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G. Gary Scoppettone [a] , Peter H. Rissler [a] , Sean P. Shea [a] & William Somer [b]

[a] U.S. Geological Survey, Western Fisheries Research Center, Reno Field Station, 1340 Financial Boulevard, Suite 161 , Reno , Nevada , 89509 , USA

[b] California Department of Fish and Game , North Central Region, Heritage and Wild Trout Program, 1701 Nimbus Road , Rancho Cordova , California , 95670 , USA

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ARTICLE

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G. Gary Scoppettone,* Peter H. Rissler, and Sean P. Shea
U.S. Geological Survey, Western Fisheries Research Center, Reno Field Station, 1340 Financial Boulevard, Suite 161, Reno, Nevada 89509, USA

William Somer
California Department of Fish and Game, North Central Region, Heritage and Wild Trout Program, 1701 Nimbus Road, Rancho Cordova, California 95670, USA

Abstract
Independence Lake (Nevada and Sierra counties, California) harbors the only extant native population of Lahontan cutthroat trout *Oncorhynchus clarkii henshawi* in the Truckee River system and one of two extant adfluvial populations in the Lahontan basin. The persistence of this population has been precarious for more than 50 years, with spawning runs consisting of only 30–150 fish. It is assumed that this population was much larger prior to the introduction of nonnative brook trout *Salvelinus fontinalis*. Brook trout overlap with cutthroat trout in upper Independence Creek, where the cutthroat trout spawn and their resulting progeny emigrate to Independence Lake. In 2005, we began removing brook trout from upper Independence Creek using electrofishers and monitored the cutthroat trout population. Stomach analysis of captured brook trout revealed cutthroat trout fry, and cutthroat trout fry survival increased significantly from 4% to 12% with brook trout removal. Prior to brook trout removal, the only Lahontan cutthroat trout progeny emigrating to Independence Lake were fry; with brook trout removal, juveniles were found entering the lake. In 2010, 237 potential spawners passed a prefabricated weir upstream of Independence Lake. Although the results of this study suggest that brook trout removal from upper Independence Creek has had a positive influence on the population dynamics of Independence Lake Lahontan cutthroat trout, additional years of removal are needed to assess the ultimate effect this action will have upon the cutthroat trout population.

Lahontan cutthroat trout *Oncorhynchus clarkii henshawi* (LCT) is one of three inland cutthroat trout subspecies federally listed as threatened (USFWS 1975). Like other inland cutthroat trout, LCT occupies a small fraction of its former range (Gresswell 1988; Behnke 1992), and its decline has been variously attributed to water diversion, dam construction (and associated disruption of spawning migrations), overfishing, disease, habitat fragmentation, and invasive species (Sumner 1939; Behnke 1992; Dunham et al. 1997; Koel et al. 2005; Neville et al. 2006). The primary obstacle to inland cutthroat trout recovery is the introduction of nonnative salmonids into their historic waters (Behnke 1992; Dunham et al. 2003; Al-Chokhachy et al. 2009). Nonnative brook trout *Salvelinus fontinalis* has been particularly problematic for stream-dwelling cutthroat trout (Griffith 1988; Dunham et al. 2003; Peterson et al. 2004). Of extant adfluvial cutthroat trout populations, few overlap with nonnative salmonids; consequently, there is relatively little information pertaining to their interactions with invasive salmonids other than lake trout *S. namaycush* (Ruzycki et al. 2003; Tronstad et al. 2010). In the Lahontan basin, extant lacustrine cutthroat trout populations persist in two small lakes (Summit Lake, Nevada and Independence Lake, California), representing only 0.4% of LCT former lake habitat (Gerstung 1988). Of the two, only the Independence Lake watershed harbors invasive salmonids—brook trout, kokanee *O. nerka*, and brown trout *Salmo trutta*. Kokanee and brown trout are restricted to Independence Lake,

*Corresponding author: gary_scoppettone@usgs.gov
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kokanee being abundant and brown trout rare. Brook trout are scarce in the lake but abundant in upper Independence Creek.

Independence Lake is also distinguished by harboring the only native extant LCT population in the Truckee River basin (Needham and Gard 1959; Gerstung 1988; Coffin and Cowan 1995; Moyle 2002). Spawner numbers have been precariously low since the mid-1950s. Before the introduction of kokanee in 1955 and 1956 (Lea 1968), spawner counts exceeded 500 fish; after kokanee introduction, numbers ranged from 30 to 150. Brook trout have been in Independence Lake and its watershed since at least the 1940s (Lea 1968). The overlap between Independence Lake LCT and brook trout occurs during the 3 to 4 weeks from late May to mid-July when LCT spawners are in upper Independence Creek, and several weeks of LCT fry emigration from the creek to the lake in late summer to mid fall (Gerstung 1988). Unlike kokanee, there is no circumstantial information that implicates the brook trout introduction in the population decline of Independence Lake LCT.

Observations from other locations that brook trout replace stream-dwelling cutthroat trout (Griffith 1988; Dunham et al. 2003; Peterson et al. 2004) led us to hypothesize that removal of brook trout would result in extended LCT stream residency, as observed in the Summit Lake population of LCT (Gerstung 1988). We further hypothesized that these changes in fry survival and shift to stream residency would result in increased LCT spawner numbers. To test this hypothesis, we removed brook trout from upper Independence Creek and its tributaries. The captured brook trout presented the opportunity to examine their stomach content and assess whether LCT fry predation is a mechanism by which brook trout negatively affect Independence Lake LCT. To study effects of removal on the Independence Lake LCT population, we compared fry survival, changes in progeny emigration patterns, juvenile residency, and spawner population number and demographics for the periods preceding and during the removal program.

STUDY SITE AND BACKGROUND

Independence Lake is an alpine lake situated in a glacier-carved basin on the east slope of the Sierra Nevada Mountains in Nevada and Sierra counties, California. It is 2,118 m above sea level and at the northwestern edge of the Truckee River drainage basin. The lake runs west to east, is 4 km long and 0.8 km wide, and has a maximum depth of 45 m. Originally, Independence Lake was two distinct lakes connected by a small stream, but in 1879 the outlet was dammed and has since been used as a reservoir (La Rivers 1962). The dam was enlarged in 1939 and now has a storage capacity of about 2,097 ha-m. The stored water is currently owned and managed by the Truckee Meadows Water Authority. Independence Lake limnology was studied by Brown and McCune (1977).

Independence Lake is the only lake within the Truckee River system retaining its historic complement of native fishes. Lahontan cutthroat trout native cohabitants are mountain whitefish *Prosopium williamsoni*, Lahontan redside *Richardsonius egregius*, tui chub *Gila bicolor*, speckled dace *Rhinichthys osculus*, Tahoe sucker *Catostomus tahoensis*, and Paiute sculpin *Cottus beldingii*. Tahoe sucker, Lahontan redside, and LCT are the only species observed to migrate from the lake into upper Independence Creek to spawn (authors' personal observation). The nonnative signal crayfish *Pacifastacus leniusculus* occurs throughout the more lotic areas of the Truckee River system (Light 2003), and is abundant in Independence Lake and rare in upper Independence Creek.

Upper Independence Creek is the main tributary to Independence Lake; discharge is at the lake's west end. The primary flow is from springtime and early summer snowmelt, flows being typically above 1.0 m^3/s, while springs and seepage supply water in later summer months. By fall, flow is typically less than 0.01 m^3/s, and some years portions of the creek may become intermittent. From late May through July, adult LCT move from the lake into the mouth of the creek, where they stage before migrating upstream to spawn. The majority of spawning habitat is within 1 km of the lake, but fish can travel upstream 2 km before being blocked by a 10-m waterfall. From late summer through fall, LCT young emerge from the gravels, and by winter the majority will have emigrated to the lake as fry. Electrofishing of upper Independence Creek in the 1970s and 1980s indicated no LCT stream residency, brook trout being the primary year-round resident (J. Hiscox, California Department of Fish and Game [retired], unpublished data). No brook trout or any other fishes occur upstream of the 10-m-high waterfall (authors' unpublished data).

METHODS

Brook trout removal.—Several types of electrofishers were used for brook trout removal from 2005 through 2010. In 2005, we began with a Dirigo electrofisher but switched to Smith-Root models 15-A and 15-B generator-powered backpack electrofishers through the remaining years of removal. In 2009, California Department of Fish and Game assisted us in using Smith-Root model LR-24 and 12-B electrofishers. Except for 2005, we initiated electrofishing in early fall after the majority of LCT fry had emigrated to the lake, when streamflow was near its lowest level and before freezing conditions. In 2005, our first electrofishing pass was conducted just before and near peak emigration; the remaining two passes were after peak emigration. Except in 2005, several days were required to complete one pass in upper Independence Creek, which consisted of electrofishing from the mouth to the natural waterfall of upper Independence Creek. In 2005, there were two electrofishing crews, and one pass took only 2 d. We made three passes from 2005 through 2007, and then one in each of 2008 through 2010 so as to reduce electrical current impacts (Kocovsky et al. 1997; Scheer et al. 2004) on residual LCT progeny.

Using electrofishers for nonnative fish removal is often unsuccessful, especially in habitat with substantial complexity

(Meyer et al. 2006; Peterson et al. 2008). We increased our chances for success by decreasing stream depth and flow starting in 2009. Stream reaches 50–120 m in length were partially dewatered by creating small sandbag dams sealed with a sheet of plastic and diverting water down 15.2-cm diameter plastic irrigation tubing or 10.2-cm diameter flex drain pipe laid along the stream thalweg. Dam and pipes were put in place 14–16 h before electrofishing, thus drying riffle and run habitat almost completely. Pools within a sample reach were typically 0.2–1.7 m in depth, and these were brought down to less than 10 cm using portable water pumps of two capacities, 273 and 575 L/min, and concentrating fish into a small area. Prior to electrofishing, we removed LCT fry via dip net.

Captured brook trout were preserved in a 10% solution of formalin from 2005 through 2009, and in 2010 they were placed in a freezer within 4 h after capture. Each fish had an identification number that referred to location and date collected. The captured LCT juveniles were measured and released downstream from the location of capture.

Brook trout predation.—We examined the stomachs of brook trout removed from upper Independence Creek to determine if fry predation was a mechanism by which brook trout negatively affect Independence Lake LCT. We focused on 2005 because this was the first year of removal and thus representative of the brook trout population before our intervention. In 2005, we conducted 6 d of removal over a 30-d period (August 15 to September 16), when a relatively large number of fry were observed and fry appeared to be emigrating. For the food habit analysis, we used a dissecting microscope to examine stomach contents. We quantified items consumed by frequency of occurrence and percent by volume (Windell 1971).

Effects of brook trout removal: spawner number and demographics.—An increase in the annual number of LCT spawners following brook trout removal is the ultimate measure of success of the removal program. Spawner number and demographics are also critical information for estimating fry survival success and the negative effect brook trout exert on this life stage. A prefabricated portable weir was used to determine number, sex, and size, and to estimate survival of spawners entering and exiting upper Independence Creek from 1998 to 2010. The weir was installed about 300 m upstream of Independence Lake in late spring, after snow had melted sufficiently to allow stream access, and flow had declined enough that the weir could be fished without threat of blowout. The weir was removed at the end of the spawning season. Two different weirs of similar design were used for the study; the original was improved to facilitate increased water flow passing through the weir. The first weir was fished from 1998 to 2004. It comprised panels 2 m long and 1.2 m high constructed of 25-mm diameter aluminum electrical conduit spaced 32 mm apart. Panels were supported in the stream using fence post. The weir had a conduit V-trap with a 1.5 × 1.5-m square conduit box. There was also a downstream V-trap of similar dimensions. To prevent erosion under the weir, 25-mm poultry wire mesh extended out 2 m on the streambed from either side of the weir, staked down with rebar as well as strategically positioned sand bags. In 2005, there were slight design changes that included converting to 20-mm diameter electrical conduit spaced at 10 mm. To reduce handling of spawners, the downstream trap was replaced in 2008 with a Biomark 30 × 80-cm swim-through passive integrated transponder (PIT) tag antenna attached to a V-shaped exit situated on the downstream side of the weir to prevent upstream migrants from entering the antenna aperture for upstream passage. The antenna was connected to a Biomark 2001F-ISO portable transceiver system and powered by an Optima 12-V deep cycle AGM battery charged by two Sunlinq folding solar power panels.

Migrating LCT captured in the upstream weir box were sedated with tricaine methanesulfonate (MS-222), sexed, measured, weighed, and scanned for the presence of a PIT tag with a Destron portable mini-reader. If no PIT tag was detected, one was inserted with a syringe subcutaneously in front and left of the dorsal fin. The adipose fin was removed to indicate the presence of a PIT tag in future captures. After processing, the fish was placed in a live-cart until it recovered from sedation and was then released in a pool approximately 35 m upstream of the weir. Migrants captured in the downstream V-trap were scanned for the presences of a PIT tag and released immediately downstream of the weir.

Fry survival and emigration.—Because of the paucity of fish, we did not sacrifice females to develop a relationship between fecundity and size, and so relied on data generated by Lea (1968). We converted Lea's standard length measurements to fork length (FL) using the conversion developed by Sigler et al. (1978) for LCT in Pyramid Lake, Nevada. Because Lea had access only to smaller (263–429-mm FL) and presumably younger females, use of his data may give erroneous results when projecting fecundity for older and larger fish (Scoppettone et al. 2000). We therefore used the formula generated by Sigler et al. (1983) for LCT 365–705-mm FL taken from Pyramid and used a regression to fit it to Lea's fecundity data. We felt this would give us the best estimate of fecundity of large LCT in Independence Lake; our female captures were 272–730-mm FL.

To track the number and size of LCT fry emigrating into Independence Lake, a prefabricated fry trap was installed approximately 300 m upstream of the stream mouth and covered 100% of the streamflow. The fry trap was constructed of a 3.2-mm hardware cloth fence held in place with steel fence posts. Within the fence was a marine plywood head box that contained a 160-mm diameter PVC pipe that ran several meters to a cube-shaped trap box with each side measuring 1.5 m. Emigrating fry entered the pipe and dropped into the trap box. Captured fry were netted and enumerated. The fry trap was fished every day until after the peak emigration (over 90% of the emigrating fry had passed); it was then run Monday to Friday. From Friday afternoon through Monday morning, the polyurethane front panel was removed to allow fry to pass freely downstream. During fishing days, biologists checked the fry box several times a day. For the nonfishing days, the number of fry was estimated by extrapolating from the previous and subsequent period. The fry trap was fished until few to no fry were being captured.

Fry survival was the quotient of the number of fry estimated to enter the fry trap divided by the estimated potential number of eggs deposited. The trap was run annually from 1998 through 2010, except for 2004 when neither the spawning weir nor the fry trap was installed. We used one-way analysis of variance to test fry survival before brook trout removal (1998–2003) and during removal (2005–2010); assumptions for homogeneity and normality variance were met.

We compared annual emigration patterns of LCT fry and their size prior to (1998–2004) and during brook trout removal (2005–2010). Annual emigration was the number of fry entering the fry trap each day from the beginning of emigration to closing of trap operations. A Kolmogorov–Smirnov two-sample test was used to identify a difference in the distribution of emigrants over time related to brook trout removal. Each day of monitoring, a random sample of 20 fry were measured to the nearest millimeter fork length then immediately released downstream from the trap box. We used a Mann–Whitney U-test to determine if there was a difference in fry length between peak emigration prior to and during brook trout removal; if there was a change in emigration pattern, size and (consequently) survivorship of fry entering the lake may be different (Houde 2002). The Mann–Whitney U-test was also used to determine if there was a length difference for the two conditions for fry remaining in upper Independence Creek for several weeks prior to emigration. Change in community structure, such as brook trout removal, may have direct and indirect influence on LCT fry growth (Werner and Peacor 2003; Sundstrom et al. 2005). All fry trapped 45 d after the beginning of emigration were compared in length because it was near the end of fall emigration, but sample size was sufficiently large to test for difference between the two treatments.

Diel emigration pattern was monitored near peak emigration and consisted of enumerating and removing fry from the trap every hour over a 24-h period. There were five diel samples conducted before brook trout removal and two during removal. Only two diel samples during brook trout removal precluded testing for differences between the before and during brook trout removal treatments.

Juvenile stream residency and emigration.—During brook trout removal (2005 through 2010), we enumerated and measured LCT 1-year-old (50–80-mm FL) and older inhabiting upper Independence Creek. In 2005 and 2006, captured LCT were released at the mouth of Independence Creek to avoid repeat shocking. From 2007 through 2010, when only one pass was made, captured resident LCT were held in a nearby live-cart until electrofishing of that area was completed, and they were repatriated to the area from which they were taken.

Independence Lake LCT fry have been reported to emigrate to Independence Lake within weeks of emergence from their respective redds (Gerstung 1988). Because a fraction of the Summit Lake Lahontan cutthroat trout progeny remain in their natal habitat one or more years (Gerstung 1988; Vinyard and Winzeler 2000), we hypothesized that brook trout removal may delay emigration for some LCT, and some may emigrate in the spring as fingerling or larger and older juveniles. From May 31, 2008, through June 21, 2008, we used a fyke net to capture fingerling and juvenile LCT moving downstream toward and presumably emigrating into Independence Lake. May 31 was selected as the start date because we were able to access upper Independence Creek and the stream had subsided sufficiently, allowing us to install and fish the net. The fyke net was 2 m long and its mouth was 0.75 m wide and 0.75 m high with 10-mm mesh (stretch). Held in place with steel fence posts on either side of the aluminum frame, the net's cod end led into a 0.16-m diameter and 3-m-long PVC pipe that terminated at a trap box 1.0 m long, 0.9 m wide, and 0.8 m high. The latter consisted of a welded metal frame lined with 3.2-mm mesh hardware cloth. Emigrating fingerling and juveniles entered the fyke net, went down the PVC pipe, and dropped into the trap box. Captured fish were netted, measured to fork length, and released several meters downstream. We ceased fishing the fyke net on June 21 because spawners were becoming entrained.

The fyke net was fished in a narrow chute approximately 400 m upstream of the mouth of upper Independence Creek, but flow through the net was a fraction of the streamflow. Presumably, LCT capture success is influenced by the portion of streamflow taken through the fyke net. Streamflow filtered through the fyke net was estimated using a General Oceanics model 2030 mechanical flowmeter suspended at the center of the fyke net mouth. The meter was read when checking for fish in the trap, a minimum of twice a day, in the morning and evening. To track streamflow, we established a gauging station approximately 10 m downstream from the fyke net. The station consisted of a meter stick vertically attached to a fence post driven into the stream. For calibration, streamflow measurements were taken several times a day during the time the fyke net was fished. Flow measurements were made adjacent to the gauge using a Marsh–McBirney model 201D digital flowmeter mounted on a calibrated rod. There was a wide range of flow during spring runoff, and the gauge was read several times a day. We used the average of morning and evening flow measurements for reporting daily flow.

RESULTS

Brook Trout Removal

Brook trout removal from 2005 through 2010 did not follow a linear depletion (Figure 1). In 2006 brook trout were larger compared with 2005, and in 2007 we removed more and smaller brook trout than any other year. After 2007, method and technique of brook trout removal changed, complicating comparisons among years. In 2008, we reverted to only one pass so as to lessen impact on LCT. Then in 2009, we began partially drying the stream and found we could draw out fish that formerly escaped the effects of our electroshocker by seeking refuge in undercut banks. In 2010 only 313 brook trout were

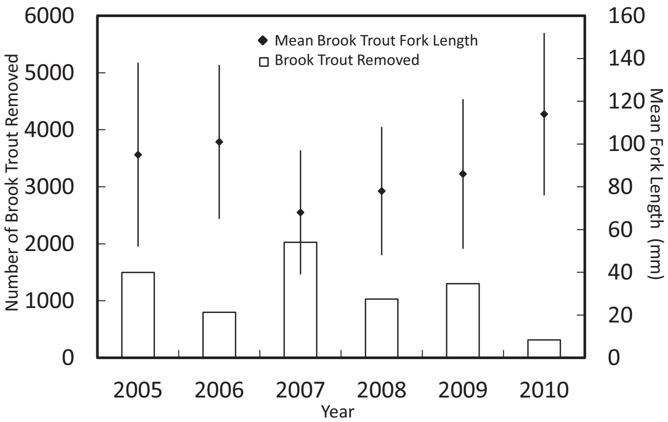

FIGURE 1. Number of brook trout removed from upper Independence Creek by year and their mean fork length; vertical line represents SD.

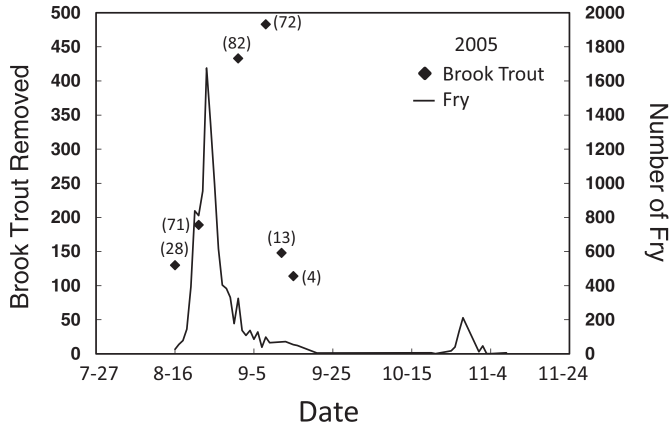

FIGURE 3. Brook trout removal dates in relation to the 2005 Independence Lake LCT fry emigration pattern from upper Independence Creek to Independence Lake; number of LCT fry recovered from stomachs of brook trout collected shown in parentheses.

taken, and these were primarily large fish; this suggests that spawning, which occurs in the fall, had been disrupted.

Brook Trout Predation

In 2005, we collected and examined the stomachs of 1,491 brook trout. The primary food item consumed by frequency of occurrence ($n = 1{,}157$) and volume (55%) was aquatic invertebrates, followed by terrestrial invertebrates (Figure 2). A total of 270 LCT fry were recovered from 135 brook trout. This represented only 6% of the total items consumed (by volume) for the 1,491 brook trout removed. Number of brook trout taken by date and in relation to the 2005 LCT fry emigration pattern is shown in Figure 3. The first brook trout sample ($n = 130$) was taken August 16, when LCT fry had begun to emerge and emigrate, while the second removal ($n = 189$) was August 22, near peak fry emigration. These two samples represented 21% of the brook trout removed and 37% of the total number of LCT fry found in stomachs.

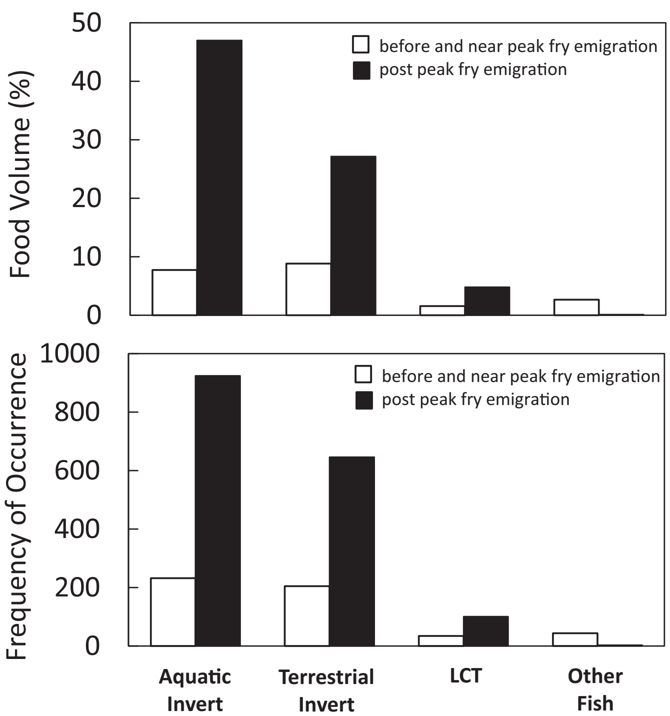

FIGURE 2. Food items consumed by frequency of occurrence and volume for 1,491 brook trout removed from upper Independence Creek in summer and fall 2005. Brook trout samples taken immediately prior to peak LCT fry emigration and near peak emigration are combined ($n = 319$), and those taken post-peak emigration are combined ($n = 1{,}172$).

The smallest brook trout to have consumed LCT fry was 48-mm FL and presumably young of the year. Other fish consumed include brook trout fingerling, Paiute sculpin, speckled dace, and Tahoe sucker larvae. The most frequently taken were Tahoe sucker larvae; there were 3,171 taken by 40 brook trout. Virtually all Tahoe sucker larvae were taken on August 16, before they had emigrated to the lake. One 185-mm FL brook trout had consumed 7 LCT fry along with 553 Tahoe sucker larvae.

Effects of Brook Trout Removal

Fry survival and emigration.—Prior to brook trout removal, LCT fry survival ranged from 0% to 8%, and during removal survival was 8–16% (Table 1); this difference was significant (df = 1, 10; $F = 18.26$; $P = 0.002$). There was no survival in 2003, the year with the fewest number of spawners (18 females and 11 males). The lowest survival (8%) during the brook trout removal years was 2005, the year removal began.

Fry emigration pattern differed slightly prior to and during brook trout removal. Peak emigration was 3 d later during the removal period (Figure 4), and proportionally a greater percentage of fry emigrated past peak emigration. Shape and locations of the peaks of the two emigration patterns are significantly different ($D = 0.319$, $P < 0.001$). In both treatments, over 75% of the fry emigrated through our fry trap within the first 20 d of

TABLE 1. Estimated numbers of potential eggs deposited and cutthroat trout fry captured and estimated survival rate for sampling years before and after brook trout removal began.

Year	Estimated egg production	Fry captured	Egg–fry survival
	Before brook trout removal		
1998	169,235	6,295	0.04
1999	164,208	13,115	0.08
2000	280,525	14,312	0.05
2001	255,348	1,896	0.01
2002	184,670	5,222	0.03
2003	53,555	0	0
2004[a]			
	After brook trout removal		
2005	147,007	11,955	0.08
2006	67,016	11,012	0.16
2007	205,658	21,707	0.11
2008	278,896	38,293	0.14
2009	291,296	40,670	0.14
2010	380,169	42,484	0.11

[a]Not sampled.

emigration. Many early emigrants showed signs of a yolk sac, indicating recent emergence from their respective redds. By 45 d after the initiation of emigration, over 95% of the fry in both treatments had emigrated.

Mean fork length at emigration was 27.5 mm (n = 120, SD = 1.5) before brook trout removal and 27.8 mm (n = 120, SD = 1.3) during. This slight difference was not significant (df = 1, $\chi^2 = 2.94$, $P = 0.09$). Young entering the fry trap past 45 d averaged 38.4-mm FL (n = 127, SD = 4.80) before removal, and 37.6-mm FL (n = 511, SD = 4.60) after removal began; the difference was not significant (df = 1, $\chi^2 = 2.49$, $P = 0.115$).

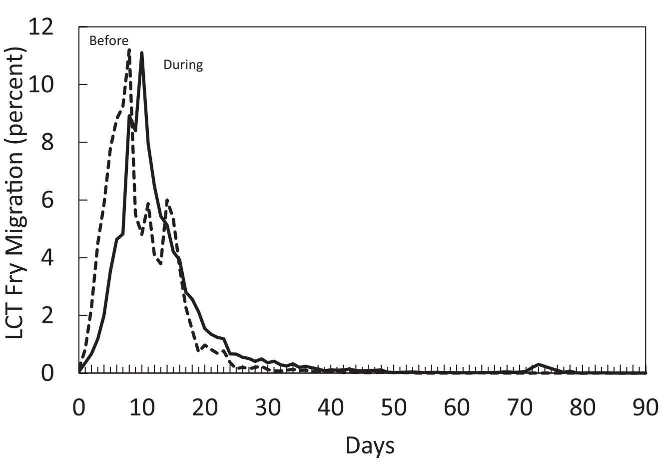

FIGURE 4. Lahontan cutthroat trout fry emigration pattern from upper Independence Creek to Independence Lake before (1998–2003) and during (2005–2010) brook trout removal.

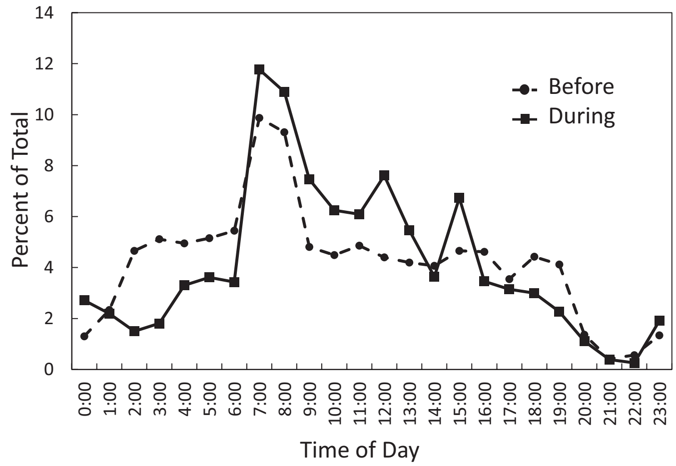

FIGURE 5. Lahontan cutthroat trout fry diel emigration pattern from upper Independence Lake to Independence Lake before (1998–2003) and during (2005–2010) brook trout removal.

Fry diel emigration patterns were similar before and during brook trout removal (Figure 5). Most fry emigrated during the daylight hours (0600–1600 hours). The peak was at the 0600 hours, and the low was from 2100 to 2200 hours.

Juvenile stream residency and emigration.—Brook trout removal led to an increase in the number of LCT progeny remaining in the stream (residents) following swim-up. In 2005, our first year of electrofishing, only two juveniles (≈150-mm FL) were captured in three passes. In 2006 the number of juveniles was 60, averaging 71-mm FL (Figure 6). In 2007, the number we captured increased again to 201. In 2008 we reverted to just one pass, resulting in fewer numbers. In 2009 and 2010 we began pumping pools, and this led to an increase in captures. Since 2006 the mean size of juveniles has steadily increased, some juveniles remaining in the stream for 2 and 3 years. In

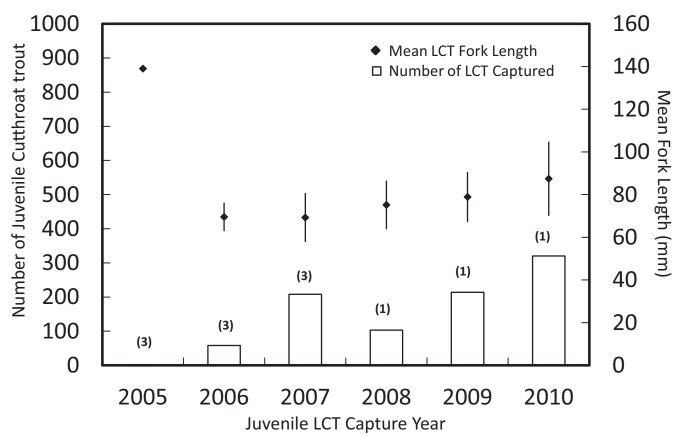

FIGURE 6. Number and mean fork length of juvenile LCT captured from upper Independence Creek from 2005 to 2010; vertical lines are SDs; number of passes made with an electrofisher on upper Independence Creeks shown in parentheses. Pools were pumped in 2009 and 2010 to facilitate brook trout removal.

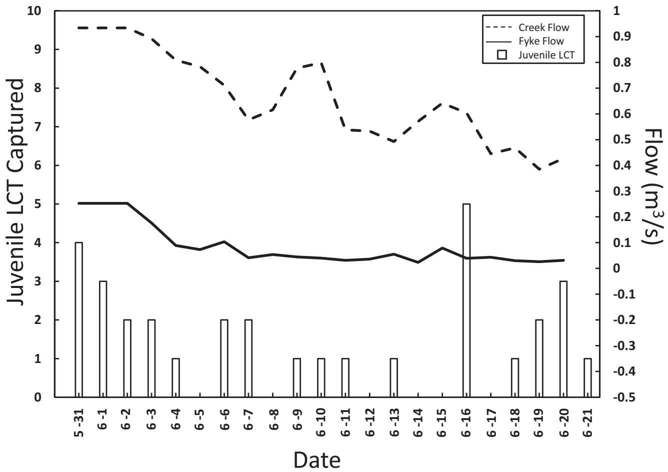

FIGURE 7. Number of emigrating juvenile LCT captured in fyke net along with streamflow and flow through fyke net from May 31 to June 21, 2011.

2010, resident (1-year-old or older) LCT captured outnumbered brook trout removed 320 to 313.

Instead of emigrating to Independence Lake as fry within several weeks of emergence, a portion of the LCT progeny emigrated during spring discharge the following year. From May 31 to June 21, 2008, we captured 32 juvenile LCT (47–89-mm FL) in 16 of the 22 d of fishing, and with our net fishing about one-fifth of the streamflow (Figure 7). There were four juvenile LCT captured the first day the trap was put in place, suggesting emigration was in progress prior to trap placement, and thus this putative springtime emigration began some indeterminate time before the adult spawning migration (which began June 9). Other fishes captured were two brook trout (66- and 206-mm FL), two Paiute sculpin, and four Tahoe suckers. In 2009 we fished the fyke net for only a day (June 6) before water was deemed too fast for sampling, and we captured four LCT ranging from 49- to 58-mm FL. We did not operate the juvenile emigration trap in 2010.

Demographics of spawners.—Since 2007 the spawner population number has increased annually, with a high of 237 entering our weir trap in 2010 (Figure 8). Females showed the greatest increase, and there were three times as many females in the 2010 spawning migration as males. The increase in the number of female spawners, coupled with increased fry survival, led to an increase in LCT fry emigrating to Independence Lake. Prior to brook trout removal, the greatest number of emigrating LCT fry was 14,313 compared with over 40,000 in 2009 and 2010 (Table 1).

Mean female LCT lengths were less in 2005–2010 than those in 1998–2003, suggesting the spawning run comprised younger females. The smallest females were in 2010, the year of the greatest number of females migrating up upper Independence Creek. Male spawners were generally larger from 2005 through 2010. There were no consistent trends from 1998 to 2003, but samples sizes were generally small.

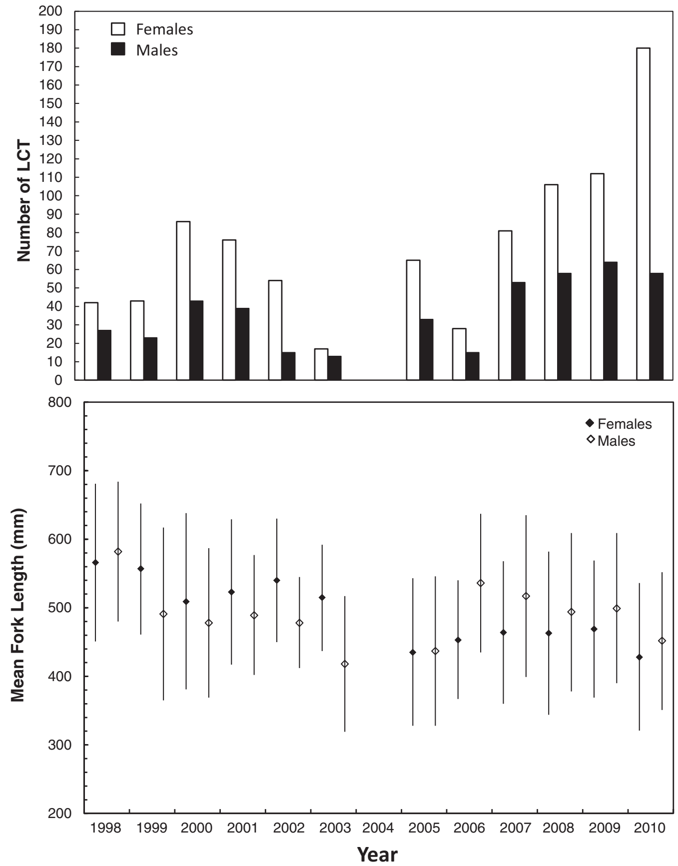

FIGURE 8. (Top) Number of female and male LCT spawners entering weir 1998–2010. (Bottom) Mean fork length and SD of LCT entering weir 1998–2010. No weir was in place 2004.

DISCUSSION

Brook trout presence within upper Independence Creek has had a negative impact on the lake's LCT population. It may, however, be feasible to eliminate them from the Independence Lake watershed or, at minimum, control the population to the benefit of the LCT population. In the late 19th century and prior to nonnative salmonid introductions into the Independence Lake watershed, there were a reported 2,000–3,000 LCT spawners (Gerstung 1988). The level to which the present day LCT population will recover as a result of brook trout removal efforts is still unfolding and may be limited by the presence of kokanee and limited spawning habitat. Kokanee feed upon zooplankton and compete with LCT for this food resource (Fuller et al. 1999). Dams have been implicated as reducing salmonid populations through the reduction of available spawning habitat (Connor et al. 2001), as is the case for Independence Lake cutthroat trout. Prior to the construction of the Independence Lake Dam, Independence Lake LCT were reported to have spawned in the outlet stream, the resulting progeny emigrating into the lake (California Deputy Fish Commissioner 1891). Inlet and outlet spawning and the innate ability of resulting progeny to emigrate to the parental lake has been well documented for the Yellowstone cutthroat trout *O. clarkii bouvieri* (Raleigh and Chapman 1971; Bowler 1975; Gresswell et al. 1993).

Similar to what has been reported in the literature (Allan 1980; Moyle 2002), the upper Independence Creek population of brook trout feed primarily on drifting aquatic and terrestrial invertebrates. Although LCT fry were a relative minor contribution to the brook trout diet, brook trout predation is suspected to have a major impact on LCT fry survival. The 1,491 brook trout removed probably represented less than 65% of the 2005 population; in 2006 we removed 798 brook trout with few young of the year, indicating that there was at least this number remaining after the 2005 removal. Presumably, had the entire brook trout population been collected, we would have recovered well over 400 ingested LCT fry. Since over 79% of brook trout were removed outside of peak LCT fry emigration period, when the stream population of fry was greatest and probably most vulnerable to predation, we consider (1) over 400 LCT fry taken a conservative estimate of fish taken within the 6 d of brook trout removal, (2) brook trout have been reported to evacuate foodstuff from the stomach over a broad time period (24–72 h), and (3) the time taken is influenced by water temperature, predator size, prey size caloric content, and activity level (Elliott 1972; Fange and Grove 1979; Boisclair and Sirois 1993; Sweka et al. 2004). There is no brook trout evacuation study tracking fry digestion rate, but the closely related Dolly Varden *Salvelinus malma* evacuated stomach contents in 24 h when predating sockeye salmon *O. nerka* fry at 13°C (Fange and Grove 1979). Mean daily water temperature in upper Independence Creek during the removal period hovered near 13°C. Assuming digestive rates of brook trout and Dolly Varden to be similar, and the number of LCT fry in brook trout stomachs was an average number ($\approx$400) per day for the 30-d window of time of our removal, approximately 12,000 were taken. The potential negative effect of brook trout predation on Independence Lake LCT fry survival is substantial, considering only 11,955 LCT fry emigrated in late summer and fall 2005. Except for the Yellowstone cutthroat trout (Benson 1960), other adfluvial cutthroat trout populations have been documented to be predated, as juveniles and in lake habitat (Cordone and Frantz 1966; Ruzycki et al. 2003).

Competition has been implicated as a mechanism by which brook trout replace native cutthroat trout in streams (Griffith 1988; Peterson and Fausch 2003; Buys et al. 2009). Brook trout predation of fluvial cutthroat young has been suspected as a means of causing population decline, but this effect has been difficult to prove (Dunham et al. 2000; Dunham et al. 2003). Peterson et al. (2004) determined that the younger life stages are most negatively impacted by brook trout. The Independence Lake and upper Independence Creek system presented an excellent opportunity to gauge the potential effect of brook trout predation on LCT fry. Adfluvial cutthroat trout are typically larger and more fecund than the fluvial form, and in upper Independence Creek they spawn in a localized area, leading to fry density that probably greatly exceeds those expected for fluvial trout, which have increased survivorship at lower densities (Elliott 1985; Elliott 1990; Brockmark et al. 2010; Brockmark and Johnsson 2010). Our large sample size (n = 1,491) of brook trout for stomach analysis also enhanced our likelihood of finding ingested LCT fry.

Salmonid fry emigrating from a natal stream to adfluvial habitat typically move during the dark hours (Raleigh 1967; Rankel 1977; Thorpe et al. 1988; Johnson 1997; Knight et al. 1999). The obvious advantage of nighttime movement is predator avoidance, a life history strategy common among many fish species (Helfman 1993; Johnson 1997). Independence Lake LCT fry emigration, however, occurred around the clock, most movement taking place from dawn to dusk and peak emigration occurring at or near dawn. Their diel emigration pattern suggested that, prior to brook trout stocking, there were no greater mortality risk in daytime emigration as opposed to nighttime. The apparent lack of genetic programming for nighttime emigration makes them particularly vulnerable to brook trout predation, as brook trout are primarily diurnal feeders (Forrester et al. 1994). The diel pattern of emigration was quite similar before and during brook trout removal, but there was not sufficient sample size to test if there was a difference. There was significant difference in fry emigration pattern before and during brook trout removal, but the difference did not appear to be biologically significant. Presumably, the fitness advantage of delayed emigration is entering lake environment at a larger size (Houde 2002), but there was no significant difference in lengths between peak LCT fry emigration before or during brook trout removal. Likewise, there was no significant difference in fry length of those entering the lake 45 d after peak emigration.

Adfluvial cutthroat trout have been reported to emigrate to lake environments shortly after swim-up, but some remain in the natal stream one or more years prior to emigration (Benson 1960; Gresswell et al. 1993; Knight et al. 1999; Vinyard and Winzeler 2000). Before brook trout removal, progeny of Independence Lake LCT spawners were known to enter Independence Lake only as fry (Gerstung 1988). During brook trout removal some stream residency was observed, progeny remaining in upper Independence Creek until the following spring and beyond. Early life stage survival is incrementally enhanced with increasing size and age (Houde 2002). The number of 1-, 2-, and 3-year-old LCT increased in subsequent years of brook trout removal. This apparent shift in life history patterns may be important for improving population status. In 2008, 3 years after initiation of brook trout removal, the adult spawner population began its upward trajectory, as 237 passed through our weir in 2010—the largest number reported in over 50 years. The increase in spawner number cannot be explained by increased fry survival alone. Spawner numbers in 2006 and 2007 were low; there were not substantially more fry emigrating to Independence Lake in those years compared with pre-brook trout removal. The number of LCT fry entering the lake did not increase appreciably until 2008, and age at maturation is typically 3–5 years. We suspect that those LCT taking up stream residency for one or more years have high survival rate and are the primary contributors to the expanding spawner population. The small size of female spawners in 2010 is consistent with this hypothesis.

The number of LCT fry holding in upper Independence Creek through the winter or longer, as well as their contribution to the spawner population, needs to be further assessed. This task is made difficult by the logistics of accessing upper Independence Creek and installing a trap prior to or at springtime snowmelt. In 2008 we were able to reach upper Independence Creek 9 d prior to the first adult migrant, but juvenile emigration was already in progress and may have begun when springtime streamflows were highest. According to the gauging station on Sagehen Creek (the next drainage to the south), flow increased substantially in late April and remained high until late May (USGS 2008). If juveniles emigrate with increased flow regardless of water temperature, most juvenile emigrants may have entered Independence Lake prior to trap installation. There had not been a reported attempt to sample springtime emigration for LCT in upper Independence Creek prior to our study, probably because before brook trout removal fry appeared absent from upper Independence Creek within several weeks after peak fry emigration. In brook trout removal years, we observed hundreds to thousands of fry remaining in the stream several weeks post-peak fry emigration and which apparently became winter residents. Presumably as a result of brook trout removal, the number of springtime emigrants is much greater than before removal.

Multipass electrofishing was suitable the first year of brook trout removal when there were virtually no juvenile LCT stream residency, but this method became a liability to our study and LCT population as residency increased; high juvenile LCT mortality was incurred, causing us to modify our method of brook trout removal. Our subjective evaluation is that the change in method (partially drying a stream reach, pumping pool habitat, and one electrofishing pass) was a more effective means of brook trout removal than making three passes within a several-week time period. Large adult brook trout that formerly escaped in deep pools and undercut banks were relegated to water only several centimeters in depth and easily removed. In addition, less time was needed to turn fish, and consequently the new method appeared to be less stressful and caused substantially less mortality to resident LCT. However, the change in method complicated the gauging and comparing of brook trout removal among years. Several more years of brook trout removal is need to quantify the effect our new method of removal contributed toward depleting the upper Independence Creek brook trout population.

We continue to monitor the effects of brook trout removal on the Independence Lake LCT population, particularly spawner numbers and the contribution to the adult population from fry migrating to the lake shortly after swim-up and those remaining in the stream until the juvenile stage. While our ultimate goal is to extirpate brook trout from the Independence Lake watershed, this study indicates that just controlling upper Independence Creek brook trout population enhances the chances for LCT persistence of the Independence Lake population. The level of brook trout control needed for persistence of the fluvial form of cutthroat trout has been investigated by Peterson et al. (2008). The level of brook trout removal effort to ensure the persistence of the Independence Lake LCT needs to be investigated.

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