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**Population connectivity of adfluvial and stream-resident Lahontan cutthroat trout:
Implications for resilience, management, and restoration**

Authors:

- Teresa Campbell, University of Nevada, Reno, Global Water Center and Biology Department, 1664 N. Virginia Street, Reno, NV 89557-0314, USA, 775-682-6066, tcampbs@gmail.com (corresponding author)
- James Simmons, University of Nevada, Reno, Global Water Center and Biology Department, 1664 N. Virginia Street, Reno, NV 89557-0314, USA, jamessimmons@nevada.unr.edu
- Jessica Sáenz, Summit Lake Paiute Tribe, 1001 Rock Blvd, Sparks, NV 89431, USA, jessaenz@gmail.com
- Christopher L. Jerde, University of California, Santa Barbara, Marine Science Institute, CA 93106, USA, cjerde@ucsb.edu
- William Cowan, Summit Lake Paiute Tribe, 1001 Rock Blvd, Sparks, NV 89431, USA, william.cowan@summitlaketribe.org
- Sudeep Chandra, University of Nevada, Reno, Global Water Center and Biology Department, 1664 N. Virginia Street, Reno, NV 89557-0314, USA, sudeep@unr.edu
- Zeb Hogan, University of Nevada, Reno, Global Water Center and Biology Department, 1664 N. Virginia Street, Reno, NV 89557-0314, USA, zhogan@unr.edu

19 ABSTRACT

20 Population connectivity between resident and migratory cutthroat trout is understudied,
21 but has implications for population viability and management. We examined evidence for stream
22 residency, studied the spatial patterns of stream use by adfluvial and stream-resident trout, and
23 measured migration rates with changing stream depth for Lahontan cutthroat trout in the Summit
24 Lake Basin, Nevada (USA). Passive Integrated Transponder (PIT) technology and a fry trap
25 were used to track fish movements and identify the distribution of resident and adfluvial trout.
26 Stream residents were distributed throughout the network. Adfluvial spawners concentrated in
27 lower reaches, but also migrated up to 12.9 km. Adfluvial juveniles migrated to the lake from
28 lower reaches and from upstream of adfluvial spawners. High stream depths coincided with more
29 adfluvial juveniles migrating to the lake and more adfluvial spawners moving into the stream,
30 which led to more accessing the upper watershed. This work shows that connectivity is central to
31 adfluvial-resident Lahontan cutthroat trout population dynamics and may lead to increased
32 probability of persistence – a characteristic of these isolated, threatened trout populations.

33 INTRODUCTION

34 Population connectivity—the rate of exchange of individuals between habitat patches or
35 sub-populations (Cowen et al. 2006)—is an integral characteristic that defines genetic structure
36 (Webster et al. 2002) and metapopulation dynamics (Harrison and Taylor 1997) of wildlife
37 populations. High connectivity can improve a populations' probability of persistence by
38 increasing resilience to environmental variation and catastrophic events (Hilderbrand 2003;
39 Stacey and Taper 1992). In contrast, habitat fragmentation caused by roads, dams, and
40 environmental degradation (among others) has demonstrably reduced genetic diversity (Epps et
41 al. 2005), restricted access to habitats required for life cycle completion (Billard and Lecointre
42 2001), and caused local extinctions (Dennis and Eales 1997). Measuring population connectivity
43 across space and time enables identification and protection of critical habitats (Webster et al.
44 2002), clarification of metapopulation dynamics (Harrison and Taylor 1997), and effective
45 management practices (Rieman and Dunham 2000; Schtickzelle and Quinn 2007) that can
46 ultimately improve the long term survival of species and populations (Frank and Wissel 1998;
47 Lande and Barrowclough 1987).

48 The salmonids are ideal organisms for the study of population connectivity across
49 landscapes, having high dispersal ability, diverse life history strategies, and varied rates of
50 homing and straying (Rieman and Dunham 2000). While metapopulation structures of
51 anadromous salmon over various spatial scales have received much attention (e.g. Schtickzelle
52 and Quinn 2007), other areas of research in salmonid population connectivity are still developing
53 (Rieman and Dunham 2000), including interactions between different migratory forms
54 occupying the same watershed (e.g. Al-Chokhachy and Budy 2008; Kendall et al. 2015).
55 Cutthroat trout (*Oncorhynchus clarkii* spp.) are particularly understudied in this area. Cutthroat

trout exhibit diverse migratory strategies, including stream-resident and adfluvial life histories (Behnke 1992). Although Kaeding and Boltz (2001) demonstrated high spatial overlap between fluvial and allacustrine Yellowstone cutthroat trout during spawning, the prevalence, distribution, and reproductive isolation of cutthroat trout life histories within watersheds require more study. Most active research on migrant-resident interactions is focused on brook trout (*Salvelinus fontinalis*; e.g. Kusnierz et al. 2014; Ridgway 2008; Scribner et al. 2012) or rainbow trout-steelhead (*O. mykiss*; e.g. Leitwein et al. 2017; Narum et al. 2004; Zimmerman and Reeves 2000) systems. These species exhibit diverse population structures: migratory and non-migratory forms can be reproductively isolated (Narum et al. 2004; Zimmerman and Reeves 2000) or genetically undifferentiated (Leitwein et al. 2017; Ridgway 2008), inhabit the same sections of stream (Mills et al. 2012) or show greater spatial separation (Kusnierz et al. 2009). Although the one consensus may be that salmonid population structures are highly variable (Dodson et al. 2013; Kendall et al. 2015; Rieman and Dunham 2000), it is clear that landscape connectivity is essential for the proper functioning of populations (Pringle 2003).

The Lahontan cutthroat trout (*O. c. henshawi*, hereafter referred to as LCT) is a species of enormous cultural, economic, and recreational value that once populated 11 lakes and numerous streams across the Lahontan Basin of northern Nevada, northeastern California, and southeastern Oregon, USA (Gerstung 1988). Eight of these native adfluvial populations were extirpated by the early 1900s due, in part, to severed connections between lakes and their tributaries (USFWS 2009). Another population in Walker Lake, Nevada followed suit in 2010 (NDOW 2017). The LCT is now federally listed as threatened and persists naturally in only two of its native lakes (USFWS 2009) – Independence Lake, California and Summit Lake, Nevada – representing only 0.4% of the historical lake-stream habitat connections. Consequently, understanding population

connections across lake and stream habitats is integral to the restoration of the species. It is well known that adfluvial LCT require lotic habitat to spawn and reproduce (Hickman and Raleigh 1982). Less well understood is the spatial pattern of spawning activity by adfluvial LCT throughout a stream or river network. Early anecdotal reports of spawning migrations indicate that LCT from Walker Lake migrated up to 200 km (Gerstung 1988) and LCT from Pyramid Lake, Nevada migrated 160 km up the Truckee River to tributaries of Lake Tahoe, California/Nevada (Sumner 1940). The degree of spawning activity in low gradient tributaries versus high gradient headwater streams has not been documented. Other migratory salmonids have been shown to use whole river networks (Mills et al. 2012) or exhibit a preference for either upstream (Saiget et al. 2007) or downstream (Isaak and Thurow 2006; Roberts and Fausch 2015) reaches. For rivers like the Truckee, where fish passage above barriers is being improved (USFWS 2009), knowledge of connectivity patterns and critical spawning areas can help prioritize fish passage and habitat restoration projects.

Stream residents contribute to population viability via resilience to environmental perturbations (Campbell 2017) and contribution of individuals and genetic material to adfluvial populations (Courter et al. 2013; Harrison and Taylor 1997). In steelhead systems, resident rainbow trout co-occur with anadromous steelhead in spawning tributaries (Mills et al. 2012) and their proportional occurrence often increases with altitude (Dodson et al. 2013). However, for LCT residing in streams with an intact hydrologic connection to a lake, the proportional occurrence of stream residents and adfluvial juveniles within the stream, and the spatial distribution and co-existence of these life histories, remain unstudied. Understanding population traits, and whether life history expression is obligate or facultative, is essential for effective

management and has direct implications for population resilience to environmental change (Rieman and Dunham 2000).

Although eighty-two percent of native LCT populations where adfluvial-resident dynamics could have been studied have been eliminated, the population in the Summit Lake Basin, Nevada remains viable and free of non-native salmonids that alter LCT distributions and ecology in other systems (USFWS 2009). There are also no artificial barriers to LCT migration in the stream network that feeds Summit Lake. Therefore, the Summit Lake Basin presents a unique opportunity to study natural adfluvial and resident LCT migrations, spatial distribution patterns, and population connections across lake and stream habitats. We studied LCT migrations between Summit Lake and its tributary, Mahogany Creek, and the distributions of resident and adfluvial fish within the stream network to assess the connectivity of the population across lake and stream environments. Our objectives were to: (1) evaluate evidence for stream residency, (2) delimit the spatial patterns of stream use by adfluvial and stream-resident LCT, and (3) assess population connectivity by quantifying the exchange of individuals between the lake and stream environments as a function of changing stream depth.

METHODS

Study Area

Summit Lake is a small, high-desert, terminal lake in Humboldt County, Nevada, USA (41.5152674°N, -119.063163°W) located on the Summit Lake Paiute Tribe Reservation (Fig. 1). It has a maximum depth of approximately 12 m and a surface area of approximately 324 ha (Curry and Melhorn 1990). Summit Lake is fed by two tributaries: Mahogany Creek and Snow Creek. Snow Creek has a tenuous connection with the lake in low water years due to past

irrigation and grazing use, which degraded the stream channel and led to a large vertical drop near the lake that is a barrier to fish passage. Surveys as recent as the early 2000s showed few to no LCT in Snow Creek (William Cowan, Summit Lake Paiute Tribe, 1001 Rock Blvd, Sparks, NV 89431, USA, personal communication). Mahogany Creek and its main tributary, Summer Camp Creek, are connected to the lake and have healthy in-stream and riparian habitats in most places due to grazing exclosures constructed in the 1970s (Dahlem 1979). Mahogany Creek and Summer Camp Creek support the spawning migration of adfluvial LCT and a population of smaller LCT thought to be composed of juvenile adfluvial fish and stream residents (juvenile and adult). Together, these streams provide approximately 24 km of stream habitat and have a mean bankfull width of 2.25 m (range = 0.5-6.46 m) and mean maximum bankfull depth of 0.42 m (range = 0.18-0.87 m). Pole Creek, a tributary to upper Mahogany Creek, is an intermittent stream that dries quickly in drought years and was dry for the duration of the study period except during peak spring flows.

From 2012 to 2015, the Summit Lake Basin was in severe drought (Hatchett et al. 2015). The lake elevation dropped 3.2 m between September 2011 and September 2015 and continued to decrease into 2016. During the summer and fall of 2015 and 2016, several areas of the stream dried completely or had extreme low flows, making them seasonal migration barriers. The affected areas included directly upstream of the lake and sections upstream on Mahogany Creek. Despite the low water conditions, in each year of the study, the adfluvial spawning migration numbered in the low hundreds and the stream population remained large (Campbell 2017).

Water depth in Mahogany Creek was measured every fifteen minutes throughout 2015 and 2016 with an Aqua Star Plus pressure transducer just upstream of the lake (Fig. 1). Water depth was used as a surrogate for stream discharge in later analyses because a ratings curve had

not yet been developed for the extreme low flows experienced during the drought. In 2015 and 2016, two stationary Biomark® Passive Integrated Transponder (PIT) tag antennas with IS1001 readers were operated year-round on Mahogany Creek: a lower antenna cable was located just above the lake and an upper cord antenna was just below the confluence with Summer Camp Creek (Fig. 1). These stationary antennas spanned the wetted width of the stream, and therefore likely detected all PIT-tagged fish that swam through (Zydlewski et al. 2006). Downstream of the lower PIT tag antenna, a fry trap was used to monitor out-migrations of small fish from the stream to the lake (Fig. 1). The trap was in place from 14 July to 14 November 2016 and was operated 52 days during that time. The trap was checked daily when it was in operation and all fish were scanned for PIT tags, counted, and measured for fork length (FL) to the nearest millimeter.

Fish Sampling and Tagging

All work followed the guidelines of the American Society of Ichthyologists and Herpetologists and was conducted under the approval of the Institutional Animal Care and Use Committee (protocol #00679). In the spring and fall of 2015 and 2016, fish were captured in the lake ($n = 916$) with trap nets at locations spread evenly throughout the lake (Simmons 2017). Fish were captured in the stream ($n = 1674$ age-0 (< 1 year old) and 693 age-1+ (≥ 1 year old)) in August 2015 and August 2016. The timing of stream fish capture was selected so that age-0 fish would have emerged from the gravel, but not yet migrated to the lake. Fish in the stream were captured by multiple-pass backpack electrofishing surveys using Smith-Root LR-24 electrofishers at sites dispersed throughout the watershed (Fig. 1). Twenty-one sites were planned to be fished, but because 2015 was an extreme drought year, five sites were not sampled due to complete or near desiccation of the stream. In 2016, water levels were high enough to

sample three of the five previously desiccated sites (Fig. 1). All fish from the stream and lake were measured for FL to the nearest millimeter. Fish greater than 100 mm FL were anesthetized with carbon dioxide gas (lake) or MS-222 (stream) and tagged with 12-mm, full duplex PIT tags. Fish greater than or equal to 250 mm FL were tagged in the pelvic girdle; fish less than 250 mm FL were tagged in the abdominal cavity between the pectoral and pelvic fins according to tagging methods recommended by Biomark®. Fish recovered in a pen until they were fully upright and able to swim strongly (at least five to ten minutes) before being returned to the lake or stream. Spot shocking was conducted in areas between stream survey sites in order to increase the sample of tagged fish. In total, 913 fish were tagged in the lake and 237 in the stream (121 in 2015 and 116 in 2016).

Adfluvial adults, age-1+ stream-dwelling trout, and age-0 stream-dwelling trout had distinct size, morphological, and color differences that allowed researchers to make accurate identifications in the field (see Fig. S1 in the Supplementary Material for more detail and photographs). Age-0 and age-1+ trout captured in the stream required additional data to be further identified as adfluvial juveniles, juvenile stream-residents, or mature stream residents.

Evidence for Stream Residency

We evaluated evidence for stream residency in three ways. First, we looked for LCT tagged in the stream in August 2015 that did not leave the stream for the duration of the study period (August 2015 to November 2016). To do this, we searched for tags that were never detected by the lower PIT tag antenna, as in Kusnierz et al. (2009)—which would indicate migration to the lake—and were also detected within the stream after tagging to confirm their presence in the stream. To detect tags within the stream, we conducted three mobile tracking surveys for PIT-tagged fish in 2016 using methods similar to those used by Cucherousset et al.

(2005). The dates for these surveys were 5-21 April, 5-19 May, and 2-20 September, which corresponded to three time periods centered around the adfluvial spawning migration: pre-spawn, during-spawn, and post-spawn. Observers used a Biomark® HPR plus reader with a BP plus mobile antenna and walked the length of Mahogany Creek and Summer Camp Creek, from the lake to the headwaters, in an upstream direction, sweeping the antenna across the stream and underneath overhanging banks. The antenna had a read range of ~30 cm and the reader recorded the time and GPS location of each detected tag. For each detection, we recorded the habitat in which the tag was found and whether the tag was in a live fish or buried in the stream bed. This was determined by whether the tag moved or remained stationary (Bateman et al. 2009) and checked by turning over cobbles. Some areas could not be sampled by mobile tracking due to impenetrable vegetation. Upper headwater habitats where channel width and depth were very small were also not sampled because of the unsuitability of the habitat for LCT and the distance upstream (> 0.5 km) from tagging sites.

Assuming that the tags detected in live fish that never left the stream were stream residents, we calculated the proportion of residents in the stream by dividing the number of resident tags by the number of tags deployed in the stream in August 2015 ($n = 121$). We also calculated the proportions of tags: (1) detected by the lower PIT tag reader, indicating the fish migrated to the lake and was therefore an adfluvial juvenile, (2) detected during mobile tracking surveys buried in the stream bed, which can indicate a shed tag or a mortality, and (3) never detected again after tagging, which represent fish with an uncertain fate.

In our second evaluation of stream residency, we examined differences in body size between fish that remained in the stream and fish that migrated to the lake. Older stream residents should clearly have a larger body size than young juvenile adfluvial trout. Additionally,

among stream-dwelling trout of similar age, larger individuals commonly exhibit residency, due to faster early growth rates causing fish to mature earlier and become residents, or higher metabolic demand at small sizes causing smaller fish to migrate to find greater food resources (Dodson et al. 2013). Therefore, we expected stream residents to have larger body sizes than juvenile adfluvial fish that have yet to migrate to the lake (Morinville and Rasmussen 2003). To examine whether body size was indicative of residency, we assumed that tagged fish remaining in the stream were residents and tagged fish detected by the lower PIT tag antenna were adfluvial juveniles (see prior methods for more detail), and applied Welch's two-sample *t*-test to compare the mean FL of resident LCT with that of out-migrating juvenile adfluvial LCT. The fork length data for out-migrating juveniles included the lengths of LCT tagged in the stream that were detected by the lower PIT tag antenna and also the LCT captured in the fry trap. Fork lengths of individuals captured in the fry trap were only included if they were equal to or greater than 100 mm to make the fry trap data comparable to the PIT tag data (since fish were only tagged if they were ≥ 100 mm FL).

In our third approach to evaluating evidence for stream residency, we looked for age-0 LCT upstream of the uppermost detected adfluvial LCT (as determined by the during-spawn mobile tracking survey in May; see below) because these age-0 fish may have been produced by stream-resident spawners. Sexual maturation and spawning activity of stream-dwelling trout is considered indicative of stream residency (Berejikian et al. 2014, Jonsson and Jonsson 1993, Robillard et al. 2014). Furthermore, we should not find age-0 progeny of adfluvial LCT upstream of where they were spawned because age-0 salmonids usually migrate downstream after emergence (Morrissey and Ferguson 2011, Northcote 1992, Vollestad et al. 2012). Although salmon fry in outlet streams are adapted to make long upstream migrations (~5 km) to reach

rearing lakes (Pon et al. 2007), there is no known evolutionary reason for Summit Lake Basin age-0 LCT to migrate upstream. Additionally, if age-0 fish are found upstream of fry migration barriers (waterfalls with a jump height > 20 cm (Brandt et al. 2005)), it provides even stronger evidence of stream-resident spawning activity. Therefore, the presence of age-0 LCT far upstream (> 1 km) of adfluvial spawners, especially above migration barriers, is indicative of stream-resident spawners in the system.

Spatial Patterns of Stream Use

Adfluvial spawning adults

To understand the distribution of adfluvial spawning LCT within the stream, fish that were PIT-tagged in the lake were detected in the stream by mobile tracking between 5 and 19 May 2016 when the majority of adfluvial spawning adults were within the stream (the spawning migration occurred between 10 April and 9 June 2016; the peak was 4 May 2016). As with the detections of fish tagged in the stream, we recorded the habitat in which the tag was found and whether the tag was in a live fish or buried in the stream bed. Untagged adfluvial spawning adults were also encountered in the stream and were distinguished from stream-dwelling fish—stream residents or adfluvial juveniles—primarily by their large size (Vinyard and Winzeler (2000) found that Summit Lake spawners migrating upstream were ~460 mm FL on average and very few were < 300 mm FL), and also by color patterns and morphology (Fig. S1). When untagged adfluvial spawners were observed, their locations were georeferenced. The GPS locations of all detected and observed adfluvial spawning adults were imported into ArcGIS 10.4.1. For PIT tags detected in the stream bed, only those detected on the lower stationary PIT tag antenna in 2016 were used in the analysis because this showed the fish had entered the stream to spawn in 2016. We used the kernel density spatial analyst tool in ArcMap 10.4.1 to

find areas of high and low spawning activity of adfluvial LCT. The output cell size was set to 10 m and the search radius 300 m. Density maps were produced for tagged and untagged spawners together as well as tagged spawners alone.

We also examined whether the number of adfluvial LCT entering the upper watershed was related to the number of LCT entering the stream at a given time. We hypothesized as more fish entered the stream together, individual fish would be more likely to perceive downstream reaches as not having enough space and choose to move farther upstream to spawn where space was not as limited. For example, Hendry et al. (2001) found that peak spawning densities of sockeye salmon (*O. nerka*) were higher closer to the lake, and certain stream sections were settled first and sustained higher densities of females throughout the spawning season. For our analysis, we used the daily number of LCT entering the stream to spawn (daily counts of tag detections on the lower PIT tag antenna) as the input variable and compared that to the number of those fish that were later detected accessing the upper watershed (counts of tag detections on the upper PIT tag antenna) as the response variable. Thus, if 10 fish entered the stream in one day, and four of those fish were detected by the upper PIT tag antenna at any time in the future, the input value would be 10 and the response value four. Inspecting the distribution of the count data from the upper PIT tag antenna revealed that a zero-inflated Poisson model was necessary for this analysis. The data had a high frequency of zero count values and a steady decline in frequency as count values increased. A zero-inflated Poisson model assumes that a secondary process contributes to the high frequency of zero count values; in this case, that process could include downstream spawning habitat availability (Hendry et al. 2001) or discharge from the upper watershed (Mellina et al. 2005; Zurstadt and Stephan 2004).

A multi-model inference framework (Burnham and Anderson 2002) was used to evaluate the effect of the number of fish entering the creek to spawn on the number entering the upper watershed. Multiple models were compared and ranked using Akaike's information criterion for small sample sizes (AIC_c), which is a model selection approach that favors simpler model structures to avoid over-fitting the data (Burnham and Anderson 2002). We constructed a global, additive model that included the daily number of tagged LCT entering the creek (counts on lower antenna) and year (2015 or 2016) as predictor variables and the number of tagged LCT that entered the upper watershed (counts on upper antenna) as the response variable. We compared this global model to two reduced models, with either year or counts of LCT entering the creek as the predictor variable, and the null model, which has no predictor variables and assumes the trend in the response variable occurs by chance. The top model (lowest AIC_c) was used to calculate variable coefficients because there were no other competitive models with $\Delta AIC_c < 2$ (Burnham and Anderson 2002). If LCT count on the lower PIT tag antenna was included in the top model with a parameter significance of $p < 0.05$, it was taken as evidence that the number of fish entering the stream to spawn had a significant effect on the number entering the upper watershed. This analysis was performed in program R using the MuMIn and pscl packages.

Adfluvial juveniles

We determined stream areas used by juvenile adfluvial LCT by identifying electrofishing sites that had age-1+ LCT that later migrated to the lake. All age-1+ LCT captured and tagged in the stream that were later detected on the lower PIT tag antenna, as in Kusnierz et al. (2009)—and were never again detected in the stream by either the lower antenna, mobile tracking, or electrofishing—were assumed to have migrated to the lake, and thus to be adfluvial juveniles. Sites from which these adfluvial juveniles originated were mapped in ArcMap 10.4.1. Due to the

inability to tag age-0 fish (many adfluvial juveniles migrate to the lake at age-0) and the discrete nature of electrofishing sites, this analysis identified the minimum amount of stream used by adfluvial juveniles.

Stream residents

To delimit the spatial pattern of stream residency, we calculated the proportion of tags classified as residents (fish tagged in the stream that remained in the stream; see prior methods for more detail) at each electrofishing site by dividing the number of residents at a site by the number of tags deployed at the site. We then mapped these proportions (along with the proportions of tags classified as adfluvial juveniles, tags found in the stream bed, and undetected tags) in ArcMap 10.4.1. The mean and range of residency rates for lower Mahogany Creek (below the confluence with Summer Camp Creek), upper Mahogany Creek (above the confluence), and Summer Camp Creek were used to compare rates between these three larger stream sections. To minimize the effects of small sample size on inferences, only sites with at least 3 tags deployed during electrofishing were used for this comparison.

Migration Magnitude and Stream Depth

We assessed population connectivity by quantifying the exchange of individuals between the lake and stream environments as a function of changing stream depth, hypothesizing that more fish would migrate as depth increased. We would have used discharge rather than depth, as stream discharge is known to affect salmonid migrations (Mellina et al. 2005; Zurstadt and Stephan 2004), but we did not have a continuous data set of discharge for the study period. Nevertheless, depth is closely linked to discharge and water depths were so low during the study period (0 cm in certain times and places) that depth was likely a significant factor in the decision to migrate. Therefore, we examined whether mean daily stream depth in lower Mahogany Creek

affected daily counts of adfluvial LCT entering Mahogany Creek to spawn or counts of age-0 and age-1+ LCT migrating from the stream to the lake. Counts of PIT-tagged LCT detected on the lower PIT tag antenna were used to estimate the number entering the stream from the lake. Fry trap capture data were used to estimate the number of juveniles leaving the stream for the lake. The analyses were restricted to the dates between the first and last days LCT were detected by the antenna or captured in the trap.

Inspecting the distribution of the count data from both the lower PIT tag antenna and the fry trap revealed that a zero-inflated Poisson model was appropriate for examining the relationship between stream depth and migration magnitude. Spawning and other migrations are initiated by environmental cues other than water depth, including water temperature and discharge (Mellina et al. 2005; Zurstadt and Stephan 2004), which could explain the high frequency of zero values. The same multi-model inference framework (Burnham and Anderson 2002) described above was used to evaluate the effect of stream depth on the number of adfluvial LCT migrating from the lake upstream through the lower PIT tag reader and the number of juvenile LCT migrating downstream through the fry trap. For adfluvial spawning migrations, we compared a global, additive model with the predictor variables year (2015 or 2016) and stream depth (m) to models with year and stream depth alone and the null model. For out-migrations through the fry trap, we compared a global, additive model with the predictor variables age class (age-0 or age-1) and stream depth (m) to models with age class and stream depth alone and the null model. For juvenile out-migrations, the top model (lowest AIC_c) was used to calculate variable coefficients because there were no other competitive models with $\Delta AIC_c < 2$. However, for adfluvial spawning migrations, model averaging was used with the set of competitive models

with $\Delta AIC_c < 2$. If stream depth was included in the top model with a parameter significance of $p < 0.05$, it was taken as evidence that stream depth was influential on migration magnitude.

RESULTS

Detection Efficiency of PIT Tag Antennas

We evaluated the detection efficiency of the lower PIT tag antenna during the study by checking to see if any adfluvial spawners that were PIT-tagged in the lake were captured in a weir on Mahogany Creek (~4 km upstream of the lake) on their upstream migration, but not detected by the lower PIT tag antenna (just upstream of the lake). This would indicate imperfect tag detection. There was no comparable method of testing the efficiency of the upper antenna. Across the two study years, 291 fish that were tagged in the lake were captured in the weir; 285 of those fish were detected by the lower PIT tag antenna. Therefore, six out of 291 lake-tagged fish that made it to the weir were not detected by the lower PIT tag antenna, giving the antenna 97.8% detection efficiency.

We were unable to directly evaluate the mobile PIT tag antenna's detection efficiency due to permit restrictions on leaving block nets in the stream long enough for newly tagged fish to fully recover and re-acclimate from tagging and re-distribute themselves through the stream. However, over the course of the three mobile tracking surveys in 2016, 51 out of the 121 tags deployed into stream-dwelling fish in 2015 were detected by mobile tracking in 2016, for a 42% detection rate, which is normal for this type of survey for salmonids (Cucherousset et al. 2010). There were some instances where tags detected in the stream by mobile tracking could not be definitively classified as being in a live fish or in the stream bed due to detections that were discovered on the reader after the fact and thus could not be verified in the field. It was also

noticed near the end of the second survey that small trout sometimes hid underneath cobbles and did not emerge while being scanned with the PIT tag antenna; therefore, there were possibly some tags classified as “stream bed” that may have been in live fish. Reviewing the data and field notes revealed a maximum of 10 out of 75 detections that may have been misclassified in these ways, yielding a maximum misclassification rate of 15%. This rate is conservative for two reasons. First, for detections that were noticed after the fact, we could use the number of times the tag was logged by the reader as an indication of whether it was in a live fish (few logs indicated it was likely in a fish that moved away from the antenna; many logs indicated it was likely in the stream bed). Second, it is probable that many of the tags identified as “stream bed” in the first two surveys were in fact in the stream bed, even if they were not verified by turning over cobbles to look for fish. Thus, misclassification is expected to have a minimal effect on the estimates of tags classified as resident and “stream bed” and the inferences thereafter. These classification errors were not a factor for adfluvial spawners because their large size made it easy to confirm their presence in the field and also prevented them from hiding under cobbles.

Evidence for Stream Residency

Twenty-four percent of fish tagged in 2015 were classified as stream residents based on the assumption that fish detected as alive within the stream in 2016 were residents. Between the lower PIT tag antenna and the three mobile tracking surveys in 2016, 58 of the 121 PIT tags implanted in stream fish in 2015 were detected. Fifty-one were detected by mobile tracking (this is less than the 75 detections listed above because some tags were detected multiple times); seven were detected by the lower PIT tag antenna and never re-detected within the stream (thus assumed to be adfluvial juveniles). One was detected by both methods, first in a live fish by mobile tracking on 7 April, then on the lower PIT tag antenna on 29 April 2016. This tag was

classified as an adfluvial juvenile. Sixty-three tags were never detected. Furthermore, of the 51 tags detected in the stream, 29 were in live fish and 28 were in the stream bed. Six of the stream bed tags were first detected in live fish on an early mobile tracking survey and then were detected again during the final, post-spawn survey in the stream bed; those six tags were classified as resident. Therefore, the total number of stream-tagged LCT in each category was: 29 resident (24% of total tagged), 7 juvenile adfluvial (6%), 22 stream bed (18%), and 63 undetected (52%).

Fork lengths of all fish captured in the stream ranged from 21–272 mm (mean = 72 mm), whereas fork lengths of fish captured in the lake ranged from 80–731 mm (mean = 489 mm). As hypothesized, fish classified as residents tended to be larger in size than those classified as adfluvial juveniles. Results of Welch's *t*-test indicated that the mean fork length of residents (134.2 mm, *SE* = 6.7, *n* = 29) was significantly greater than that of adfluvial juveniles (118.1 mm, *SE* = 1.3, *n* = 67). Although residents spanned nearly the entire size distribution of tagged fish, ranging from 102 to 272 mm, adfluvial juveniles were only the smaller sizes, ranging from 100 to 146 mm.

Age-0 LCT were also found upstream of adfluvial spawners, indicating spawning activity of stream residents. Two electrofishing sites above the upstream-most detected adfluvial spawner in Summer Camp Creek (9.7 km; see below) in May 2016 had age-0 LCT present in August 2016. These sites were the second and third upstream-most sites on Summer Camp Creek (Fig. 1) and were 1.7 and 2.4 km upstream of the upstream-most adfluvial LCT. A waterfall with a jump height of 56 cm was located between those two sites, forming an impassable barrier for age-0 fish (Brandt et al. 2005). One-hundred fifty age-0 fish were found at the site 1.7 km upstream and 3 age-0 fish were found at the site 2.4 km upstream. Anecdotally, age-0 LCT were

also observed by one of the authors in July 2015 at the upstream-most site on Summer Camp Creek (Fig. 1), which is both above the waterfall and 3.4 km upstream of the upstream-most adfluvial spawner in 2016. In further support of these age-0 fish being produced by stream residents was the observation of large age-1+ LCT (> 150 mm FL) at all of these sites in both years that may have been the stream-resident parents of these offspring (Downs et al. 1997).

Spatial Patterns of Stream Use

Adfluvial spawning adults

The highest densities of adfluvial spawning LCT were in the lower part of the stream below the confluence with Summer Camp Creek (Fig. 2). Fifty-eight PIT-tagged and 72 untagged adfluvial LCT were detected and observed during the mobile tracking survey. The average migration distance was 4.9 km upstream from the lake ($SE = 0.19$) and the maximum migration distance was 12.9 km. Three PIT-tagged and one untagged adfluvial LCT were detected above the Summer Camp Creek confluence: one tagged and one untagged fish were observed alive 9.7 km upstream from the lake in Summer Camp Creek; two adfluvial tags were found in the sediment 9.9 and 12.9 km upstream from the lake in Upper Mahogany Creek. We also mapped the adfluvial spawning densities excluding the observations of untagged fish, and the distribution of densities was nearly identical to that with both detections and observations shown in Figure 2.

As hypothesized, the number of adfluvial LCT that entered the upper watershed increased with the number that entered the stream to spawn during a given day (Fig. 3). On the lower PIT tag antenna, 221 adfluvial LCT were detected in 2015 and 310 in 2016. On the upper PIT tag antenna, 21 were detected in 2015 and 94 in 2016. The global model that included the predictor variables year and LCT count on the lower PIT tag antenna was the only model supported by

multi-model inference ($\Delta AIC_c = 0$, $w = 0.999$; Table 1), indicating that both year and the number of LCT entering the stream at a given time impacted the number of LCT that accessed the upper watershed to spawn. All other models had a $\Delta AIC_c > 13$, showing they were not supported. In the global model, LCT count had a highly significant, positive effect ($c = 1.05$, 95% CI [1.04, 1.06]) on the number entering the upper watershed (Table 2), showing that when more fish entered the stream together on a given day, then more of those fish entered the upper watershed at some time in the future. The year effect was non-significant, but indicated that the number of spawners entering the upper watershed was greater in 2016 than 2015 for a given number of spawners entering the creek ($c = 1.43$, 95% CI [0.85, 2.43]).

Adfluvial juveniles

Juvenile adfluvial out-migrations originated predominantly from locations in lower Mahogany Creek, but also from farther upstream (Fig. 4a-b). Of the 121 LCT tagged in the stream in August 2015, seven migrated to the lake (see prior results for more detail). These fish were detected on the lower PIT tag antenna between 27 March and 28 May 2016 and migrated from sites both above and below the confluence with Summer Camp Creek (Fig. 4a). None of the fish tagged in 2015 out-migrated in the fall of 2015. Of the 116 fish tagged in the stream in August 2016, three migrated to the lake between 22 September and 24 October 2016. These three migrated from sites below the confluence with Summer Camp Creek (Fig. 4b).

Stream residents

Fish classified as stream residents were detected at sites throughout the system, but in varying proportions (Fig. 4c). The highest residency rates were found at sites in Summer Camp Creek (mean = 44%, range = 33-55%, $n = 5$), followed by lower Mahogany Creek (mean = 16%, range = 0-38%, $n = 4$) and upper Mahogany Creek (mean = 8%, range = 0-17%, $n = 2$). Despite

the observed variation, the small sample sizes precluded statistical evaluation of the spatial distribution of stream residents.

Migration Magnitude and Stream Depth

Higher numbers of adfluvial LCT tended to enter the stream to spawn when water depths were greater (Fig. 5). Adfluvial LCT were detected entering Mahogany Creek by the lower PIT tag antenna between 27 March and 23 June 2016. Modeling results supported stream depth as influencing the daily number of adfluvial spawning migrations. The most supported model ($\Delta AIC_c = 0.00$, $w = 0.667$) was the global model that included stream depth and year as predictor variables, indicating that both of these variables affected the daily number of spawners entering the creek, but the second-best model was also competitive ($\Delta AIC_c = 1.39$, $w = 0.333$) and only included stream depth, showing that the year effect was not as important (Table 1). Models without the stream depth parameter were not supported ($\Delta AIC_c > 30$, $w = 0.00$). In the top and second-best models, stream depth had a highly significant, positive effect on the number of adfluvial LCT entering the stream to spawn; in the top model, year had a non-significant, negative effect (Table 2). The averaged model also showed a highly significant, positive effect of stream depth and a non-significant, negative effect of year. The model-averaged coefficients for stream depth and year were 686.98 (95% CI [27.03, $1.7E^4$]) and 0.81 (95% CI [0.60, 1.10]), respectively, indicating that a 0.1 m increase in stream depth led to 69 more fish migrating per day, and that 19% fewer fish were likely to spawn in 2016 than 2015 for a given depth.

Higher counts of LCT in the fry trap also corresponded to greater stream depths (Fig. 5). LCT were found in the fry trap beginning 14 July (when the trap was set up) and ending 7 November 2016. Three hundred ten age-0 and 74 age-1+ fish were captured. PIT-tagged out-migrants probably migrated during times when the trap was not in operation because none of the

fish captured in the trap already had been previously PIT-tagged. Ninety-six percent of the age-0 out-migration and 89% of the age-1+ out-migration occurred between 21 September and 7 November. The only model of daily out-migrations that was supported by multi-model inference was the global model with stream depth and age as predictor variables ($\Delta AIC_c = 0.00$, $w = 1$; Table 1). All other models without either stream depth or age had a $\Delta AIC_c > 90$ and $w = 0$. These results indicated that stream depth and age affected the daily number of out-migrations. In the top model, both stream depth and age had highly significant effects on the magnitude of daily out-migrations (Table 2), although the effect size for stream depth ($c = 8.8E^6$, 95% CI [$3.0E^5$, $2.5E^8$]) seemed higher than reality, indicating that $8.8E^5$ more fish out-migrated for a 0.1 m increase in water depth. The effect size for age ($c = 0.21$, 95% CI [0.16, 0.27]), indicating that 79% fewer age-1 than age-0 fish migrated for a given water depth, seemed more reasonable, but still lower than expected after visual examination of the data presented in Figure 5. These results were probably heavily influenced by the three outliers in age-0 out-migration days (Fig. 5).

DISCUSSION

Much of LCT restoration in lakes is focused on the success of the adfluvial component of the population (USFWS 2009). However, the population of stream-dwelling LCT in the Summit Lake Basin showed signs of a self-sustaining, stream-resident component that could be important to the health and viability of the broader population. Multiple lines of inquiry provided evidence for stream residency in this population, including a high proportion (24%) of tagged fish that remained in the stream over the two-year study period and were larger than fish that migrated to the lake. There was also strong evidence of stream-resident spawning activity in Summer Camp Creek. In fact, the high proportions of fish classified as residents (Fig. 4c), evidence of resident

513 spawning activity, and little to no adfluvial spawner presence in Summer Camp Creek (Fig. 2)
514 suggest a robust population of stream residents in this tributary. It was also from this area that
515 one adfluvial juvenile in 2015 migrated to the lake from above the detected upstream limit of the
516 adfluvial spawning migration in 2016 (Figs. 2 and 4a,c) and also above the waterfall on Summer
517 Camp Creek. Although it is not definitive, this individual could be the offspring of stream-
518 resident parents and could represent population connectivity between resident and adfluvial
519 populations. The phenomenon of stream-resident offspring adopting migratory life histories,
520 known as partial migration (Jonsson and Jonsson 1993), is documented in closely-related species
521 (Courter et al. 2013) and can explain the current success of reintroduced LCT to Pyramid Lake
522 (Schweber 2013, Springer 2007). Emigration of individuals from stream-resident to adfluvial
523 populations can reduce the extinction risk of the adfluvial population even if it occurs at low
524 rates (Hilderbrand 2003, Stacey and Taper 1992). This dynamic is especially relevant in drought
525 contexts, during which lake populations have been shown to decline steeply while stream
526 populations remain robust (Campbell 2017). It also may be the mechanism by which Walker
527 Basin LCT repopulated Walker Lake after it dried out approximately 2,000 years ago (Bradbury
528 et al. 1990, Gerstung 1988). While this study focused on movement patterns, genetic testing may
529 be necessary to test for true connectivity between stream-resident and adfluvial populations.

530 Although we observed a single instance of potential out-migration from the stream-
531 resident to the adfluvial population, the contribution of stream residents to the adfluvial
532 population could increase in years with increased water depth and fish mobility. The stream
533 depths in 2016 were low enough in places to suppress fish movement. As depths return to
534 normal, we may see increased movements from the stream to the lake. As an illustration, in
535 2015, we saw no tagged individuals migrate from the stream to the lake in the fall, but in 2016

536 we detected three out-migrations between 22 September and 24 October. This could be due to
537 the slightly greater water depths in 2016 compared to 2015 during that time period (Fig. 6).
538 Additionally, the fry trap tended to capture higher numbers of juvenile adfluvial LCT during
539 periods of greater stream depth and stream flow surges caused by precipitation events (Fig. 5),
540 suggesting stronger population connectivity with better hydrologic connectivity. In highly-
541 regulated rivers, maintaining appropriate stream depths will facilitate movement between
542 habitats and preserve exchange and gene flow between adfluvial and resident trout. This dynamic
543 can promote the recolonization of unoccupied habitats and the resilience of the population as a
544 whole (Harrison and Taylor 1997). We recommend leaving depth gauges in the stream so that
545 these relationships can be investigated on a longer time scale across a greater range of water
546 levels. Long-term monitoring of these relationships is also important for understanding any
547 temporal or spatial dependencies that may be present in these models (including the spawner
548 upstream migration model).

549 We demonstrated that resident and adfluvial LCT in the Summit Lake Basin have high
550 spatial connectivity. Adfluvial spawners migrated as far as the headwaters to spawn (Fig. 2) and
551 adfluvial juveniles and stream residents were found at sites throughout the stream network (Fig.
552 4c). We have some evidence that the pattern of residency observed in the Summit Lake system
553 was habitat driven. Despite a weak tendency for residency to increase with altitude from lower
554 Mahogany Creek up through Summer Camp Creek, upper Mahogany Creek had the lowest rates
555 of residency out of the three stream sections (Fig. 4c). During our study period, Summer Camp
556 Creek had more gravel and cobbles, greater wetted depths, and more pools than upper Mahogany
557 Creek. These characteristics are not only good for cutthroat trout in general (Hickman and
558 Raleigh 1982; Young 1996), but stream-resident trout prefer pools over riffle habitats

(Morinville and Rasmussen 2006). For LCT restoration, protecting stream habitat that sustains residents is just as important as protecting habitat for adfluvial spawners and juveniles.

In contrast to findings by Saiget et al. (2007) with coastal cutthroat trout (*O. c. clarkii*), adfluvial LCT in the Summit Lake Basin used low-altitude reaches the most intensely. These reaches had the highest densities of adfluvial spawners (Fig. 2) and saw the majority of adfluvial juvenile out-migrations (Fig. 4a-b). Higher adfluvial use in these downstream reaches was probably due to greater water depths (Zimmerman and Reeves 2000) combined with smaller costs of migration associated with shorter migration distances (Jonsson et al. 1997). In river systems, these low-altitude reaches tend to be the most severely degraded (Pringle 2001), as is the case for several native LCT lakes (USFWS 2009). Channelization of and dams on the Truckee River alter the natural flow regime and impede fish passage from Pyramid Lake (USFWS 2009). The Walker River, Nevada has poor water quality, high sedimentation, and rarely connects to Walker Lake due to water diversions that severely reduce stream flows (USFWS 2009). Habitat restoration in these areas is critical to the restoration of viable LCT populations. We also demonstrated that the magnitude of LCT spawning migrations increased with water depth and there was likely a threshold water depth below which adfluvial LCT would not enter the stream to spawn (Fig. 5). Appropriate flow regimes and water depths are critical to spawning and reproductive success (Muhlfeld 2002). Therefore, returning LCT populations to a self-sustaining state will also require appropriate water depth and flow.

Although we found the highest adfluvial stream use in low-altitude reaches, the importance of high-altitude reaches to the adfluvial population should not be discounted. Even in a low water year, four spawning migrations above the Summer Camp Creek confluence were observed (Fig. 2). Additionally, more spawning LCT accessed the upper watershed as more

entered the stream (Fig. 3), which in turn increased with stream depth (Fig. 5). Isaak and Thurow (2006) found that certain stream reaches were always the most heavily accessed by spawning Chinook salmon (*O. tshawytscha*), but that salmon expanded into other reaches in years of higher abundance. With the small increase in stream depth in our system between 2015 and 2016 (Fig. 6), we already observed a larger adfluvial spawning migration; as the basin recovers from drought, we may see increased numbers of adfluvial LCT accessing the stream and the upper watershed to spawn. Therefore, spatial connectivity between lower and upper reaches can not only provide an avenue for stream-resident offspring to supplement the adfluvial population, but can also help maximize the reproductive success of adfluvial adults by providing access to more spawning habitat.

We acknowledge that the high rate of tags found in the stream bed during our study indicates either high mortality or that fish were shedding their tags, which could bias the estimates of residency and migrancy present within the stream population. The six tags that were detected in live stream-dwelling fish during early mobile tracking surveys and then detected as “in the stream bed” during the post-spawn survey may have been shed during spawning. Also, personnel were new to PIT-tagging in 2015, which is known to decrease tag retention rates (Meyer et al. 2011). The size distribution of fish whose tags were later found in the stream bed was similar to the distribution of sizes of all tagged fish, indicating there was no size-dependency in the rate of tag loss. If these tags are in fact sheds, we do not believe it changes the implications of our results. If there were more migrants or residents than what we have shown here, it would only strengthen the conclusion that whole-watershed connectivity is central to the long-term success of native, self-sustaining populations of cutthroat trout. Additional years of surveying and tagging with experienced personnel will help refine these estimates.

Although the detection efficiency of the lower PIT tag antenna was very high (97.8%) and that of the mobile antenna (42%) was within the normal range for salmonids (Cucherousset et al. 2010), many tags (52%) deployed into stream fish were never detected. The most likely reasons for not detecting tags were: 1) imperfect detection on mobile tracking surveys due to limited read range (not detecting tagged fish that were present in the stream, but out of range of the antenna); 2) fish movement within the stream (e.g. a fish moving from a reach that had not yet been sampled to a reach that had already been sampled in between survey days); and 3) fish being removed from the stream by predators and consumed away from the stream such that their tags would not be present in the stream bed. One tag was found on the bank during a mobile tracking survey, suggesting consumption by a predator. Imperfect detection during mobile tracking also applies, albeit to a lesser degree, to detecting adfluvial spawners within the stream during their spawning migration. Adfluvial spawners were easier to detect due to their large size that makes them more visible, but it is likely that many were missed between survey days due to their movement within the stream. Thus, it is also possible that the upper extent of the spawning migration was farther upstream than detected. We believe it is unlikely that spawners migrated much farther than detected for two reasons: 1) the during-spawn tracking survey was conducted during the peak of the spawning migration and should have captured a good representation of the spawner distribution; 2) during the study, stream depth decreased rapidly with distance upstream from the Summer Camp Creek confluence and probably precluded the majority of spawners. However, these justifications do not eliminate the possibility that adfluvial spawners migrated farther upstream than the upper detected extent. Ways to improve detection efficiency of mobile tracking include development of mobile antennas with a longer read range and development of a

627 method of charging the reader battery in the field so researchers can perform the survey in a
628 more continuous fashion without having to return to camp to charge batteries.

629 We also recognize that our first two approaches to evaluating stream residency depend on
630 the assumption that the fish we classified as residents do not migrate to the lake in the future.
631 The significant difference in body size between fish that remained in the stream and fish that out-
632 migrated lends some support to the assumption that, especially for larger fish, there may in fact
633 be some difference in physiology or life history. However, the question of whether these fish will
634 never out-migrate at some future date is something that can only be evaluated with long-term
635 monitoring and a factor to consider when drawing conclusions from this study. It also speaks to
636 the importance of long-term monitoring of movement and additional research on the age
637 structure, growth rates, and maturation of stream-dwelling LCT in order to truly understand the
638 composition of stream-residents and adfluvial juveniles, and the broader ecological significance
639 of the stream-dwelling group of fish to the population as a whole.

640 This study highlighted the importance of maintaining strong connections between healthy
641 lake and stream habitats for adfluvial populations of cutthroat trout. This may be the first attempt
642 to document these dynamics in a freshwater, resident-adfluvial cutthroat trout system. Therefore,
643 these findings can be useful to managers of other cutthroat species, most of which are protected.
644 Conserving stream or river habitat that promotes the stream-resident life history, especially in
645 upstream reaches, should increase population resilience to environmental stochasticity via
646 exchange of individuals between resident and adfluvial populations. Interactions between
647 adfluvial and resident fish should increase with better hydrologic connectivity. Extensive use of
648 the stream network by both adfluvial and resident trout, and increased migration rates with
649 increasing stream depth, show that landscape connectivity contributes to the viability of this

population. Preserving or enhancing that connectivity will increase the probability of persistence of threatened populations of cutthroat trout.

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TABLES

Table 1. Model selection table for all models considered in the study.

Model Set ^a	Model ^b	AIC _c	ΔAIC _c	weight
Spawner upstream migration	CountLMC + Year	187.5	0.00	0.999
	CountLMC	201.5	13.97	0.001
	Year	311.5	124.06	0.000
	Null	322.7	135.19	0.000
Spawner migration	Water + Year	1261.0	0.00	0.667
	Water	1262.4	1.39	0.333
	Year	1292.6	31.59	0.000
	Null	1308.0	46.94	0.000
Juvenile out-migration	Water + Age	540.1	0.00	1.000
	Age	632.7	92.59	0.000
	Water	666.4	126.32	0.000
	Null	691.3	151.24	0.000

^aModel sets: The *spawner upstream migration* models explain the number of adfluvial spawners that enter the upper watershed as detected by the upper PIT tag reader; the *spawner migration* models explain the daily number of adfluvial spawners that enter the stream from the lake; the *juvenile out-migration* models explain the daily number of juvenile out-migrations to the lake.

^bModels are defined by their parameters: *CountLMC* is the daily number of adfluvial spawners that enter the stream from the lake as detected by the lower PIT tag reader (LMC = Lower Mahogany Creek); *Year* is a categorical variable for study year; *Water* represents mean daily water depth; *Null* is for the null model (no covariates); + indicates an additive relationship.

Table 2. Exponentiated parameter estimates of the competitive models ($\Delta AIC_c < 2$) from all model sets considered in the study.

Model Set ^a	Model ^b /Parameters ^c	Estimate	LCI ^d	UCI ^d	<i>p</i>
Spawner upstream migration	Top				
	CountLMC	1.05	1.04	1.06	$2.0E^{-16}$
Spawner migration	Year	1.43	0.85	2.43	0.18
	Top				
	Water	1216.20	49.80	$3.0E^4$	$1.3E^{-5}$
	Year	0.81	0.60	1.10	0.17
	2nd-best				
	Water	219.26	34.07	1410.92	$1.4E^{-8}$
Juvenile out-migration	Averaged				
	Water	686.98	27.03	$1.7E^4$	$7.6E^{-5}$
	Year	0.81	0.60	1.10	0.38
Juvenile out-migration	Top				
	Water	$8.8E^6$	$3.0E^5$	$2.5E^8$	$2.0E^{-16}$
	Age	0.21	0.16	0.27	$2.0E^{-16}$

^aModel sets are defined in Table 1.

^bModel names: *Top* is the model in the set with the lowest AIC_c score as shown in Table 1; *2nd-best* is the model with the second-lowest AIC_c score as shown in Table 1; *Averaged* is the model produced from averaging models with $\Delta AIC_c < 2$.

^cParameter names are defined in Table 1.

^d*LCI* and *UCI* are the lower and upper 95% confidence intervals, respectively.

869 **FIGURES**

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873 Fig. 1. Summit Lake and its tributaries. The black crosses on the stream represent the stationary
874 PIT tag antennas. The pressure transducer used to measure stream depth is located near the lower
875 PIT tag antenna that is closest to the lake. The open diamond is the fry trap. Filled circles on the
876 stream indicate sites that were electrofished in both 2015 and 2016. Open circles indicate sites
877 that were planned to be electrofished in 2015 and 2016, but were not due to dry conditions. Open
878 circles with small black circles inside indicate sites that were not electrofished in 2015, but were
879 electrofished in 2016. Map data were obtained from the U.S. Geological Survey's (USGS)
880 National Map (2016b) and National Hydrography Dataset (2016a).

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885 Fig. 2. Kernel densities of spawning adfluvial Lahontan cutthroat trout between 5 and 9 May
886 2016. Densities were calculated using detections of PIT-tagged fish ($n = 58$) and observations of
887 untagged fish ($n = 72$). A 100-m buffer was created around the stream to visualize the change in
888 density across space. Some parts of the stream were not sampled during mobile tracking either
889 due to impenetrable vegetation, dry stream bed, or headwater habitat. These areas are indicated
890 by hatching. Map data were obtained from the USGS National Map (2016b) and National
891 Hydrography Dataset (2016a).

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897 Fig. 3. Relationship between the daily number of adfluvial Lahontan cutthroat trout detected on
898 the lower Mahogany Creek PIT tag antenna and the number of those individuals that were
899 detected by the upper PIT tag antenna at any time afterwards. Sample sizes (number of days that
900 adfluvial spawners were detected on the lower PIT tag antenna) were $n = 48$ for 2015 and $n = 47$
901 for 2016. Many of the zero counts for 2015 are obscured by the 2016 data.

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907 Fig. 4. Migrations of Lahontan cutthroat trout PIT-tagged in the stream during electrofishing
908 surveys and spot shocking. **(a-b)** Migrations of LCT from stream to lake. Open triangles are sites
909 from which no fish migrated to the lake; filled triangles are sites from which fish migrated to the
910 lake; black cross is the lower PIT tag antenna. Two numbers next to each site show the number
911 of fish tagged at the site (left) and the number of tagged fish that was later detected by the lower
912 PIT tag antenna (right). Panels **a** and **b** show data from tags deployed in 2015 and 2016,
913 respectively. **(c)** Electrofishing sites (pie charts) showing classifications of LCT tagged at those
914 sites in 2015 based on tag detections. *Juv. adfluvial* = tags detected by the lower PIT tag antenna;
915 *resident* = tags detected in live fish within the stream; *stream bed* = tags detected in the stream
916 bed; *undetected* = tags that were never detected. The number of fish tagged at the site is noted
917 next to the pie chart. **(a-c)** The number of fish *tagged* does not represent the number of fish
918 *captured*; many were too small to tag. Map data: USGS National Map (2016b) and National
919 Hydrography Dataset (2016a).

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924 Fig. 5. Relationship between mean daily stream depth and migration magnitude of Lahontan
925 cutthroat trout. **(Left)** Daily counts of PIT-tagged adfluvial LCT entering Mahogany Creek from
926 the lake in 2015 and 2016. **(Right)** Daily counts of age-0 and age-1+ LCT out-migrating to the
927 lake through the fry trap in 2016.
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931 Fig. 6. Mean daily water depth in lower Mahogany Creek as measured by the pressure transducer
932 in the stream just above the lake. Data were not recorded from 9 to 28 July 2015.

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