University of Nevada, Reno

Movement Patterns, Habitat use, and Survivorship of Lahontan Cutthroat Trout (*Oncorhynchus clarkii henshawi*) in the Truckee River.

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

Master of Science in Biology

by

Alexander V. Alexiades

Dr. Mary Peacock/Thesis Advisor

May 2010

The Graduate School

We recommend that the thesis

Prepared under our supervision by

Alexander V. Alexiades

entitled

Movement Patterns, Habitat use, and Survivorship of Lahontan Cutthroat Trout (*Oncorhynchus clarkii henshawi*) in the Truckee River.

be accepted in partial fulfillment of the requirements

for the degree of

Master of Science, Biology

Mary Peacock, Ph.D., Advisor

Matthew Forister, Ph.D., Committee Member

Jill S. Heaton., Ph.D., Graduate School Representative

Marsha H. Read, Ph.D., Associate Dean, Graduate School

May 2010

Abstract

Populations of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*, hereafter LCT), along with most other cutthroat trout subspecies, are in decline throughout their range. Habitat fragmentation, hybridization, and competition with non-native salmonids are viewed as major threats to LCT. Understanding LCT movement and habitat use behaviors will be a useful step in the reintroduction and establishment of a naturally reproducing LCT population in the Truckee River. Little is known about the movement patterns of LCT, which are listed as threatened under the U.S. Endangered Species Act (ESA).

In this work, weekly radio telemetry monitoring was used to examine movement patterns, habitat use, and survivorship of hatchery-reared LCT in a 16.5 km stretch of the mainstem Truckee River, Nevada, across three reaches separated by dams. Nearly all fish movements took place during autumn and winter tracking seasons with significantly higher total movement during the autumn.

Fish weight did not influence total movement or home range size. Males and females did not differ in home range size or total movement. Turnover rates were higher for males than females; however the difference was not significant. Turnover rates were similar for LCT among reaches.

Location in the watershed influenced total movement and home range sizes of fish, with fish moving the largest distances in the middle section (Crystal Peak Park) followed by the upper section (Fleish). Nearly all fish movements were in an upstream direction, into large pools formed below the dam structures. No fish moved upstream over dams/barriers. Fish used slow water habitat units more than fast water habitat units in all three sections. Body size also influences habitat use, with larger fish using pools more frequently than other habitat types. AIC model rankings indicated season, flow rates, and stream temperature covariates to have the most influence on survival. Monthly survival was lowest during the autumn season (October to January), which coincided with the lowest flow rates and temperatures during the entire study period. These results verify the mobility of LCT, highlighting the importance of barrier-free movement corridors within the Truckee River. The differential movement patterns between reaches could be useful to resource managers in future habitat restoration efforts and reintroduction attempts of LCT into the Truckee River.

Acknowledgements

First and foremost I would like to thank my major advisor Mary Peacock for giving me the opportunity to carry out this project. Funding was provided by the USFWS, and fish for the study were provided by the Lahontan National Fish Hatchery (LNFH) in Gardnerville, NV. A special thanks to Tim Loux at USFWS for help, advice, and equipment in the field. I also thank Robert Al-Chokhachy for advice and guidance throughout the project. For help at the LNFH during surgeries, I'd like to thank Jay Bigelow, James Hoang, and Al Duncan. For teaching me how to implant fish with radio-tags and tracking in the field, I thank John Umek and Joe Sullivan. For help with electro-fishing and snorkeling for fish, I'd like to thank Roger Peka and Eric Hoergen. I thank my field assistants, Chris Fikovsky and Kirsha Fredrickson for help tracking while I was out of town or too busy to get out in the field. For software support, study design, and statistical issues, I thank Miles Becker. For help with GIS, Adobe Illustrator, and poster making, I thank Abbey Grimmer. I also thank Mike Meeuwig for comments on thesis drafts. Finally, I appreciate all the helpful advice from my committee members Matt Forister and Jill Heaton.

Table of Contents

List of Tables

List of Figures

Introduction

Many native populations of freshwater stream fish and invertebrates are in peril worldwide (Lodge and Taylor 2000; Rieman and Peterson 2006; Pascual and Cussac 2007). This decline can be attributed to numerous threats including non-native species interactions, habitat fragmentation and degradation, dams, loss of genetic diversity, overharvesting, and environmental/climatic changes (e.g., droughts and temperature fluctuations) (Allan and Flecker 1993; Dunham et al. 1997; Magalhães and Beja 2007). Although many of these factors persist today in North America, habitat degradation and non-native species are considered the dominant factors affecting the distribution and abundance of many native fish populations (Allan and Flecker 1993; Harig et al. 2000; Hilderbrand and Kershner 2000a; Rosenfeld and Boss 2001). Today, many native salmonids occur only as isolated populations in previously large, interconnected habitats with complex metapopulation dynamics (Rieman et al. 2003).

Fragmentation has been shown to reduce habitat area, complexity, and connectivity thereby increasing extinction risk of native salmonids (Rieman and McIntyre 1993; Dunham et al. 1997). Land use practices such as mining, logging, and road construction have substantially affected the ecology and natural hydrology of streams, often contributing to declines in fish populations (Burns 1972; Allan and Flecker 1993; Kondolf 1997; Tonina and Buffington 2009). Agricultural inputs of fertilizers to rivers and streams have also been shown to greatly alter or degrade the water quality of the systems (Schulz and Liess 1999). While hydropower and diversion structures (e.g., dams) can also negatively affect native stream fish by isolating populations and causing mortalities when fish try to move through these structures (Collins and Jenkins 1996; Thurow et al. 1997; Morita and Yamamoto 2002; Coyler et al. 2005). These anthropogenic practices have led to major variations and fluctuations in the water temperatures and flow rates of rivers and streams, further impacting the viability of native salmonid populations.

The distribution of salmonids can be significantly affected by water temperature (Dunham et al. 2004; Bear et al. 2007), and flow regimes (Bunn and Arthington 2002; Propst and Gido 2004). Temperature may also affect the degree of spatial overlap between non-native salmonids and native cutthroat trout species (Glova 1986; Heggenes et al. 1996; Jakober et al. 1998). Additionally, anthropogenic activities that alter flow regimes (e.g., dam construction and operation) have negative effects on freshwater fishes that have evolved in response to natural flows (Poff et al. 1997). Low flows also decrease the availability of pools, which are a critical habitat feature for stream-dwelling salmonids, and the connectivity between populations. Water temperatures in downstream reaches often exceed the thermal limits of salmonids (Robinson et al. 2008). Historically, the inland salmonid species dealt with this temporal variation in temperature by living in large interconnected stream systems which enabled them to find refugia from these lethal temperature extremes through upstream migrations (Peterson 1996; Rosenfeld et al. 2000). In highly managed stream systems, the flow regimes can be manipulated to provide optimal flow rates for salmonids. Therefore, understanding the response of native salmonids to altered flow regimes could be important in their long-term conservation and management.

Knowledge of stream salmonid movement patterns can contribute to our understanding of energy transfer in streams, source-sink dynamics of fish population, and colonization of potential habitat following disturbances (Hall 1972; Rodriguez 2002). There is some evidence that fish mobility differs according to species, subspecies, size, and sex of individuals (Gowan et. al 1994;

Schrank and Rahel 2006), which can be important for fisheries managers making decisions about stocking and re-introductions. Knowledge of fish movement in undisturbed stream systems can also help predict how anthropogenic influences (i.e., damming, flow manipulation, habitat degradation, etc.) may impact these movement patterns and ultimately population persistence (Shrank and Rahel 2006).

Gerking's (1959) study demonstrating restricted movements of stream fish had led most biologists to regard fluvial trout populations as sedentary (restricted movement paradigm), therefore few studies examined fish movement when studying stream network dynamics. With improved study design and technological advances in fish tracking, the Gowan et al. (1994) study suggests some river-dwelling trout may be more mobile (utilizing sections of stream greater than 50m) than previously thought. Rodriguez (2002), showed that while the majority of individuals are sedentary, a fraction of individuals in populations exhibit mobile behavior. In addition to mobile behavior, it has been shown that many species of stream dwelling trout exhibit two different life history strategies, migratory and resident; where migratory individuals move from mainstem rivers into tributaries for spawning (Rieman and McIntyre 1993; Gresswell et al. 1997; Swanberg and Geist 1997; Schmetterling 2001). Clearly, stream dwelling salmonids are more mobile and migratory than earlier studies have suggested; however, there is variability in the degree of motility among populations or systems and movement patterns may be influenced by anthropogenic and natural disturbances.

Historical disagreements concerning movement patterns in salmonids may largely be a function of the spatial and temporal scales of individual studies (Rodriquez 2002). The importance of scale in ecological studies has been well documented (Wiens 1989). Historically, many stream ecology studies monitored fish movement at small spatial scales and over short time frames because individuals were thought to be sedentary (spending their lives within a 20-50m section of stream). These data were then used to describe the entire river system, missing many of the complexities, interactions, and contributing factors to behaviors of riverine fish (e.g., Hunt 1976). Many researchers are now studying fish movement intermediate and large spatial scales to incorporate both local and larger watershed level movement patterns of fish (e.g., Fausch et al. 2002). Many of these studies have found evidence that stream fish are more mobile than previously thought, requiring large, un-fragmented stream networks (Dunham et al. 1997). Connectivity, however, is often impeded by barriers and non-native salmonids such as brook trout (*Salvelinus fontinalis*) which displace native cutthroat into upstream reaches (Dunham et al. 2003).

Many of the fourteen subspecies of cutthroat trout (*Oncorhynchus clarkii* spp.) in North America are currently considered threatened or endangered under the Endangered Species Act or sensitive species by state game and fish agencies (Peacock and Kirchoff 2004; Utter 2003, Kozfkay and Campbell 2007; Federal Register Vol. 40, p. 29864). As with many salmonids, declines in the distribution of these subspecies are due in part to habitat loss and fragmentation (Rieman and Dunham 2000; Fausch et al. 2002; Schrank and Rahel 2006), competition with non-native salmonids (Coffin and Cowan 1995; Sabo and Pauley 1997; Van Kirk and Benjamin 2001; Hasegawa and Maekawa 2008), and hybridization with closely related rainbow trout (*O. mykis*s) (Utter 2003; Peacock and Kirchoff 2004). Non-native rainbow, brown (*Salmo trutta*), and brook (*Salvelinus fontinalis*) trout have been introduced extensively across much of the Western U.S, representing an impediment to the recovery of viable, native cutthroat trout populations within their historical ranges (Young 1995; Dunham et al. 1997; Dunham et al. 1999; Rieman and Dunham 2000; Rubidge et al. 2005). Hybridization with rainbow trout poses the greatest threat to many cutthroat trout populations which can result in genetic introgression and ultimately produce hybrid swarms and dilution of cutthroat trout genomes (Bartley and Gall 1991; Peacock and Kirchoff 2004; Bettles et al. 2005; Kozfkay and Campbell 2007; Boyer et al. 2009). In addition, rainbow trout compete for resources (e.g., food and spawning gravels) with native salmonids. Many non-native salmonids are now naturalized (naturally reproducing) in river systems historically occupied only by cutthroat trout, which has forced native cutthroat trout populations into less favorable areas in the upper headwaters of river systems (Little and Fabacher 1994; Dunham et al. 1997; Novinger and Rahel 2003). Often there are no barriers separating cutthroat trout and non-natives, allowing possible future negative interactions to occur (Muhlfeld et al. 2009 a,b). Populations isolated within upper headwater systems are disconnected from other populations making them susceptible to genetic bottlenecks or local extirpation due to floods, droughts, or other environmental effects. Removals of these naturalized populations of non-natives are difficult, expensive, and controversial (Peterson et al. 2004); thus, managers have focused on the use of barriers to separate cutthroat trout from non-native species (McHugh et al. 2006; Novinger and Rahel 2003). Unfortunately, the use of barriers can be problematic, as barriers can isolate populations and reduce long-term viability due to small effective population sizes (Hilderbrand and Kershner 2000b; Fausch et al. 2009). Since isolation techniques have often been ineffective, management of these declining populations in interconnected habitat has been difficult due to lack of data regarding the distribution and natural movement patterns of native cutthroat trout compared to non-native salmonid species.

Lahontan cutthroat trout

The Lahontan cutthroat trout (LCT), native to riverine and lacustrine systems in the Lahontan Basin of Northern Nevada, Eastern California, and Southern Oregon is currently listed as threatened under the Endangered Species Act. LCT historically occurred throughout the Truckee River drainage, from Lake Tahoe to Pyramid Lake (Figure 1). Currently there are no naturally reproducing fluvial LCT populations in the mainstem Truckee River. There remains a small population of naturally reproducing native LCT in Independence Lake, which have been used historically as broodstock for hatchery programs. A small population of these Independence Lake strain LCT has been successfully reintroduced in the Little Truckee River, a tributary of the Truckee River upstream of Lake Tahoe. The long-term persistence of this population is uncertain, however, due to the presence of brook trout. The California Department of Fish and Game (CDFG) have attempted to remove these brook trout with mechanical methods (i.e., electro-fishing) for years, with limited success. Re-introduction of LCT in additional, connected habitats in this watershed is an important step in the recovery of the species.

Currently, the major concerns for successful LCT re-introduction in the mainstem Truckee River are habitat fragmentation and degradation, competition with non-natives, and hybridization with rainbow trout. Rainbow and brown trout have been introduced throughout the drainage, and have naturally reproducing populations throughout the watershed. Successful re-introduction of LCT into the Truckee River watershed will require a better understanding of the interactions among sympatric populations of non-native salmonids as well as other limiting factors.

LCT were extirpated from the Truckee River watershed by a suite of factors but primarily by barriers, which prevented access to spawning gravels and refugia to escape lethal water temperatures, ice, and predators (Dunham and Rieman 1999) . Installation of barriers limited LCT distribution to small, unconnected streams and high mountain lakes. Studies have shown that inland cutthroat trout populations historically were able to persist in highly variable environments by living in large interconnected stream and river systems (Figure 1) (Dunham et al. 1997; Ray et al. 2000; Rieman and Dunham 2000; Neville et al. 2006; Schrank and Rahel 2006). Peacock and Ambruzs (2004) found LCT displaying sedentary, mobile, and/or migratory behaviors in the Mary’s River Basin, Nevada. The current isolated populations, therefore, are not viable alternatives to interconnected populations occupying large interconnected stream and lake systems. The Truckee River itself has over 40 dams/diversions, preventing access for LCT to the many upstream tributaries necessary for spawning and blocking access to refugia from temperature extremes.

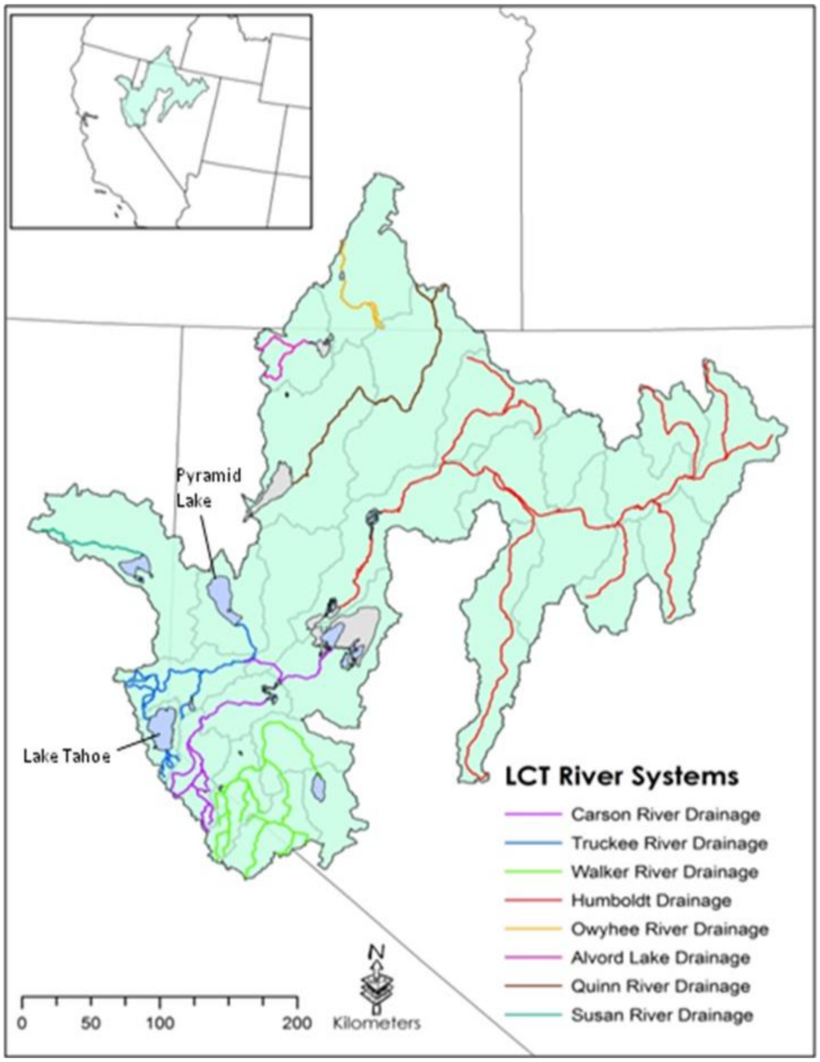

Figure 1. River and lake systems in the hydrographic Lahontan Basin (shaded area) historically occupied by Lahontan cutthroat trout.

The current ESA listing of LCT led the U.S. Fish and Wildlife Service to formulate a "Short-term action plan for the recovery of LCT in the Truckee River Basin" in 2003. The purpose of the action plan is to identify conditions that led to the decline of LCT populations and impediments to the re-establishment of naturally reproducing populations (Coffin and Cowan 1995). It is imperative to understand the interactions of non-native salmonids and Lahontan cutthroat trout in order to utilize potential opportunities for co-existence (Dunham et al. 2002) and prioritize management actions (e.g., flow regulations/barriers/etc.) that may lead to successful reintroductions or translocations.

Objectives

The primary goal of this study was to characterize movement dynamics of hatchery raised LCT reintroduced into the mainstem Truckee River in western Nevada, a highly managed ecosystem with nonnative predators and competitors. Based upon movement patterns documented for other cutthroat trout, the following predictions concerning reintroduced LCT were made: (1) LCT would migrate through the river during high flows, but would be unable to move upstream due to barriers (dams and diversions); (2) LCT would utilize pool habitats during low flow conditions; and (3) based upon reach characteristics, LCT would have differential movement patterns and survivorship among reaches. Individual LCT were radio-tagged and movement was monitored for 50 weeks to incorporate seasonal movement patterns into this study. Radio telemetry was used to evaluate:

(1) Movement of LCT in relation to fish size/condition, fish sex, season, and location within the study area.

(2) Habitat use and electivity by LCT.

(3) Survival rates of LCT in the Truckee River based on reach, season (flow and temperature), individual size and sex, and recovery period.

This study is a useful step in the recovery process of LCT in the Truckee River because LCT will be introduced into a highly fragmented, modified system, in the presence of rainbow trout (and other non-native salmonids). Based on results of this study, the flows of the Truckee River could be managed to mimic a more natural hydrograph, improving connectivity for LCT throughout the Truckee River basin. Connectivity could be advantageous for LCT because they have higher temperature, total dissolved solids (TDS), and alkalinity tolerances than other non-native salmonids, allowing LCT to inhabit portions of the Truckee River and tributaries that are unsuitable for other salmonids.

Methods

Study Area

The Truckee River begins at Lake Tahoe, California, flows 230 kilometers downstream to endorheic Pyramid Lake, Nevada, and varies in elevation from 1,897 to 1,160 meters above sea level (Figures 1, 2). The mainstem Truckee River contains greater than forty barriers to fish movement that limit migration and access to tributaries for spawning (Truckee River Recovery and Implementation Team 2003). This study occurred in the Truckee River between the border of California and Nevada and the city of Reno, Nevada (Figure 2). The study area is variable in habitat type, discharge, and temperature; therefore, the response of LCT to these factors can be evaluated. The study area was also determined based on permit limitations that precluded the re-introduction of hatchery LCT into California sections of the Truckee River. The study site was divided into three reaches separated by dams or diversions that were considered to be barriers to upstream dispersal. The uppermost section (Fleish) began at the Steamboat Diversion Dam extending 5.6 km to the Verdi Power Dam. This section contained several deep pools scattered between long sections of high gradient riffles and fairly deep (0.5-0.75 m) flatwater (i.e., runs). The middle section (Crystal Peak Park) began just downstream of the Verdi Power Dam and extended 5.7 km to the Washoe Highlands Dam. This section contained few quality deep pools, consisting mostly of long sections of flat, shallow water and low gradient riffles. The lower section (Washoe) spanned 5.4 km from the Washoe Highlands Diversion Dam to the Last Chance Diversion Dam. This section contained more deep water pools, found in the other sections. In the upper section, fish were released 3.5 kilometers downstream of Steamboat Diversion Dam. In the middle section, fish were released at Crystal Peak Park on the first release date. Due to high pressure from anglers at the park, an alternate site 640 meters upstream of the park was selected for the second release date. At the lower site, fish were released 525 meters downstream of the Washoe Highlands Diversion Dam. Temperatures in the study area varied from -0.18°C to 18.46°C and discharge varied from 8.5 to 22.7 m^3/s [Farad monitoring station, U.S. Geological Survey (USGS)]. Discharge in the Truckee River is regulated through management of water diversions and reservoirs (e.g., Prosser, Stampede, and Boca reservoirs) to satisfy water-rights demands.

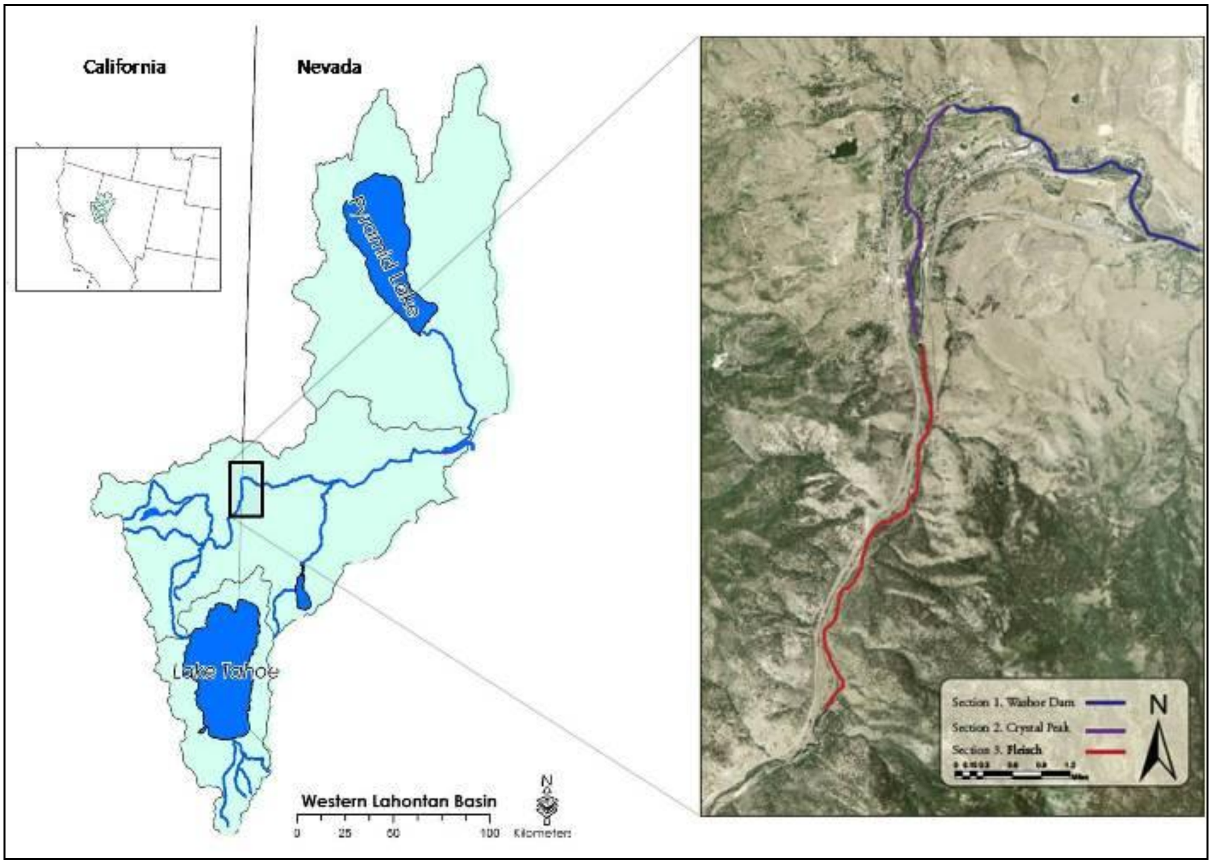

Figure 2. Detailed map of the study area and three reaches and overview map of the Truckee River Basin.

Table 1. The length, elevation change, average gradient, and average annual discharge (1994-present) for the three study reaches on the Truckee River, Nevada.

Reach	**Total Length(km)**	**Elevation(m)**	**Gradient (%)**	**Average Discharge(m^3/s)**
Fleish	5.4	1489-1536	0.8	22.6
Crystal	5.7	1490-1450	0.5	20.7
Washoe	5.4	1406-1450	0.6	19.9

Table 2. Number of different habitat types (Number) and percent of total stream surface area (Percent) available in the three reaches of the Truckee River examined in this study. Habitat types are divided into fast water and slow water units following the California Salmonid Stream Habitat Restoration Manual (CSHRM 1994) Level I habitat types.

	Fleish		Crystal		Washoe	
Level I habitat type	Number	Percent	Number	Percent	Number	Percent
Fast water unit						
Riffle	14	32	13	44	5	36
Cascade	7	5	0	0	2	2
Flatwater	12	45	14	47	4	39
Slow water units						
Main channel pool	11	17	6	9	5	20
Backwater pool	2	< 1	1	< 1	2	2
Scour pool	1	< 1	0	0	1	< 1

Study Species

The hatchery LCT used in this study were from the Pilot Peak strain broodstock. In the 1970's Lahontan cutthroat trout were found in a small stream near Pilot Peak in western Utah, far outside the LCT native range. Genetic comparison indicated that the Pilot Peak strain have the strongest phylogenetic relationship to museum preserved LCT of known Truckee basin origin (Peacock and Kirchoff 2007). Sample fish of this wild strain were captured and used to create a broodstock at the LNFH. This strain of LCT may be the most genetically adapted to the abiotic conditions found in the Truckee River Basin, and may represent a better alternative to reintroduction of Independence Lake strain LCT.

Species Assemblage

Native fish species found in the Truckee River include Lahontan redside shiner (*Richardsonius egregius*), speckled dace (*Rhynichthys ocsulus*), Paiute sculpin (*Cottus beldingii*), mountain sucker (*Catastomus platyrhynchus*), Tahoe sucker (*C. tahoensis*), and mountain whitefish (*Prosopium williamsoni*). The most prevalent non-native salmonids in the Truckee River include rainbow trout and brown trout (*Salmo trutta*). Rainbow trout were stocked until as recently as 7 years ago. A population was founded with Independence Lake LCT in the upper Truckee River, but non-native brook trout threaten long term persistence of this population. There are no native fluvial populations of Pilot Peak LCT in the Truckee River basin (Peacock and Kirchoff 2007).

Season Characterization

Seasons were defined based on stream temperature thresholds and flow rates. With this, I delineated the calendar year into four seasons: 1) Spring, which was a period of high flows and stream temperatures greater than 4°C (April – June); 2) Summer which corresponded to reduced variability and general decline of flow (July – September) and high stream temperatures (up to 22°C); 3) Autumn, which was defined as a period of cooling temperatures that remained above 0°C with relatively stable, low flows (mid October-mid January); and 4) Winter (mid January-March), which was considered as a period of stable, low flows with cold stream temperatures, periodically dipping below 0°C, and often remaining below 4 °C, a threshold considered to be physiologically stressful for potadromous fishes (Cunjak 1988). Flow data were obtained from USGS monitoring gauges located in the Truckee River at Boca, Farad, and Mogul. Temperature data loggers where placed within each of the three study reaches and recorded temperature every hour for the duration of the study. Temperature data was incomplete from September 24, 2008 to June 1, 2009 in the Crystal Peak Park reach because the datalogger was vandalized, so the average temperature from Fleish and Washoe Highlands sections was used for this period.

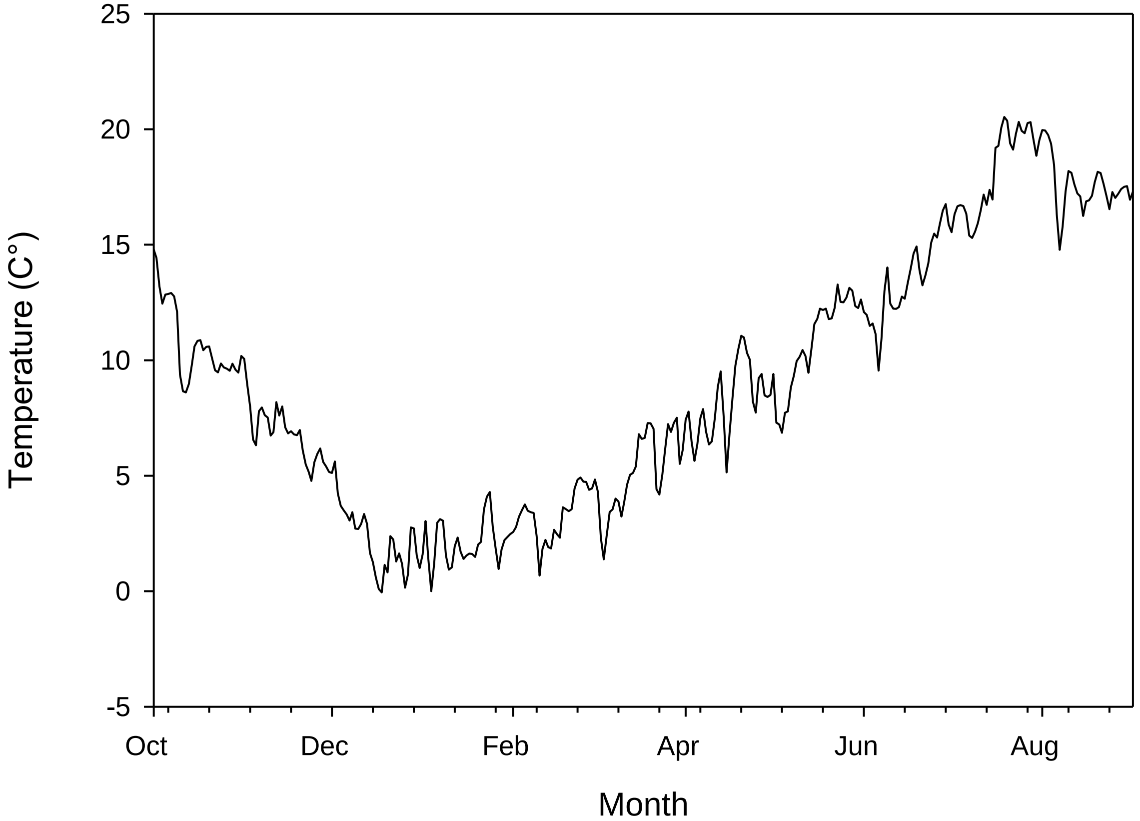

Figure 3. Mean stream temperature in degrees Celsius of the study area from October 2008 to September 2009.

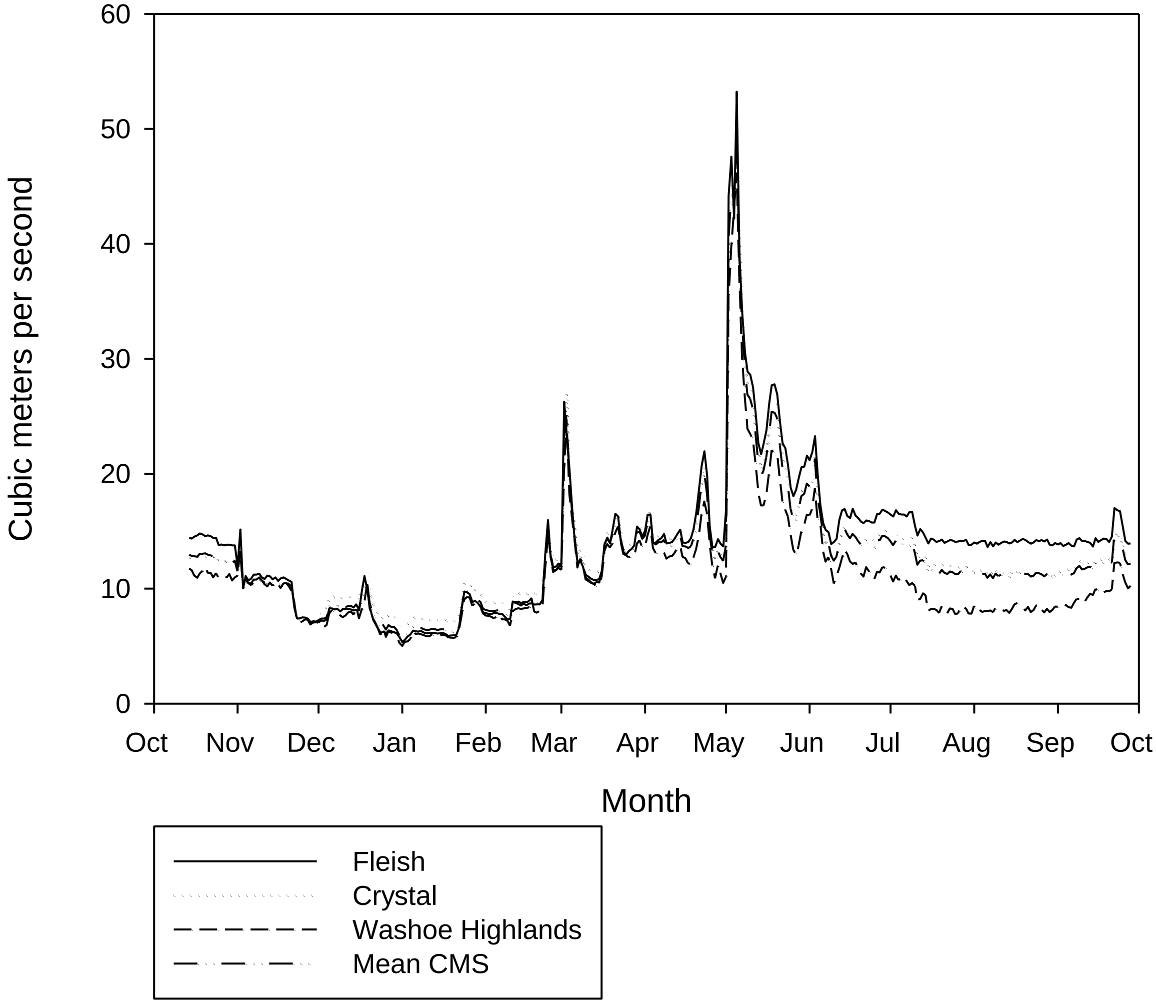

Figure 4. Average daily discharge from October 2008 to October 2009 for the three study reaches and mean daily discharge for the entire study area.

Field Methods

Forty-six individual LCT (Tables 3, 4) obtained from the Lahontan National Fish Hatchery (LNFH) in Gardnerville, Nevada were introduced into the Truckee River. I used an equal number of males (*N*=23) and females (*N*=23) from the LNFH's 2006 brood stock.

Individuals were anesthetized using clove oil or CO_2 intubation and 4.5-gram Lotek wireless NTC 6-2 Nanotags (radio-tags) were surgically implanted intraperitoneally anterior of the pelvic girdle of the fish. Each tag emitted a unique signal on six separate frequencies, allowing for identification of individual fish. It has been shown that tags weighing less than 3.9% of the body weight of an individual fish will not negatively affect swimming performance (Adams et al. 1998, Brown et al. 1999). I used only large LCT (> 300 g) from the brood stock of the LNFH, thereby increasing the survivability of the introduced fish.

I limited tagging to fish where tag weight was ≤ 2% of the fish's body weight (Winter 1983), to avoid affecting swim performance of the individuals. The average length and weight of all fish was 35.60 ± 20.70cm and 555.80 ± 140.05g, respectively.

One individual died three days after surgery (October 19, 2008); the tag from this fish was removed and implanted in another individual. Twenty-one LCT were released within the three study reaches on October 14, 2008 after a post-surgery recovery period in the hatchery of two weeks. Four tags were found to be faulty during reintroduction at the Washoe Highlands site. Individuals containing these faulty tags were returned to LNFH. Two weeks later, the remaining tagged individuals were released, after a recovery period of four weeks. I used a Lotek SRX 400 receiver fitted with a four element Yagi antenna to relocate individuals. Relocations began one week after release. Individuals were monitored every week for 50 weeks (lifespan of Nanotag) or until mortality could be confirmed. I recorded locations of tagged fish using a Garmin 76SX handheld GPS unit, accurate to within three meters. If movement was not detected for an individual LCT for more than 100 days, I attempted to confirm the individual's fate by a combination of snorkeling and electro-fishing.

Table 3. Standard length (mm; mean ± SD), wet weight (g; mean ± SD), and average condition factor (K; mean ± SD) of female and male Lahontan cutthroat trout implanted with radio-tags and released into the Truckee River, Nevada.

Sex	Mean Standard Length(mm) ± SD	Mean weight(g) ± SD	Mean Condition Factor (K) ± SD
Male	343.05 ± 26.71	605.00 ± 143.20	1.50 ± 1.32
Female	326.78 ± 18.68	508.80 ± 136.85	1.41 ± 1.33

Table 4. Standard length (mm; mean ± SD), and wet weight (g; mean ± SD) of Lahontan cutthroat trout implanted with radio-tags and released into three reaches in the Truckee River, Nevada.

Reach	Average standard length(mm) ± SD	Average weight(g) ± SD
Fleish	336±28.60	509.63±140.90
Crystal Peak Park	345.88±21.93	581.34±142.59
Washoe	331.69±25.53	535.69±145.02

Objective 1: Movement of LCT in relation to fish size, fish sex, season, and location within the study area.

I examined fish mobility based on three movement parameters: (1) turnover rates were calculated as the proportion of new relocation sites relative to the total number of relocations (Schrank and Rahel 2006); (2) home range was defined as the difference between the most upstream movement of a fish and the most downstream movement in relation to the release site (Young 1996); (3) total movement was the sum of all movements during the monitoring period. Using these movement parameters I was able to examine movement behaviors. Data were tested for normality using a Kolmogorv-Smirnov test. If fish movement showed a leptokurtic distribution (Fausch et al. 2002; Skalski and Gilliam 2000; Young 1996), I used a Friedman factorial analysis of variance by ranks test (non-parametric) to determine differences in fish mobility behavior based on season (autumn and winter), fish size, body condition, sex, and location in the watershed (reach). When data were normally distributed I used a simple one-way analysis of variance (ANOVA) to test for main effects. I used a factorial ANOVA to test for interaction effects between body condition and sex, reach and sex, as well as reach and body size.

Objective 2: Habitat use and electivity by LCT.

Habitat units within the study were classified as either pool (slow water units) or riffle (fast water units) based on the California Salmonid Stream Habitat Manual (CSSHM) Level I Habitat Types (Table 2). Habitat was characterized in this way to minimize subjective assumptions about habitat types. Other salmonid habitat use studies on medium sized rivers have also used a simple characterization of surface mesohabitats; pools, runs (flatwater), and riffles (Rimmer et al. 1983, 1984; Dare et al. 2002). Pools were characterized as slow moving water with a depth of one meter or greater. I further characterized pools as main channel, backwater, or scour pools according to CSSHM protocol (Table 2).Main channel pools were the dominant (> 55% by surface area) slow water unit. Riffles, or fast water units, were subdivided as riffles, cascades, and flatwater. In order to estimate habitat availability, the entire area where fish were relocated was inventoried following methods similar to those of Dare et al. (2002) and Rimmer et al. (1983) (using Level I Habitat types from the CSSHM) from May 28 to June 9, 2009. Each time a fish was relocated, the habitat type in which it was found was recorded and depth was measured using a 2-m graduated staff and a GPS waypoint was taken, allowing me to examine the habitat use of the fish. I used an ANOVA to test for differences in use of pools, flatwater, and riffles. I also tested for differences in use of pools between small and large fish as wells as males and females, using a one-way ANOVA. Ivlev’s (1961) Electivity Index (E) was used to indicate habitat preference based on percentage of relocations within habitat types and availability habitat types.

Objective 3: Survival rates of LCT in the Truckee River based on reach, season (flow and temperature), individual size and sex, and recovery period

A Nest Success Model was implemented in program MARK version 5.1 (White 2008) to examine differences in survivorship between sexes of LCT, sizes of LCT, seasonality, and reaches. The Nest Success Model provides a flexible framework for conditional open population modeling and incorporates uncertainty in radio telemetry data when the exact date of mortality is unknown (Rotella et al. 2004). I pooled weekly encounter histories (the number of times that a fish was successfully relocated and determined to be alive) into monthly encounter histories (4 weeks) to obtain monthly survival rates, and then converted to daily, weekly, and annual survival rates (e.g., Powell 2007). I developed a rule set for assumption of mortality where:

1) If a fish did not move > 50m for a period of 26 weeks, an attempt was made to push the fish out of its habitat using a Smith-Root LR-24 backpack electro-fisher. Attempts for visual confirmation were also made. If fish did not move after electrofishing, the fish was assumed dead.
2) For individuals residing in holes deeper than 1.5m, fish were assumed alive since there was no way to confirm mortality using electro-fishers that have a depth range of 1 to 1.5 meters.
3) Fish with failed tags, that moved out of the system (presumably by anglers), were censored (i.e., taken out of the pool of available individuals) at the last time of detection, and assumed dead, for more conservative estimates.

Using the Nest Success model, I was able to incorporate weight, standard length, sex, and recovery period length as individual covariates, with the three different reaches modeled as separate groups. Flows, temperatures, seasons, and time trend (i.e., changes in survivorship as a function of time after release) were modeled as group covariates and incorporated directly into the design matrices for individual models.

Ranking of models in the candidate set of 17 models was based on Akaike Information Criteria (AIC) adjusted for small sample size (AICc: Burnham and Anderson 2002). To account for uncertainty among models and gain the most inference from a multi-model approach, I used model averaging of all candidate models (Burnham and Anderson 2002). As suggested by Burnham and Anderson (2002), when the difference in ΔAIC between models is less than 2, models were assumed to have approximately equal weight in the data.

Results

During the first week following reintroduction three fish were caught and removed by anglers (according to a personal interview with an angler on site) and three additional fish were never relocated, therefore only 35 fish were tracked from October 2008 to September 2009 (Table 5). I recorded a total of 865 relocations.

Objective 1: Fish movement in relation to fish size, fish sex, season, and location within the study area.

There were statistically significant differences in home range size of individual fish among the three reaches (ANOVA; F=12.98, df=2, P<0.001, Figure 5). Total movement distance differences were also statistically significant among the three reaches (ANOVA; F=15.85, df=2, P<0.001). Turnover rate was higher for males than females, however the difference was not significant (ANOVA; F=1.65, df=1, P=0.21). Turnover rates were similar for LCT among reaches (ANOVA; F=1.08, df=2, P= 0.35). Fish with higher condition factors (K) had higher turnover rates (ANOVA; F=3.39, df=2, P= 0.08) and home ranges (ANOVA; F=1.68, df=2, P= 0.25) than those with lower body condition, though the differences were not significant. There was a negative relationship between standard length and home range size, however, the difference was not significant (Friedman test, χ^2= 3.67, *df*= 1, *P*=.056). Fish weight did not appear to influence total movement distances (ANOVA; *F*=1.72, *df*=1, *P*=0.079). There was a significant difference in turnover rate between autumn and winter seasons among reaches (ANOVA; *F*= 4.42, *df*=1, *P*= 0.039). None of the interactions tested for were significant, and are not discussed further.

Table 5. Turnover rate (mean ± standard deviation), home range (mean ± SD), total distance (mean ± standard deviation) moved per fish by reach, and number of radio tagged Lahontan cutthroat trout in the Truckee River, Nevada (2008-2009).

Reach	Turnover rate	Average home range (range; m)	Average distance moved(range; m)	*N**
Fleish	0.27±0.12	877.45±573.97 (260-2000)	878.00±638.45 (134-2165)	12
Crystal Peak Park	0.28±0.13	1208.00±737.58 (498-2400)	1804.62±971.95 (717-3824)	13
Washoe	0.27±0.16	403.00±122.06 (100-415)	758.00±202.78 (469-1400)	10

*42 LCT were reintroduced into the Truckee, however seven fish were never relocated, and are not included in these data.

Objective 2: Habitat use by LCT.

Tagged fish used pools preferentially over fast water habitat types (ANOVA; *F*= 45.90, *df*=2, *P*< 0.02; Figure 7) in all three sections. Large fish were found more often in pools than smaller fish, however the difference was not significant (ANOVA; *F*=.37, *df*=1, *P*<0.55, Figure 8). Males and females did not exhibit significant differences in habitat use (ANOVA; *F*=0.749, *df*=2, *P*<0.50) between groups, however both were found more often in pools (43%) than riffles (25%) or flatwater (33%) despite the higher availability of fast-water habitats (84%; Table 2). Electivity analysis indicated that LCT appeared to prefer pools (E= 0.44) over flatwater (E = -0.30) or riffles (E = -0.05).

Objective 3: Survival rates of LCT in the Truckee River based on reach, season (flow and temperature), individual size and sex, and recovery period

Using monthly survival rate estimates from model averaged results, I derived annual, weekly, and daily survival rates (Table 6). Annual survival probability for LCT, based on the 50 week monitoring period, was only 17.05% for LCT in the entire study area. Survival rates did not differ significantly among the three reaches (Figure 9). The ranked models all included a term for the "autumn" season (mid October-mid January). The top 6 models included group covariates (temperature and flow) as well as three individual covariates (sex, recovery period, and standard length) differed by less than 2ΔAIC's and were considered to have approximately equal representation in the data (Table 7). The seventh model, which included the individual covariate for weight (g), ranked highly, being only 2.07ΔAIC's behind the top model (Table 7). The direction of effect and cumulative model weights for the top covariates are shown in Table

8. Models including the term for autumn accounted for 96% of cumulative model weights, with survival rate decreasing (beta estimate) during this period (Table 8). Temperature and flow terms had the second and third highest cumulative model weights respectively (Table 8), with survival rates increasing as water temperatures and flow rates increased.

Table 6. Annual, monthly, weekly, and daily survival rates of reintroduced hatchery LCT in the Truckee River derived from model averaged estimates. Standard errors and confidence intervals were calculated using the Δ method.

Time period	**Survival Rate**	**Standard Error**	**Lower 95% CI**	**Upper 95% CI**
Annual (50 week)	0.170502	0.000146	0.170210	0.170794
Monthly(4 week)*	0.872775	0.045640	0.781495	0.964055
Weekly	0.966553	0.010303	0.949511	0.983753
Daily	0.995152	0.001430	0.981287	1.009040

Table 7. Performance of top survival models for LCT from October 2008 to September 2009 where "." denotes the most parsimonious model.

Model	AICc	Delta AICc	AICc Weights	Num. Par
{Season(autumn) + time}	159.5	0	0.2361	4
{Season(autumn)+time+temperature}	159.6	0.0914	0.22555	5
{Season(autumn)+time+flow}	160.6	1.0486	0.13976	5
{Season(autumn)+ gender}	161.3	1.7199	0.09991	5
{Body length+Season(autumn)}	161.4	1.9084	0.09093	5
{Post-surgery recovery+autumn}	161.5	1.935	0.08973	5
{Body weight+autumn}	161.6	2.0799	0.08345	5
{ 2 season(cold low flow)}	163.5	3.9555	0.03267	6
{Season(autumn)+temperature}	171.8	12.2905	0.00051	3
{.}	173.1	13.5217	0.00027	1

Table 8. Cumulative model weights and direction effects of group and individual covariates based on beta estimates.

Covariate	Direction of Effect	AICc Weight
Autumn season	-	0.96621
Temperature	+	0.22616
Flow	+	0.14018
Sex(females)	-	0.10004
Standard length(mm)	+	0.09104
Recovery	-	0.08984
Weight(g)	+	0.08355

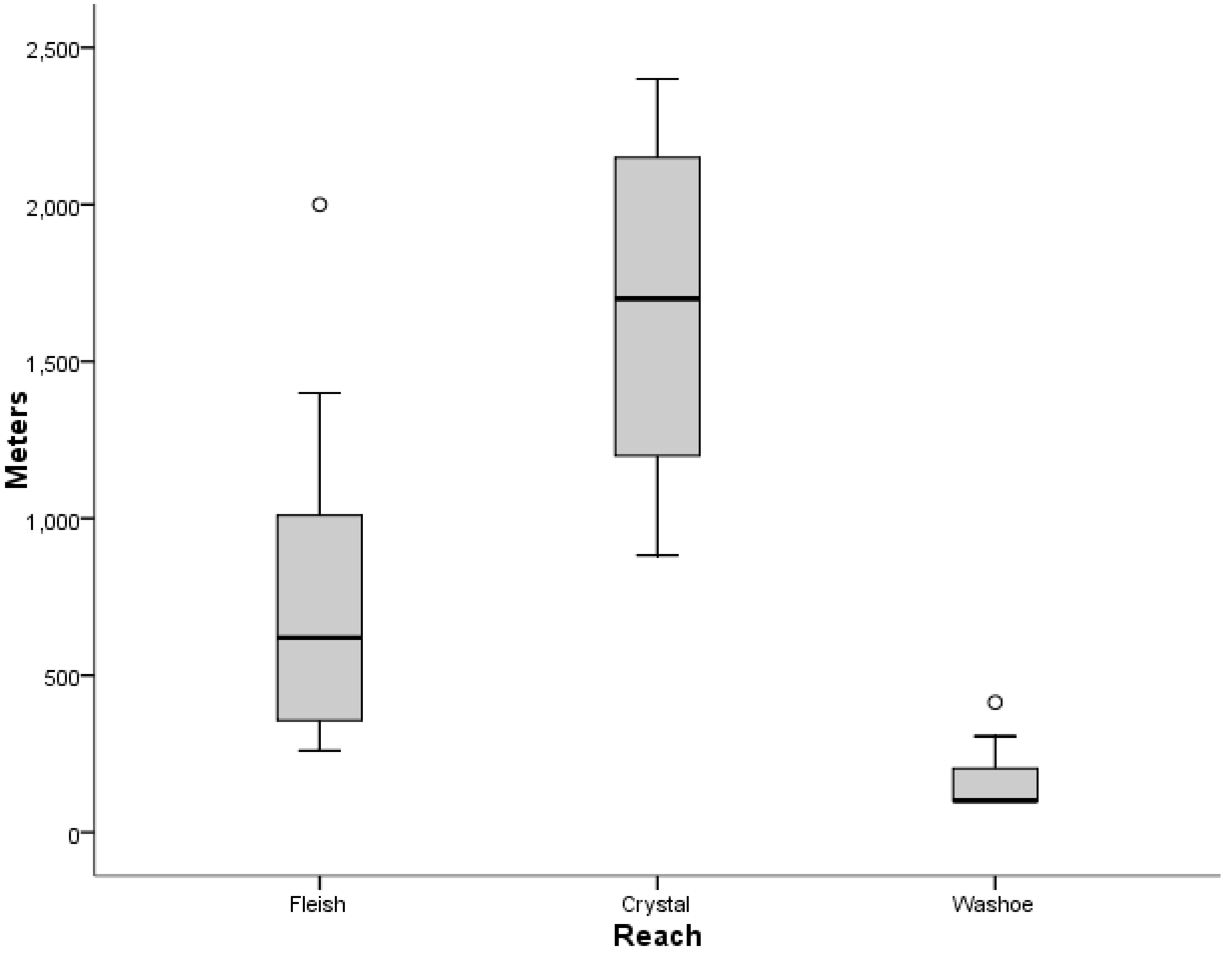

Figure 5. Mean home range size ± standard deviation of LCT in the three study reaches. Box plots show median and inter-quartile range and the upper and lower 95% confidence interval for the data.

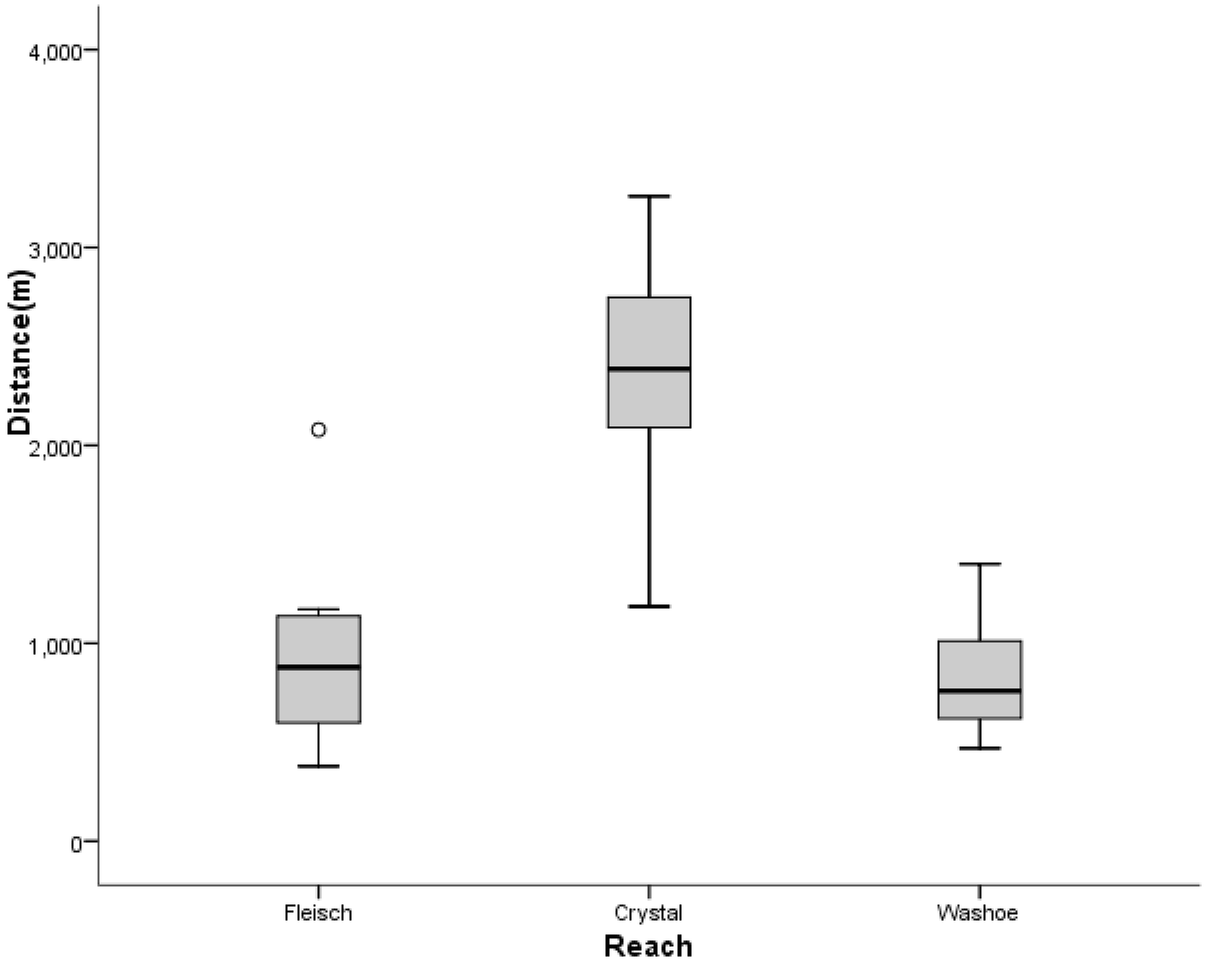

Figure 6. Total movement distances (m) of individual LCT between the three reaches. Box plots show median and inter-quartile range and the upper and lower 95% confidence interval for the data.

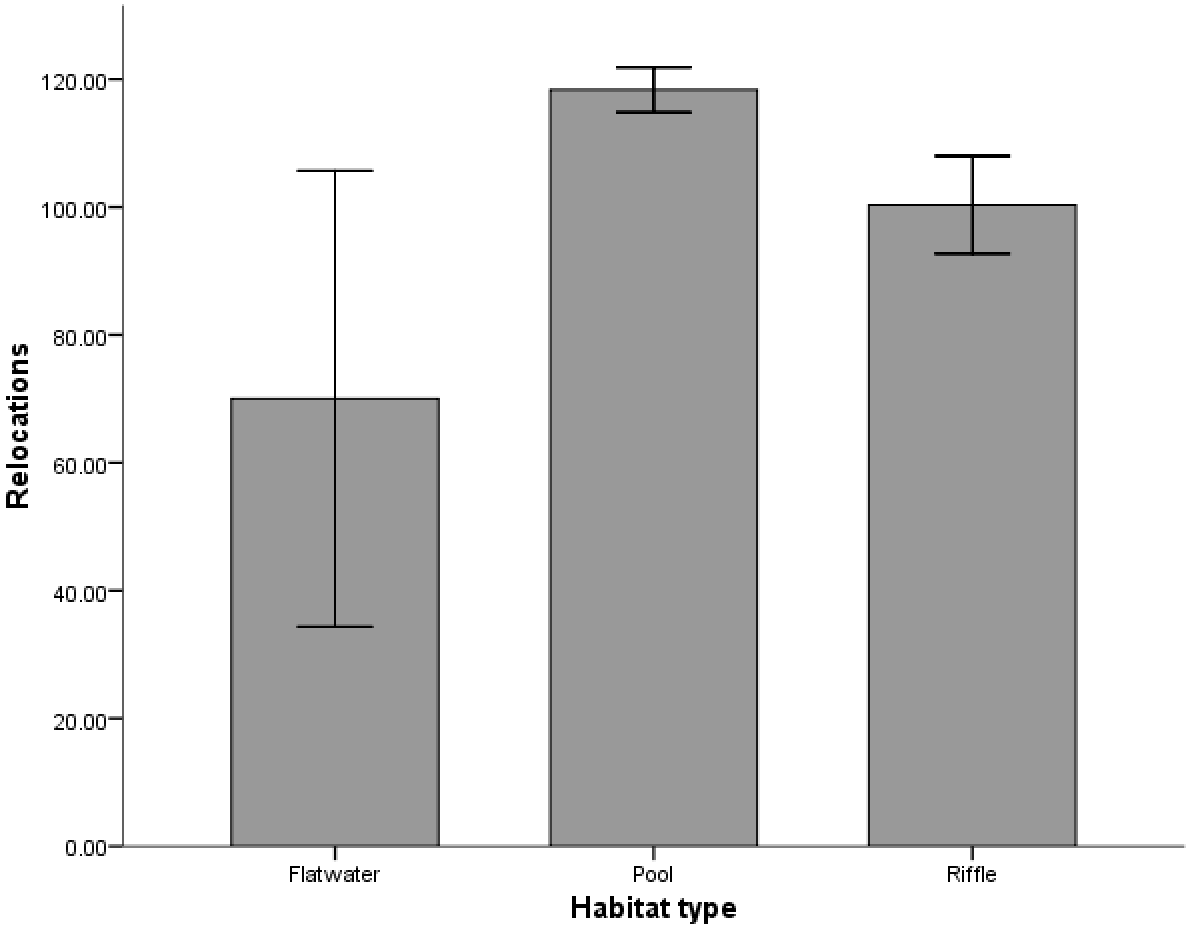

Figure 7. Number of relocations ± standard deviation of LCT in the Truckee River study area by habitat type from October 2008 to September 2009.

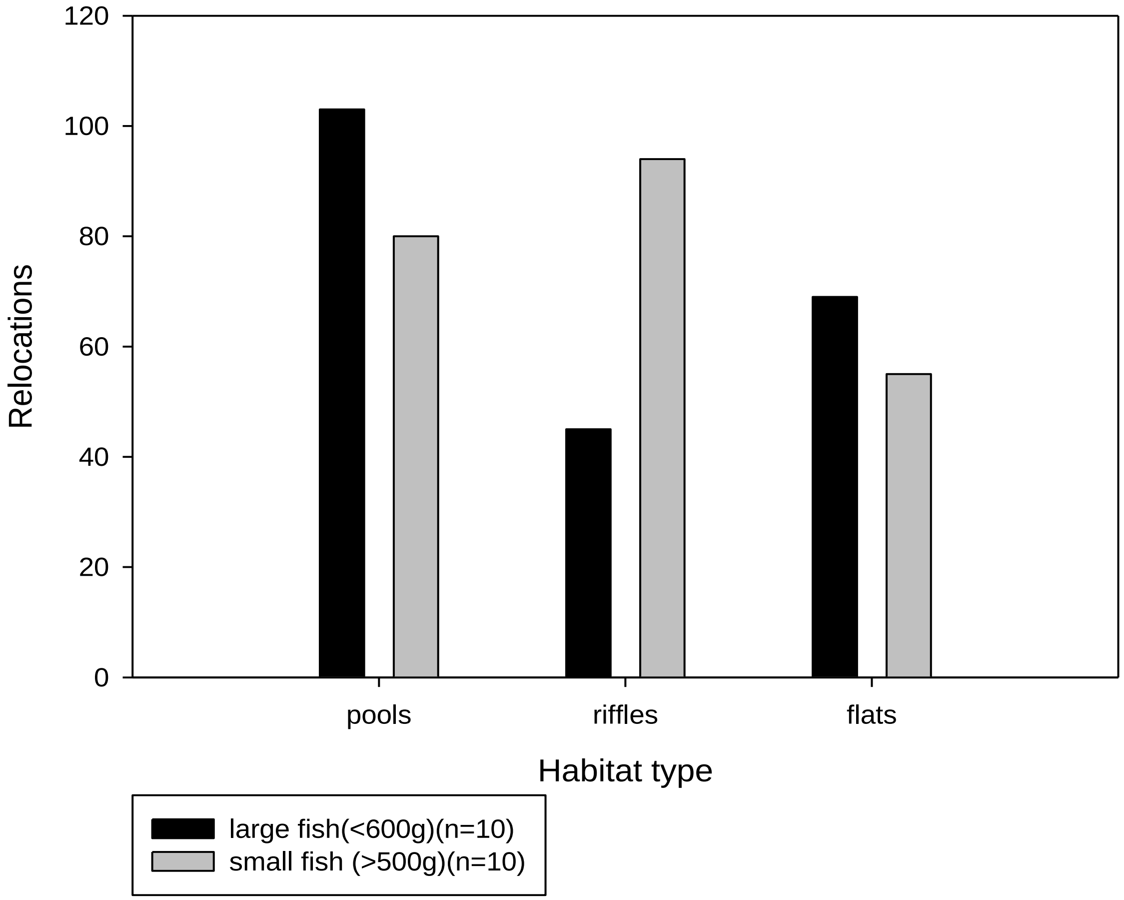

Figure 8. Habitat use differences of small and large fish in the study.

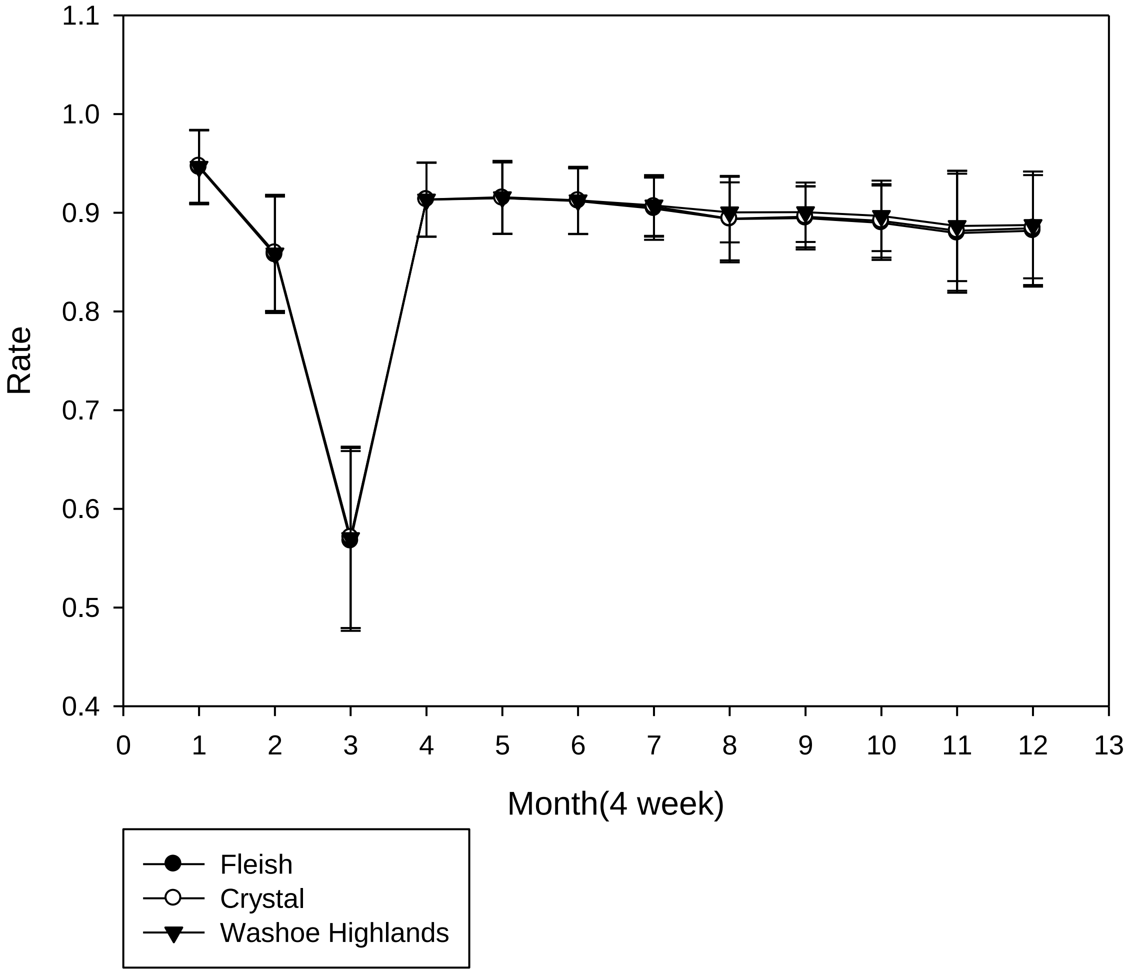

Figure 9. Average monthly (4 week) survival rates ± standard errors of LCT in the three Truckee River study reaches from October 14, 2008 to September 28, 2009.

Discussion

LCT were highly mobile within the mainstem Truckee River and used slow moving, deep water pools more than other habitat types during the autumn and winter. However, no fish moved upstream past putative barriers. Additionally, the low survivorship of LCT introduced in this study highlight the need to evaluate different reintroduction scenarios for LCT in the Truckee River.

Movement of LCT in relation to fish size, fish sex, season, and location within the study area

The average home range of these LCT was 853m, with only 24% of individuals moving less than 100m. Nearly all fish were relocated in at least two different habitat types. LCT exhibited significant upstream movement during the autumn, followed by movement into overwintering refugia (deep pools) in the winter. By early February, nearly all individuals showed relatively little movement, remaining sedentary in water deeper than their original relocations during the autumn. Nearly all of the radio tagged fish that were relocated (97%) moved at least 100m from their original relocation site. This finding is inconsistent with the Gerking's (1959) "restricted movement paradigm" where fish rarely move more than 20 m from their original location site. These LCT seemed to direct their movements upstream rather than downstream. Only seven of the 33 individuals showed any movement downstream, with only two fish moving from an upper section to a lower section. Movement upstream from one section to another was impeded by the three dams within the study area; however, these barriers did not appear to prevent downstream movements. One of the two fish that moved to a downstream reach was caught in the Verdi power dam and diverted to the Verdi canal, where it died shortly thereafter.

There was a significant difference in home range size of fish between the three reaches. The three reaches had similar lengths, flows, gradients, and temperatures (Table 1); however, they varied in their proportions of fast water to slow water habitat habitats (Table 2), which could have influenced fish movement. Crystal Peak Park had a relative lack of deep water pools characterized by long stretches of riffle and flatwater. This section also had the highest turnover rates and largest home ranges, suggesting that a lack of suitable habitat (i.e., deep pools) increased movement (Bjornn 1971; Cunjak 1986).

I found no significant relationship between movement patterns and fish size (standard length). This is most likely due to the relatively large, homogenous size of all individuals in the study. Schrank and Rahel (2006) found larger Bonneville cutthroat trout tended to be more sedentary than smaller fish, as large fish tended to remain in localized suitable habitats.

Males had slightly higher turnover rates, home ranges, and total movement distances than females in all three reaches, though differences were not significant. While not significant, these findings are consistent with sex-biased dispersal documented for other salmonid species, where males typically exhibit larger dispersal distances (Hutchings and Gerber 2002).

Examination of movement patterns between the two seasons where most movement took place, autumn and winter, revealed substantially higher movement distances during the autumn among reaches (Friedman test, $\chi^2=28.71$, $df=5$, $P<0.001$). From late February to September 2009, however, LCT rarely made movements larger than 50m, which is consistent with the “restricted movement paradigm” (Gerking 1959). Coyler et al. (2005) found that salmonids show considerable variation in movement behavior during the autumn and winter, while Brown and Mackay (1995) have further shown that salmonid movement decreases from autumn to winter, consistent with my findings. LCT also moved much more frequently (i.e., higher turnover rate) during the autumn. It is important to note that the “autumn” season was also the first 3 months of reintroduction for the LCT, which could explain the higher movement rates and larger movement distances during this period.

Habitat Use

Several studies of cutthroat trout have demonstrated higher use of deep pools by adult fish relative to other habitat types (Glova 1987; Bisson et al. 1982, 1988; Fausch and Northcote 1992; Young 1996). Heggenes et al. (1991) went further in demonstrating that cutthroat trout prefer deep water pools, slower water velocities, and cover provided by large woody debris. The results from this study for LCT concur with these findings, however, there were few pools formed or covered by woody debris in the Truckee River study area. In each of the three sections, deep pools represented a smaller proportion of habitat types than flatwater or riffles (Table 2), yet LCT used deep water pools more frequently than other habitat types. Electivity analysis also quantified a strong preference for pools over other types. The Truckee River is a highly managed system, with major historic and current land alterations, which could explain the lack of large woody debris found in the study area. Although a more detailed habitat analysis is necessary, it appears that hatchery LCT reintroduced into the Truckee River exhibit similar habitat use behaviors to that of cutthroat trout in other systems (Glova 1987; Bisson et al. 1982, 1988; Heggenes et al. 1991; Fausch and Northcote 1992; Young 1996).

Survivorship

Survival estimates for introduced hatchery LCT in the Truckee River, while low initially, tended to stabilize over time. The lowest monthly survival estimate for all three reaches occurred in January, corresponding with the lowest temperatures and flow rates during the study period. Fish might have been unable to find refugia from the cold temperatures during this period due to the low flows, where shallow riffles and flatwater sections could have acted as barriers to fish movement. The top models all contained the term for “autumn” with a negative direction of effect indicating decreasing survival over the autumn (October through January) period. This is consistent with Harvey et al. (2006) who showed that early winter brings a substantial reduction in suitable habitat and subsequently decreases survivorship for salmonids. Not surprisingly, fish with higher standard lengths and weights also showed slightly higher survival rates than smaller fish. The recovery covariate accounted for a small percent of AIC model weights and had a negative effect on survival rate. I had assumed that fish with a longer post-surgery recovery period (4 weeks) would show higher survival than fish with only a 2 week recovery period. This did not occur, possibly indicating that the implantation surgery had little negative effect on LCT survival, and that a longer recovery period may not be necessary. These estimates of LCT survival may assist managers with future monitoring and reintroduction efforts.

Limitations

Despite well documented methodologies for radio telemetry studies in fisheries, there were inherent limitations in the data collected in this study. The telemetry equipment used in my research only allowed me to determine the location of a fish to within 3 meters, making it difficult to be absolutely certain in some instances of the habitat a tagged fish was in. I tracked fish using weekly intervals; therefore movements between sampling intervals could have gone unnoticed, causing me to underestimate movement parameters (Horton et al. 2004). Survivorship was especially difficult to estimate, as the tags do not include mortality sensors. Attempts to visually confirm mortality proved largely unsuccessful due to the depth, velocity, and visibility in the Truckee River. Instead, mortality was inferred if a fish did not move for a period of 238 days and could not be induced to move by electro-fishing. This may be a very conservative estimate of mortality as it is possible the fish was alive, yet undisturbed by the electro-fisher, as cutthroat trout may remain in suitable habitat for long periods (Schrank and Rahel 2004). Additionally, 16 fish were unaccounted for at the end of the monitoring period. The lack of signal could be attributed to several possibilities including capture/mortality, tag failure or ejection, or movement outside of the study area. If these 16 individuals were all assumed alive at the end of the study period, the annual survival rate would be much higher, nearly 54%. Despite these uncertainties, the Nest Success Model framework within Program Mark allowed me to provide useful survival rate estimates by only incorporating the number of fish available at a given sample occasion in the survival estimate for that occasion.

Conclusions

The results of this study show that LCT were highly mobile within the mainstem Truckee River, while their upstream movements was limited by in-stream barriers. In the Washoe study reach, 90% of LCT moved upstream into pools at the base of the Washoe Highlands dam, though none were able to move above the dam, probably because of the unmaintained fish ladder. This fish ladder was clogged with woody debris throughout the study period. In the Crystal Peak Park section, 54% of fish moved nearly 2.5 km upstream to the pools at the base of the Verdi power dam, though none moved above the dam. Studies have shown that cutthroat trout need a large interconnected habitat to persist in extreme high desert environments (Dunham et al. 1997; Ray et al. 2000; Rieman and Dunham 2000; Schrank and Rahel 2006). Therefore barriers limiting LCT movement might present an obstacle in the reintroduction of a viable LCT population in the Truckee River as fish may not be able to move to suitable refugia habitat when necessary. Improvements to fish ladders on existing barriers should also be made to facilitate LCT movements. The habitat preferences shown in this study indicate that LCT prefer slow moving, deep water pools during the colder months of autumn and winter. Although a more detailed habitat analysis would be needed, habitat restoration and enhancement of existing pools could provide more preferred habitat for LCT, increasing their chances for survival. Although LCT in this study exhibited relatively low survival rates, nearly 17% of the released LCT survived the duration of the study. Perhaps if a larger number of suitable size/age class LCT were released into the Truckee River, there could be potential for some of the fish to survive long enough to spawn successfully. Apart from the low survival during the autumn season, LCT in this study exhibited a relatively stable rate of survival for the duration of the study. The low survival in this period was likely due to the adjustment period following introduction, rather than the season during which the LCT were introduced. The implantation of tags necessitated the use of large (>300g), older (> 2 years), broodstock fish for this study, though this age class might not be the best suited fish for reintroduction. Older hatchery fish may have become overly habituated to the hatchery environment, making them less competitive in their native habitat than naturalized non native rainbow and brown trout. Managers often introduce large numbers of small juvenile fish in reintroduction attempts. In many systems, these smaller juveniles are likely susceptible to high levels of predation by non-native trout populations, resulting in extremely limited survivorship (Young 1995; Dunham et al. 1997; Harig et al. 2000). Managers might consider introducing intermediate age classes of hatchery LCT, which are not completely habituated to the hatchery, and are large enough to avoid predation by nonnative trout.

Perhaps the most important step in successfully LCT recovery would be to manage the Truckee River flow regimes to mimic natural patterns that vary seasonally and across years. This would increase the connectivity of the system because barriers would be more easily bypassed by LCT, predominately during high release periods (April-June). A more connected Truckee River Basin would allow LCT, because of their high TDS, alkalinity, and temperature range tolerances, to occupy portions of the Truckee unsuitable for RBT and other non-native salmonids. Higher connectivity would also allow LCT to escape temperature and extremes by accessing deep pools in different altitudinal reaches of the river. LCT might also be able to access historic spawning tributaries with higher amounts of spawning gravel than the main-stem Truckee River. A more natural hydrograph for the Truckee River could give LCT the necessary advantage over non-native salmonids needed for successful re-establishment.

References

Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile Chinook salmon. Transactions of the American Fisheries Society 127:128-136.

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. BioScience 43:32-43.

Bartley, D. M., and G. A. Gall.1991. Genetic identification of native cutthroat trout (*Oncorhynchus clarki*) and introgressive hybridization with introduced rainbow trout (*O. Mykiss*) in streams associated with the Alvord Basin, Oregon and Nevada. Copeia 3:854-859.

Bear, E. A., T. E. McMahon, and A.V. Zale. 2007. Comparative thermal requirements of westslope cutthroat trout and rainbow trout: implications to species interactions and development of thermal protection standards. Transactions of the American Fisheries Society 136:1113-1121

Bettles, C. M., M. F. Docker, B. Dufour., and D. D. Heath. 2005. Hybridization dynamics between sympatric species of trout: loss of reproductive isolation. Journal of Evolutionary Biology 18:1220-1233.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73. *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Portland, Oregon.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile Coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117:262-273

Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100:423-438.

Boyer, M. C., C.C. Muhlfeld, and F.W. Allendorf. 2009. Rainbow trout, *(Oncorhynchus mykiss)*, invasion and spread of hybridization with native westslope cutthroat trout (*Oncorhynchus clarkii lewisi)*. Canadian Journal of Fisheries and Aquatic Sciences 138:1036-1051.

Brown, R., and W. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124:873-885.

Brown, R. S., S. J. Cooke, W. G. Anderson, and R. S. McKinley. 1999. Evidence to challenge the "2% rule" for biotelemetry. North American Journal of Fisheries Management 19:867-871.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492-507.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd Edition. Springer-Verlag, New York, New York.

Burns, J. W. 1972. Some effects of logging and associated road construction on northern California streams. Transactions of the American Fisheries Society 101:1-17.

California Department of Fish and Game. 1998. California Salmonid Stream Habitat Restoration Manual, 3rd Edition. Inland Fisheries Division, Sacramento, California.

Coffin, P. D., and W. F. Cowan. 1995. Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon.

Coyler, W. T., J. L. Kershner, and R. H. Hilderbrand. 2005. Movements of fluvial Bonneville Cutthroat Trout in the Thomas Fork of the Bear River, Idaho-Wyoming. North American Journal of Fisheries Management 25:954-963.

Collins, R., and A. Jenkins. 1996. The impact of agricultural land use on stream chemistry in the Middle Hills of the Himalayas, Nepal. Journal of Hydrology 185:71-86.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by brook char and rainbow trout. Canadian Journal of Fisheries and Aquatic Sciences 43:1970-1981.

Cunjak, R. A. 1988. Physiological consequences of overwintering: the cost of acclimatization? Canadian Journal of Fisheries and Aquatic Sciences 45:443-452.

Dare, M.R., W.A. Hubert, and K.G. Gerow. 2002. Changes in habitat availability and habitat use and movements by two trout species in response to declining discharge in a regulated river during winter. North American Journal of Fisheries Management 22:917-928.

Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North American Journal of Fisheries Management 17:1126-1133.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642-655.

Dunham, J. B., B. S. Cade, and J. W. Terell. 2002. Influences of spatial and temporal variation on fish, habitat relationships defined by regression quantiles. Transactions of American Fisheries Society 131:86-98.

Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2003. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12:373-391.

Dunham J. B., D. S. Pilliod, and M. K. Young. 2004. Assessing the consequences of non-native trout in headwater ecosystems in western North American Journal of Fisheries 29:18-26.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682-693.

Fausch, K. D., C. E. Torgeson, C.V. Baxter, and W. L. Hiram. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52:483-498.

Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D.P. Peterson. 2009. The invasion versus isolation dilemma: tradeoffs in managing native salmonids with barriers to upstream movement. Conservation Biology 23:859-870.

Gerking, S. D. 1959. The restricted movement of fish populations. Biological Review 34:221-242.

Glova, G. J. 1986. Interaction for food and space between experimental populations of juvenile Coho salmon *(Oncorhynchus kisutch)* and coastal cutthroat trout *(Salmo clarki)* in a laboratory stream. Hydrobiologia 131:155-168.

Glova, G. J. 1987. Comparison of allopatric cutthroat trout stocks with those sympatric with Coho salmon and sculpins in small streams. Environmental Biology of Fishes 20:275-284.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Science 51:2626-2637.

Gresswell, R. E., W. J. Liss, G. L. Larson, and P. J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. North American Journal of Fisheries Management 17:1046-1064.

Hall, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53:585-604.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of Greenback cutthroat trout translocations. North American Journal of Fisheries Management 20:994-1004.

Harvey, B. C., R. J. Nakamoto, and J. L. White. 2006. Reduced stream flow lower dry-season growth of rainbow trout in a small stream. Transactions of the American Fisheries Society 135:998-1005.

Hasegawa, K., and K. Maekawa. 2008. Potential of habitat complexity for mitigating interference competition between native and non-native salmonid species. Canadian Journal of Zoology 86:386-393.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48:1364-1370.

Heggenes, J., S. J. Saltveit, and O. Lingaas. 1996. Predicting fish habitat use to changes in water flow: modeling critical minimum flows for Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Regulated Rivers: Research and Management 12:331-344.

Hilderbrand, R. H., and J. L. Kershner. 2000a. Conserving inland cutthroat trout in small streams: how much stream is enough? North American Journal of Fisheries Management 20:513-520.

Hilderbrand, R. H. and Kershner, J. L. 2000b. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho-Utah. Transactions of the American Fisheries Society 129:1160-1170.

Horton, T. B., C. S. Guy, and J. S. Pontius. 2004. Influence of time interval on estimations of movement and habitat use. North American Journal of Fisheries Management 24:690-696.

Hunt, R. L. 1976. Long term evaluation of trout habitat development and its relationship to improving management related research. Transactions of the American Fisheries Society 105:361-364.

Hutchings J. A., L. Gerber. 2002. Sex-biased dispersal in a salmonids fish. Proceedings of the Royal Society of London B 269:2487-2493.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223-235.

Kondolf, G. M. 1997. Hungry water: effects of dams and gravel mining on river channels. Environmental Management 21:533-551.

Kozfkay, C. C., and M. R. Campbell. 2007. Incidence of hybridization between naturally sympatric westslope cutthroat trout and rainbow trout in the Middle Fork of the Salmon River drainage, Idaho. Transactions of the American Fisheries Society 136:624-638.

Little, E. E., and D. L. Fabacher. 1994. Comparative sensitivity of rainbow trout and two threatened salmonids, Apache trout and Lahontan cutthroat trout, to ultraviolet-B radiation. Advances in Limnology 43:217-226.

Lodge, D. M., and C. A. Taylor. 2000. Non-indigenous crayfishes threaten North American freshwater biodiversity: Lessons from Europe. Fisheries 25:7-20.

Magalhães, M. F., and P. Beja. 2007. Effects of multi-year droughts on fish assemblages of seasonally drying Mediterranean streams. Freshwater Biology 52:1494-1510.

McHugh, P., P. Budy, G. Thiede, and E. VanDyke. 2006. Trophic relationships of nonnative brown trout (*Salmo trutta*) and native Bonneville cutthroat trout (*Oncorhynchus clarkii utah)* in a northern Utah, USA river. Environmental Biology of Fishes 81:3-75.

Morita, K., and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling char populations. Conservation Biology 16:1318-1323.

Muhlfeld, C., T. E. McMahon, and D. Belcer. 2009a. Spatial and temporal dynamics of spawning between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), introduced rainbow trout (*O. mykiss*), and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences 66:1153-1168.

Muhlfeld, C., T. E. McMahon, M. C. Boyer, and R. E. Gresswell. 2009b. Local-habitat, watershed, and biotic factors in the spread of hybridization between native westslope cutthroat trout and introduced rainbow trout. Transactions of the American Fisheries Society 138:1036-1051.

Neville, H. M., J. B. Dunham, and M.M Peacock. 2006. Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. Landscape Ecology 21:901-916.

Novinger, D. L. and F. J. Rahel. 2003. Is isolating cutthroat trout above artificial barriers in small headwater streams an effective long-term conservation strategy? Conservation Biology 17:772-781.

Pascual, M. A., and V. Cussac. 2007. Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change. Aquatic Ecosystem Health and Management 10:212-227.

Peacock, M. M, and V. S. Kirchoff. 2004. Assessing the Conservation Value of Hybridized Cutthroat Trout Populations in the Quinn River drainage, Nevada. Transactions of the American Fisheries Society 133:309-325.

Peacock, M. M, and S. Ambruzs. 2004. Seasonal Movement Patterns of Lahontan cutthroat trout(*Oncorhynchus clarki henshawi*) in the Mary’s River basin determined through radio tracking. Final report to U. S. Fish and Wildlife Service, Region 6, Reno, Nevada.

Peacock, M. M, and V. S. Kirchoff. 2007. Analysis of genetic variation and population genetic structure in Lahontan cutthroat trout (*O. clarki henshawi)* extant population. Final report to U. S. Fish and Wildlife Service, Region 1, Reno, Nevada.

Peterson, N. P. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile Coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555-1564.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population Ecology of an Invasion: Effects of Brook Trout on Native Cutthroat Trout. Ecological Applications 14:754-772.

Poff, N. L, J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The Natural Flow Regime. BioScience 47:769-784.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109:950-955.

Propst, D. L., and K. B. Gido. 2004. Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. Transactions of the American Fisheries Society 133:922-931.

Ray, C., M. M. Peacock, and J. B. Dunham. 2000. Population structure and persistence of Lahontan cutthroat trout: results from a comparative study of isolated and networked streams. Interim report for Cooperative Agreement FSW 14-48-0001-95646 to United States Fish and Wildlife Service, Reno, Nevada.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service General Technical Report INT-302, Ogden, Utah.

Rieman, B. E. and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51-64.

Rieman, B., D. Lee, D. Burns, R. Greswell, M. Young, R. Stowell, J. Rinne, and P. Howell. 2003. Status of native fishes in the western United States and issues for fire and fuels management. Forest Ecology and Management 178:197-211.

Rieman, B. E., and J. T. Peterson. 2006. Have brook trout (*Salvelinus fontinalis*) displaced bull trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams? Canadian Journal of Fisheries and Aquatic Sciences 63:63-78.

Rimmer, D. M., U. Paim, and R. L. Saunders. 1983. Autumnal habitat shift of juvenile Atlantic salmon *(Salmo salar)* in a small river. Canadian Journal of Fisheries and Aquatic Sciences 40:671-680.

Rimmer, D. M., U. Paim, and R. L. Saunders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon *(Salmo salar)* at the summer-autumn transition in a small river. Canadian Journal of Fisheries and Aquatic Sciences 41:469-475.

Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecological Society of America 83:1-13.

Robinson, M. L., L. Gomez-Raya, W. M. Rauw, and M. M. Peacock. 2008. Fulton's body condition factor K correlates with survival time in a thermal challenge experiment in juvenile Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*). Journal of Thermal Biology 33:363-368.

Rosenfeld, J., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and Coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 57:766-774.

Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58:585-593.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187-204.

Rubidge, E., P. Corbett, and E. B. Taylor. 2005. A molecular analysis of hybridization between native westslope cutthroat trout and introduced rainbow trout in southeastern British Columbia, Canada. Journal of Fish Biology 59 (supplement A):42-54.

Sabo, J. L., and G. B. Pauley. 1997. Competition between stream-dwelling cutthroat trout (*Oncorhynchus clarki*) and Coho salmon (*Oncorhynchus kisutch*): effects of relative size and population origin. Canadian Journal of Fisheries and Aquatic Sciences 54:2609-2617.

Schrank A. J. and F. J. Rahel. 2004. Movement patterns in inland cutthroat trout (*Oncorhynchus clarki utah*): management and conservation implications. Canadian Journal of Fisheries and Aquatic Sciences 61:1528-1537.

Schrank, A. J., and F. J. Rahel. 2006. Factors influencing summer movement patterns of Bonneville cutthroat trout(*Oncorhynchus clarkia utah*). Canadian Journal of Fisheries and Aquatic Sciences 63:660-669.

Schulz R., and M. Liess. 1999. A field study of the effects of agriculturally derived insecticide input on stream macroinvertebrate dynamics. Aquatic Toxicology 46:155-76

Skalski, G. T., and J. F. Gilliam. 2000. Modeling diffusive spread in a heterogeneous population: A movement study with stream fish- ecology. Ecology 81:1685-1700.

Schmetterling, D. A. 2001. Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot River drainage, Montana. North American Journal of Fisheries Management 21:507-520.

Swanberg, T. R., and D. R. Geist. 1997. Effects of intraperitoneal transmitters on the social interaction of rainbow trout. North American Journal of Fisheries Management 17:178-181.

Thurow, R. F., D. C. Lee, and B. Rieman. 1997. Distribution and status of seven native salmonids in the interior Columbia River Basin and portions of the Klamath River and Great Basins. North American Journal of Fisheries Management 17:1094-1110.

Tonina, D., and J. M. Buffington. 2009. A three dimensional model for analyzing the effects of salmon redds on hyporheic exchange and egg pocket habitat. Canadian Journal of Fisheries and Aquatic Science 66:2157-2173.

Truckee River Recovery and Implementation Team. 2003. Short term action plan for Lahontan cutthroat trout *(Oncorhynchus clarki henshawi)* in the Truckee River Basin. Report for U.S Fish and Wildlife Service, Reno, Nevada.

Utter, F. M. 2003. Population genetics, conservation and evolution in salmonids and other widely cultured fishes: some perspectives over six decades. Reviews in Fish Biology and Fisheries 14:125-144.

Van Kirk, R. W., and L. Benjamin. 2001. Status conservation of salmonids in relation to hydrologic integrity in the Greater Yellowstone Ecosystem. Western North American Naturalist 61:359-374.

White, G. C. 2008. MARK: mark and recapture survival rate estimation. Version 5.1.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Winter, J. D. 1983. Underwater biotelemetry. Pages 371-395 *in* Nielsen, L. A., and D. L. Johnson editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Young, M. K. 1995. Resident trout and movement: consequences of a new paradigm. U.S. Department of Agriculture Forest Service Fish Habitat Relationship Technical Bulletin number 18:1-5.

Young, M. K. 1996. Summer movements and habitat use by Colorado River cutthroat trout in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences 53:1403-1408.