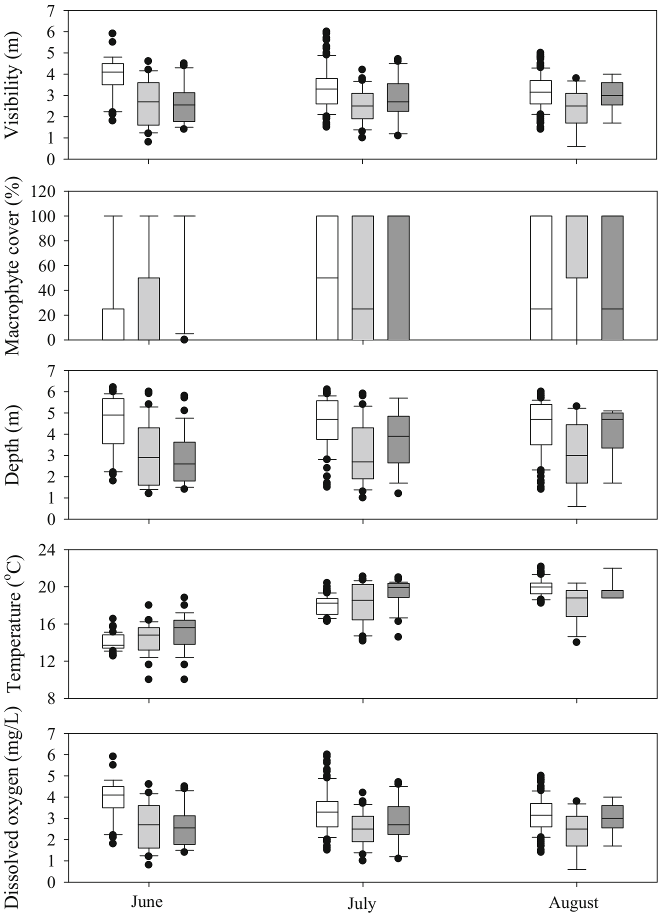

FIGURE 4. Box plots of habitat availability and use for Henrys Lake, Idaho (2019–2020). Habitat characteristics are reported for lakewide availability (white boxes), Yellowstone Cutthroat Trout use (light-gray boxes), and Utah Chub use (dark-gray boxes).

periods of warm temperatures, suggesting that maintenance of coldwater refugia may be important for adfluvial trout populations. Utah Chub are not as thermally sensitive as YCT and were associated with warm water temperatures. Protecting springs and tributaries (e.g., maintain flows, riparian restoration) is important for YCT to cope with rising summer water temperatures and may provide spatial separation from UTC. Both YCT and UTC were associated with macrophytes and were likely using vegetation as a source of protection from predators. Nevertheless, species distribution patterns and resource selection modeling indicate minimal overlap between YCT and UTC. Results from this research suggest that UTC are likely not having a direct effect on the YCT population.

Fish locations in June were likely associated with spawning and water temperature. Yellowstone Cutthroat Trout in Henrys Lake ascend tributaries to spawn from February to June (Campbell et al. 2002; Gresswell 2011; Heckel et al. 2020). Several YCT were detected in the tributaries in June, likely due to spawning. Utah Chub have been documented moving from deep to shallow water for spawning purposes in early summer (Sigler and Sigler 1996). Spawning UTC have been observed from mid-May to mid-August in other systems when water temperatures were between 11.1°C and 20.0°C (Graham 1961; Sigler and Sigler 1996). In June, water temperatures (14.0°C) were within the thermal requirements for spawning and UTC were observed in shallow areas of the lake along the shoreline. Although spawning was not documented during this study, distribution and habitat relationships suggest that spawning of both species likely occurred in June.

Consistent with our hypothesis, some YCT moved to areas of cold water during peak summer temperatures. Yellowstone Cutthroat Trout are thermally sensitive and typically found in systems with water temperatures between 4.5°C and 15.5°C (Gresswell 2011). During peak summer water temperatures (~22.0°C), YCT were documented in tributaries, near the mouths of tributaries, and near springs. Summer water temperatures in the lake averaged 18.9°C (SD = 1.4°C) in July and August, but some YCT were located in water as cool as 11.6°C during the same time period. Water temperatures at springs and tributaries were about 5°C cooler than the rest of the lake, which suggests that at least some YCT were seeking thermal refuge. Although few studies have investigated YCT distribution in lakes, YCT have been documented using thermal refugia in rivers and streams (Varley and Gresswell 1988; Harper and Farag 2004; Gresswell 2011). In Yellowstone National Park, YCT exist in geothermally heated streams with water temperatures up to 27°C (Varley and Gresswell 1988). Yellowstone Cutthroat Trout are able to survive high water temperatures by using thermal refugia (Gresswell 2011). In Henrys Lake, some YCT did not selectively use colder habitats and were located throughout the lake in water temperatures that reflected lakewide water temperatures. The warmest water temperatures used by YCT were 19.6°C in 2019 and 20.4°C in 2020. The variety of YCT locations may indicate a lack of sufficient thermal refuge or that factors other than temperature are influencing YCT distribution. Whatever the mechanism, diversity in phenotypic characteristics is vital to a population's persistence in a system (Watters et al. 2003; Fox 2005) and maintaining this variation in behavior could be important for YCT conservation, particularly in response to climate change (Al-Chokhachy et al. 2013).

Distribution patterns of UTC also appeared related to water temperatures. Utah Chub presence was positively associated with warm water temperatures in Henrys Lake, and they were not typically located near coldwater sources, such as springs and tributaries, during the summer, contrary to our hypothesis. Unlike YCT, UTC tolerate a wide variety of summer water temperatures (i.e.,

TABLE 2. Top multiple regression models for resource selection of Yellowstone Cutthroat Trout (YCT) and Utah Chub (UTC) in Henrys Lake, Idaho (2019–2020). The response variable is binary for fish presence or absence (i.e., 1 for present, 0 for absent). Explanatory variables include depth, percent macrophyte cover, water temperature, and dissolved oxygen. The probability of UTC was included as a covariate in YCT models, and probability of YCT was included as a covariate in UTC models. Models were ranked by Akaike's information criterion corrected for small sample size (AIC_c). Delta AIC_c, number of parameters (K), weight of the model (w_i), and McFadden's pseudo-R^2 are reported. Direction of relationship between presence of YCT or UTC and each of the covariates is indicated (positive [+], negative [−]).

Response variable	Month	Model parameters	AIC_c	ΔAIC_c	K	w_i	R^2
YCT	Jun	− Depth − Dissolved oxygen	92.7	0.00	3	0.28	0.23
		− Depth + Temperature	92.9	0.15	3	0.26	0.23
		− Depth	93.7	0.96	2	0.17	0.20
		− Depth − Dissolved oxygen + Probability of UTC	94.5	1.75	4	0.12	0.23
	Jul	− Depth + Probability of UTC	115.5	0.00	3	0.31	0.20
		− Depth	116.3	0.83	2	0.21	0.18
		− Depth + Dissolved oxygen + Probability of UTC	117.4	1.91	4	0.12	0.20
	Aug	− Temperature − Dissolved oxygen + Macrophyte cover	48.6	0.00	4	0.52	0.46
		− Temperature − Dissolved oxygen − Depth	48.9	0.37	4	0.43	0.46
UTC	Jun	+ Temperature + Macrophyte cover	69.1	0.00	3	0.26	0.40
		+ Macrophyte cover	69.7	1.31	2	0.20	0.38
		+ Macrophyte cover + Probability of YCT	70.2	1.43	3	0.15	0.39
	Jul	+ Temperature + Probability of YCT	97.8	0.00	3	0.43	0.22
	Aug	− Dissolved oxygen + Macrophyte cover	39.5	0.00	3	0.45	0.43
		− Dissolved oxygen − Depth	40.6	1.06	3	0.27	0.41

15.6–31.1°C; Sigler and Sigler 1996) and movements of UTC may not be motivated solely by temperature. In July and August, a shift in UTC locations from nearshore habitat to deeper habitats was observed. The shift in UTC locations could be explained by the completion of spawning, response to seasonal temperature changes, or protection from predation (Graham 1961; Sigler and Sigler 1996). Furthermore, UTC were frequently observed in large congregations from July to August. The formation of large shoals, as observed for UTC in Henrys Lake and elsewhere (e.g., Hebgen Lake, Montana; Graham 1961), has been documented to reduce predation risk in several species of fish (Moyle and Cech 2004).

Many species, including Cutthroat Trout, are often found in association with some form of cover (Harper and Farag 2004; Heckel et al. 2020). For instance, Heckel et al. (2020) found that the abundance of Westslope Cutthroat Trout *O. clarkii lewisi* in the Saint Maries River, Idaho, was positively related to the amount of instream cover, especially large wood. Similar results were reported by Harper and Farag (2004) and Berger and Gresswell (2009) for Cutthroat Trout subspecies in streams. In Henrys Lake, YCT regularly used areas with high densities of macrophytes. Given the shallow depth of Henrys Lake, YCT were likely using macrophytes as a form of cover from predators (e.g., American white pelicans *Pelecanus erythrorhynchos*, bald eagles *Haliaeetus leucocephalus*). Utah Chub also used macrophytes in Henrys Lake. Similar to YCT, UTC likely used vegetation as protection from predators. In addition, plant material is a common food resource for UTC and has been found to compose up to 70% of the food volume in UTC stomachs (Graham 1961; Sigler and Sigler 1996).

Winter distribution patterns differed between YCT and UTC. We predicted that both species would be distributed throughout the lake in the winter with no distinct pattern, but this was not the case. The majority of YCT were documented nearshore and particularly near the mouths of Targhee and Howard creeks. Garren et al. (2009) conducted a small-scale telemetry study with YCT, Brook Trout, and hybrid trout in Henrys Lake and found that 73% of radio-tagged fish ($n = 40$) were in shoreline habitats during the winter. In river systems, YCT have been documented moving into areas with groundwater influence when water temperatures drop below 1.0°C (Harper and Farag 2004). Unlike YCT, UTC were located in deeper waters away from the shoreline. Likewise, UTC in Hebgen Lake were documented moving into deeper water during periods with ice cover (Graham 1961).

The current study provides much-needed insight into UTC and YCT distribution and habitat relationships. Utah Chub have been associated with declines in salmonid growth and abundance in other systems (Hazzard 1935; Davis 1940; Schneidervin and Hubert 1987; Teuscher and Luecke 1996; Winters and Budy 2015). Limited information

TABLE 3. Parameter estimates and 95% confidence limits (CLs) from averaged top regression models for resource selection of Yellowstone Cutthroat Trout (YCT) and Utah Chub (UTC) in Henrys Lake, Idaho (2019–2020). Explanatory variables include water depth, percent macrophyte cover, water temperature, and dissolved oxygen. The probability of UTC was included as a covariate in YCT models, and probability of YCT was included as a covariate in UTC models.

Model set	Parameter	Parameter estimate	Upper CL	Lower CL
YCT habitat Jun	Depth	−0.88	−0.43	−1.34
	Dissolved oxygen	−0.18	0.33	−0.70
	Temperature	0.11	0.52	0.30
	Probability of UTC	0.01	0.15	−0.13
YCT habitat Jul	Depth	−0.84	−0.45	−1.23
	Probability of UTC	0.26	0.81	−0.28
	Dissolved oxygen	0.01	0.22	−0.19
YCT habitat Aug	Temperature	−1.74	−0.70	−2.78
	Dissolved oxygen	−1.52	−0.33	−2.71
	Macrophyte cover	0.02	0.06	−0.02
	Depth	−0.68	0.93	−2.29
UTC habitat Jun	Temperature	0.13	0.54	−0.29
	Macrophyte cover	0.04	0.05	0.02
	Probability of YCT	0.05	0.26	−0.17
UTC habitat Jul	Temperature	1.19	1.78	0.60
	Probability of YCT	0.18	0.45	−0.09
UTC habitat Aug	Dissolved oxygen	−3.37	−1.36	−6.09
	Macrophyte cover	0.02	0.05	−0.02
	Depth	−0.35	0.67	−1.37

exists about UTC ecology and the potential for UTC and salmonids to occupy similar habitats. In Henrys Lake, minimal spatial overlap was observed between YCT and UTC. Water temperature, macrophyte cover, and depth appeared to influence distribution patterns of both YCT and UTC. Although water temperatures in Henrys Lake have exceeded 25.0°C in other years, water temperatures peaked at 21.7°C during this research. Patterns in YCT and UTC spatial overlap during a year with higher water temperatures may differ from what we observed during our study. Continued monitoring is important during periods of warmer water temperatures and as the UTC population continues to increase. Distribution and overlap patterns may be different for YCT and UTC at early life stages. Not all age-classes and size-classes were included in this study due to the nature of telemetry equipment and the difficulty in sampling small fishes. Evaluation of distribution and habitat relationships of YCT and UTC at early life stages is warranted. Even so, results of this study fill knowledge gaps in UTC and adfluvial YCT ecology. Habitat relationships and distribution patterns identified in this study are likely not unique to Henrys Lake, but additional research is needed to make comparisons across systems. Nevertheless, results from this study can inform management of UTC and adfluvial trout. Adfluvial trout provide economically and socially important fisheries that function differently than other life histories, so understanding their ecology is critical for management and conservation. Resource managers can use information provided by this study to guide conservation efforts for adfluvial trout and mitigate potential negative effects of introduced UTC across the western United States.

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