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Abstract approved:

Guillermo R. Giannico

I used contiguous whole stream surveys and Digital Elevation Models to examine how landscape topography and in-stream habitat affected the distribution, growth, and survival of Lahontan Cutthroat Trout *(Oncorhynchus clarki henshawi)* (LCT) in a High Desert Watershed. The work was carried out in a sub-basin of the Quinn River system, McDermitt Creek, which drains the sagebrush desert of southeastern Oregon and northern Nevada. My results showed that topography affected LCT distribution in all reaches. LCT numbers were highest in areas with greater numbers of nick-points (the transition zones between less confined and more confined valley segments) and greater valley confinement. Additionally, in the downstream portion of our headwater reaches, more LCT were found in nick-points than expected based on the availability of this habitat type. My data suggest that hyporheic inputs may be high in such areas, thus providing LCT with shelter from warm water in the summer, anchor ice in the winter and shallow stream depths during all seasons. I found greater trout growth, but lower survival, in relatively warmer and more open reaches than in cooler reaches. Additionally, undercut banks (predation shelter) were more important to trout in cooler stream reaches than in warmer ones, where habitat choice responded first to cold water input (which was influenced by topography). My results will be useful in identifying and describing areas of high quality LCT habitat in low order streams throughout the Great Basin, thus allowing informed management decisions to facilitate the recovery of the species.

The Effect of Landscape Topography and In-Stream Habitat on the Distribution, Growth, and Survival of Lahontan Cutthroat Trout *(Oncorhynchus clarki henshawi)* in a High Desert Watershed

By
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APPROVED:

Major Professor, representing Fisheries Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

George D. Boxall, Author

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CONTRIBUTION OF AUTHORS

Dr. Guillermo Giannico, and Dr. Hiram Li were involved in the editing of Chapter 2 and Chapter 3.

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CHAPTER 1: INTRODUCTION

Measuring habitat quality is vital not just to guide restoration and monitoring efforts but also to gain a better understanding of how an organism functions in its environment. Traditionally, density is often used as an indicator of habitat quality, with higher quality habitats in theory supporting higher densities of individuals. Densities however may not always accurately reflect habitat quality, particularly for endangered or threatened species, which often occur in anthropogenically altered or fragmented habitats.

At least two assumptions must be met for density to be a true correlate to habitat quality. First, individuals must have unrestricted access to habitats; and, second, individuals must be able to correctly detect differences in habitat quality. Under the Ideal Despotic Distribution model (Fretwell and Lucas 1970), an expansion of the Ideal Free Distribution theory (IFD; see Kacelnik et al. 1992 for a review), dominant individuals prevent subdominant ones free access to habitats. Thus, density may not correlate with habitat quality because the highest quality habitats may be occupied by a single dominant individual, while lower quality habitats are occupied by many subdominant individuals. Animal density-habitat quality correlations may also break down under the conditions described in the perceptual limit model (Abrahams 1986), which also has its origins in IFD theory. In the perceptual limit model, individuals are restricted in their ability to perceive differences in habitat quality due to sensory constraints. In this scenario, density may not accurately indicate habitat quality because individuals cannot accurately determine resource availability; therefore, high quality habitats may remain unoccupied or *under*-occupied while lower quality habitats are occupied or even *over*-occupied.

Habitat fragmentation can also prevent an individual from reaching a high quality habitat, or isolate individuals in low quality habitats. A study by Virgós (2001) found that patch isolation explained badger (*Meles meles L.*) distribution in areas with fragmented habitat, while in less fragmented habitats distribution was best explained by habitat characteristics. Individuals occupying fragmented habitats may not select the best habitat but rather the best of the available habitats. As a result, individuals may be found in high densities in habitats which function as population sinks (where death rates exceed birth rates) or in habitats where individuals have low or even negative growth rates, at the same time as isolated high quality habitats remain unoccupied.

In anthropogenically altered habitats, ecological traps (Gates and Gysel, 1978) may cause individuals to also select poor quality habitats. An organism identifies a high quality habitat by detecting a set of environmental cues which historically have been linked to high quality habitats. Ecological traps occur when an organism chooses a low quality habitat because it has some characteristics that are similar to those of a historically high quality habitat. These traps can be created when anthropogenic alterations leave environmental cues that historically were associated with an intact habitat, yet simultaneously reduce habitat quality at a faster rate than species can adapt evolutionarily (Schlaepfer et al. 2002). Thus, individuals are "trapped" by their genetic response to environmental cues into selecting a poor quality habitat even when higher quality habitats are available to them or the poor quality is relatively rare (Donovan and Thompson 2001).

Using organism density to quantify habitat quality has limitations. One alternative is to use metrics which are related to an organism's fitness such as mortality, fecundity and growth to quantify habitat quality. Metrics such as mortality, fecundity, and growth may be better indicators of habitat quality because they directly relate to an organism's fitness in that habitat. Patches in which animals have higher fecundity, growth, or survival rates are arguably higher quality habitats than patches with lower rates. However, this analysis does not take into consideration differences in organism densities between the habitats, and density can affect fecundity, growth, and mortality. Perhaps the best method to measure habitat quality would be to incorporate both approaches and use habitat-specific organism growth, fecundity, mortality, and standing crop (biomass or number of individuals) to calculate production. Clearly patches with high production are higher quality habitat than patches with low or no production.

Lahontan Cutthroat Trout (LCT) offered an ideal organism to test the use of production as a way to measure habitat quality. First, LCT populations are generally small which made the unique marking of entire populations feasible thus allowing us to accurately determine survival, growth, and movement patterns for most of the population. Second, LCT populations often occur in small isolated headwater streams, which limit the amount of habitat LCT can occupy. The relatively small size of available habitat facilitated the frequent and relatively easy relocation of individuals, providing detailed information on movement patterns. Third, LCT often occupy streams with small, shallow pools which allow for both high capture and recapture rates. This enabled us to collect survival and growth data for most individuals in the population. Thus, the use of LCT as our model organism let us calculate habitat specific production by combining contiguous whole stream surveys, tagging methods that allowed for fish tracking with minimal disturbance, and end-of-season recaptures that provided growth and survival related data.

This study had two main objectives: First, to determine if coarse scale patterns in landscape topography affect the distribution of LCT; second to use LCT movement, survival and growth to determine habitat quality. The results of this study not only contribute to improving our understanding of LCT habitat requirements, but also provide key information towards the identification of stream reaches that may still offer adequate conditions for the re-establishment of viable populations of this sub-species. The technique we employed to determine habitat quality is applicable not just to other populations of LCT but to other terrestrial and aquatic species as well.

CHAPTER 2:

Landscape topography and the distribution of Lahontan cutthroat trout *(Oncorhynchus clarki henshawi)* in two high desert streams

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Abstract

Lahontan cutthroat trout (LCT) *(Oncorhynchus clarki henshawi)* are currently limited in their distribution to a patchwork of small isolated populations, the result of habitat degradation and natural variation in landscape and in-stream conditions. The objectives of this study were to determine how landscape level topographic features influence LCT distribution patterns. The work was carried out in a sub-basin of the Quinn River system, McDermitt Creek, which drains the sagebrush desert of southeastern Oregon and northern Nevada. Headwater tributaries of this creek consist of alternating canyon-confined and valley bounded reaches and LCT within these systems are challenged by low discharge and high temperatures during the summer, and anchor ice during the winter. Contiguous whole stream surveys were used to look at trout distribution during the summer of 2003 and spring and fall of 2004. Our results showed that topography affected LCT distribution in all reaches. LCT numbers were highest in areas with greater numbers of nick-points (the transition zones between less confined and more confined valley segments) and greater valley confinement. Additionally, in the downstream portion of our headwater reaches, more LCT were found in nick-points than expected based on the availability of this habitat type. Our data suggest that hyporheic inputs may be high in such areas, thus providing LCT with shelter from warm water in the summer, anchor ice in the winter and shallow stream depths during all seasons. Spatial occurrence of these areas of refugia can be taken into consideration when planning land-use activities and restoration efforts.

Introduction

Lahontan cutthroat trout (*Oncorhynchus clarki henshawi)* have been listed as threatened for over thirty years (Office of Federal Register 40:29864). Their distribution is currently reduced to a patchwork of small isolated populations, most likely as a result of various land-use related habitat alterations and interactions with non-native salmonids (Coffin and Cowan 1995). Additionally, the high desert streams that LCT and other salmonids occupy can be a harsh environment with large fluctuations in water temperature, high water temperatures, and desiccated reaches (Dunham et al. 1999, Ebersole et al. 2001, Zoellick 1999). Temperature patterns can regulate patterns in LCT distribution, and both field (Dunham et al. 1999, Jones et al. 1998) and laboratory (Dickerson and Vinyard 1999) studies suggest that LCT distribution may be limited, at least in part, by elevated summer temperatures. Desiccated reaches can also limit movement of trout; movement is potentially important for the growth and survival of salmonids. Thus, cold water patches and areas of greater discharge may be important resources for LCT.

Streams are comprised of both surface flows and subsurface flows. The hyporheic zone has been defined as the region of mixing between surface and ground water (Orghidan 1959), but can also be thought of as the area of saturated subsurface sediments containing stream water (Kasahara and Wondzell 2003). Hyporheic exchange, or the movement of water between surface flows and hyporheic flows, occur both vertically through the streambed in the form of upwelling and downwelling (Harvey and Bencala, 1993), and horizontally by entering and exiting surface flows through the stream banks (Gibert et al. 1995). Areas of hyporheic input (where hyporheic flows join surface flows) offer thermal refugia for fish because they are generally cooler in summer, warmer in winter and more thermally stable than surface flows (Malard et al. 2001, Williams 1984).

Although there is limited evidence that groundwater inputs provide thermal refugia for LCT, (but see Dunham et al. 1999) there are many studies showing that thermal refugia are used by and benefit other salmonids at a variety of life history stages. For example, many species choose areas of upwelling for spawning, including sockeye salmon (*Oncorhynchus nerka*) (Lorenz and Eiler 1989), brook trout (*Salvelinus fontinalis*) (Webster and Eriksdottir 1976, Curry and Noakes 1995) and bull trout (*Salvelinus confluentus*) (Baxter and Hauer 2000). Sowden and Power (1985) found that embryo survival increased linearly with increased groundwater seepage, as long the dissolved oxygen levels were greater than 5.3mg/L in the groundwater. Juvenile salmonids also prefer habitats with groundwater inputs. Latta (1965) found a significant, positive relationship between groundwater levels and young-of-the-year (YOY) rainbow trout (*Oncorhynchus mykiss*) numbers for an entire basin. Groundwater inputs also increased the winter survival of YOY rainbow trout in the Snake River, Idaho (Smith and Griffith 1994). And in the Grande Ronde River, Oregon, a strong relationship was found between the density of cold water patches (formed from hyporheic input) and the density of both juvenile chinook salmon (*Oncorhynchus tshawytscha*) and rainbow trout. (Ebersole et al. 2003).

Groundwater inputs also explain adult fish distribution patterns across a range of scales from multiple sub-basins to single pools, and provide thermal refugia during both winter and summer. At the multiple-basin scale, Zorn et al. (2002) found that the amount of groundwater inputs (measured by low flow yield) appeared to strongly dictate fish community structure for small streams. At the single basin scale, in a study of the John Day River, thermal refugia created by groundwater inputs explained adult chinook salmon distribution within stream reaches (Torgersen et al. 1999). At the reach scale, groundwater inputs have been reported to explain trout distribution patterns during winter. Harper and Farag (2004) and Brown and Mackay (1995) found that cutthroat trout selected off-channel pool habitat with groundwater inputs even though that kind of habitat was rare in the study sections. The authors of both studies hypothesized that such groundwater-influenced pool habitats offered refugia from anchor and frazzle ice. Brook and brown trout also preferred pools with groundwater inputs as winter habitats (Cunjak and Power 1986). Groundwater inputs may affect patterns of salmonid pool use even within habitat units. Nielsen and Lisle (1994) found that juvenile, YOY and adult steelhead all used the cooler, lower portion of thermally stratified pools. These stratified pools were often created by groundwater inputs and averaged as much as 3.5° C cooler than the surrounding stream water. While these and other studies show that groundwater inputs can be useful in explaining salmonid distribution patterns, detecting groundwater inputs using traditional methods can be costly.

While no studies to date have examined relationships between topographic features and LCT presence, bedrock topography can regulate patterns in stream depth and hyporheic input, and thus patches of thermal refugia and deep water. Habitat units within a stream reach alternate between erosional units such as pools and depositional units such as riffles. At a larger scale, reaches within streams often alternate between erosional zones such as topographically confined canyon segments and aggraded or depositional zones such as less confined valley segments (Lisle 1982). While "valley" and "canyon" segments or alternatively valley confinement describes the surface topography, these exposed characteristics are the visible extension of sub-surface bedrock topography. Surface topography has been linked to patterns in hyporheic exchange (Kasahara and Wondzell 2003). These reach-specific differences in the depth to bedrock and channel confinement can affect patterns in vertical and horizontal hyporheic exchange and thus stream discharge and temperature (Hinton et al. 1993, Stanford and Ward 1993).

In confined canyon segments, the depth to bedrock (distance from stream bed or stream bank to bedrock) is generally small, and canyon walls narrow both the wetted width and flood plain (Montgomery et al. 1996). As a result of this lack of permeable substrate, the volume of the hyporheic zone is reduced in these sections (Wondzell, 2006), and surface flows are generally greater than in less confined valley segments. Inversely, in less topographically confined valley segments, the depth to bedrock is generally much greater, and valley confinement less constrictive of flood plain and steam width. The volume of the hyporheic zone in these sections is increased, and surface flows are usually smaller than in more confined valley segments. Thus confined segments generally have a more limited hyporheic zone than unconfined segments (Kasahara and Wondzell 2003).

These changes in the hyporheic zone associated with changes in topography can influence the location and magnitude of hyporheic exchange. Multiple studies have found areas of upwelling and downwelling in the transition zone between confined canyon segments and less confined valley segments (Fernald et al. 2001, Baxter and Hauer 2000). As stream flow leaves confined canyon segments and enters more open valley segments, valley confinement decreases and depth to bedrock increases. These changes in bedrock topography and valley confinement allow some of the surface flows to enter the hyporheic zone vertically through the substrate and horizontally through the stream bank and into the flood plain. In contrast, as stream flow transitions from less confined valley segments to more confined canyon segments, hyporheic input into surface waters increases (Baxter and Hauer 2000, Hinton et al. 1993). The narrowing of the canyon walls and the reduction in the size of the hyporheic zone (Wondzell, 2006) forces hyporheic flow from the flood plain to enter surface flows horizontally through the stream bank. At the same time, the decreasing depth to bedrock causes hyporheic flow to also enter the stream vertically through the substrate. Thus where the stream channel enters a more confined valley segments, hyporheic input with cooler and more stable water temperatures may provide fish with thermal refugia during summer.

Bedrock topography can also affect stream discharge and thus affect the location of desiccated reaches and low water. As discussed earlier, canyon-confined stream segments are largely erosion zones with small amounts of alluvial deposits, while open valley segments are largely deposition zones with large amounts of alluvial deposits. Sediment supply can in turn affect the volume of the hyporheic zone (Edwards 1998). In confined canyon segments, bedrock topography, small amounts of alluvial deposits and channel confinement by canyon walls can limit the hyporheic zone. In contrast, in less topographically confined valley segments, greater alluvial deposits, greater depth to bedrock and accessible floodplain allow for a larger hyporheic zone. As a result, in confined canyon segments, hyporheic flow may only comprise a small proportion of total flow (surface and hyporheic) while in less confined valley segments hyporheic flow may comprise a relatively greater proportion of total flow. This can result in greater stream depths in bedrock canyon segments versus alluvial valley segments. Hinton et al. (1993) found that stream segments flowing through bedrock canyons had greater mean depths than segments flowing through alluvial valleys. This difference in water depths between reach types can affect how quickly a reach becomes desiccated during summer and thus stream connectivity. Pools in areas with thicker alluvial deposits have been shown to lose connectivity and desiccate sooner than pools in areas with thin alluvial deposits over bedrock (May and Lee 2004).

Topographic information promises to be useful in explaining trout distribution patterns in arid zone basins because it can help identify channel sections likely to receive hyporheic inputs (Baxter and Hauer 2000) and segments with greater depth and connectivity. These areas could be important for LCT by enabling them to cope with summer high temperatures and low flows as well as winter low temperatures and anchor ice. Hyporheic input may be even more important in the small streams which LCT occupy throughout their range because small streams generally have a proportionally greater hyporheic zone than larger streams (Thomas et al. 2001). Understanding how these landscape features affect LCT distribution and habitat selection patterns may be critical to the successful recovery of this sub-species. Unfortunately, basic information on LCT habitat requirements is very limited (Nelson et al. 1992), and nothing is known about the possible influence of landscape level geomorphic features on LCT. If strong relationships between topographic features and LCT distribution patterns can be identified, then managers can recognize key habitat patches in systems throughout the region using readily available topographic data sets. This will make it possible to quantify a stream's potential for recovery/reintroduction/translocations and, thus, prioritize restoration efforts accordingly.

This study had two objectives: first, to identify patterns between surface topography and LCT distribution; second, to determine if water temperature affects LCT use of stream segments adjacent to topographic features associated with hyporheic input.

Methods

Study Site

The Trout Creek Mountains are located in southeastern Oregon and northern Nevada. They range in elevation from 1200 to 2600 meters, and are comprised of basalt and ash flow tuffs (Orr et al. 1992). Throughout the range, a series of small low order streams flow through narrow basalt canyons and lacustrine and fluvial deposit dominated valleys. Our study was conducted in two headwater tributaries, Sage and Line Creeks, of McDermitt Creek, a sub-basin of the Quinn River. The McDermitt Creek sub-basin straddles the border between Oregon (Malheur and Harney Counties) and Nevada (Humboldt County) as it drains the eastern slopes of the Trout Creek Mountains (Figure 1). These two first- and second-order high desert streams are spring fed, and both flow through a variety of geology types, including canyons and hills of basalt, welded tuffs, and tuffaceous sedimentary rocks, and valleys dominated by lacustrine and fluvial deposits. Temperatures range from -34° C to over 40° C with a winter mean of – 2° C and a summer mean of 18.8° C. The majority of the limited precipitation in the area (mean annual of 22.6 cm) accumulates during winter and spring, and desiccated pools occur in the downstream reaches during summer low flows (Climate Data from WRCC). Discharge is highly variable both within a year and between years. Annual mean discharge between 1948 and 2004 in McDermitt Creek was 0.92 m^3/s, and ranged between 2.65 m^3/s and 0.09 m^3/s with a standard deviation of 0.62 m^3/s (USGS Gauging Station). Monthly mean discharge values between 1948 and 2004 were generally low from July through January with medians ranging from 0.07 m^3/s in September to 0.27 m^3/s in January and were greatest during March, April, and May with medians of 1.84 m^3/s, 1.89 m^3/s, and 1.68 m^3/s respectively. Riparian vegetation consists mainly of alders *(Alnus spp.)* in the upstream reaches, with willows *(Salix spp.)* becoming increasingly common in lower portions and roses *(Rosa woodsii)* predominately in downstream canyon areas. Beyond the riparian corridor, the vegetation is dominated by a sage brush *(Artemisia spp.)* complex which includes bitterbrush (*Purshia tridentate)* and gray rabbitbrush (*Chrysothamnus nauseosus)* among other species. Physical barriers to fish movement are common in both streams, and include plunges, debris jams, and push-up dams. The main land-use activity in the area is cattle grazing, with the entire land surrounding both streams owned or leased by a single family ranch. Approximately 10% of the catchment area for both Sage and Line Creeks is privately owned, and the remaining is government property controlled by the Bureau of Land Managament (BLM). The current grazing regime is planned for minimal impact with most allotments receiving two or more years of rest between periods of light use. While Sage Creek shows limited signs of land-use impacts, Line Creek has reaches with marked incisement (up to 3 meters), headcutting and sedimentation. McDermitt Creek is the only stream open to fishing in the system, and we only observed anglers on one occasion during the two years of our study.

Topographic Data Sets

Geographical information system (GIS) software was used to create topographic and stream data sets. The stream layer was digitized using 1 to 24,000 digital ortho quad maps (doq) (United State Geological Survey; USGS) and air photos rectified to control points on the doq map using ERDAS Imagine. Each stream was then divided into 10 m longitudinal segments using ARC GIS software. For the topographic data set, 10 m Digital Elevation Models (USGS, DEMs) were used to create a map of percent hillslope with Spatial Analyst (ARC GIS 9). Percent hillslope was calculated as the change in surface elevation over distance, expressed as a percentage. For example, a rise in elevation of 27 m over a distance of 30 m describes a 90% hillslope. To measure the hillslope surrounding the stream, a latitudinal buffer was created around each 10 m stream segment (hereafter referred to as 10 m buffer segments), extending 10 m into the riparian zone on both sides of the stream. Within each 20 m wide by 10 m long buffer polygon the mean percentage hillslope was calculated using Spatial Analyst (ARC GIS 9). These data describing the mean hill slope around each 10 m stream segment were used to examine patterns in valley confinement.

Five metrics relating to stream and valley topography were analyzed using data sets generated from our DEM and valley confinement maps (see Appendix 1). Average stream gradient was calculated as the change in elevation (using 10 m DEMs) divided by the length of the stream segment (500 m). Our valley confinement map was used to calculate the variation in valley confinement, median valley confinement, number of nick-points and length of bounded valley segments (BVS). For the analysis of our four topographic metrics, data from our 10 m long buffer segments were pooled into 500 m long stream segments. We examined the variation in valley confinement because we hypothesized that reaches with greater variance in confinement may have greater hyporheic exchange. Variation in valley confinement was calculated as the variance in mean hill slopes of all 10 m segments within a 500 m reach. Median valley confinement was included in our analysis because stream segments flowing through more confined reaches may have greater depth than segments flowing through less confined reaches. Median valley confinement was calculated as simply the median hill slope among all 10 m segments within a reach.

Because both nick-points and bounded valley segments (after Baxter et al. 2000) have been associated with areas of hyporheic exchange (Figure 2), we also looked at patterns between LCT distribution and both the number nick-points and the length of bounded valley segments per 500 m reach. Nick-points are the transition zone between less topographically confined valley segments and more confined canyon segments. Upstream nick-points occur when stream discharge travels from more to less topographically confined areas, while downstream nick-points occur when stream discharge travels from less to more topographically confined areas (Figure 2). In our study, we identified nick-points based on changes in the mean hill slope between adjacent 10 m buffer segments (Figure 3). A downstream nick-point occurs when the mean hill slope of a 10 m buffer segment is at least 10% greater than the 10 m buffer segment immediately upstream of it. An upstream nick-point occurs when the mean hill slope of a 10 m buffer segment is at least 10% greater than the segment immediately downstream of it. In Figure 3, segment B would be considered an upstream nick-point because the mean hill slope of the 10 m buffer segment B is at least 10% greater than the adjacent downstream segment C (19%-7%=12%). Segment G would be considered a downstream nick-point because the mean hill slope of the 10 m buffer segment G is at least 10% greater than the adjacent upstream segment F (21%-6%=15%). Bounded valley segments (BVS) where defined as the stream segments upstream of a downstream nick-point and downstream of an upstream nick-point, and their length was calculated as BVS length = (10 m * the number of stream segments between an upstream and downstream nick point + 10 m for the downstream nick point). For example, in Figure

3, segments C through G are all BVS with a length of 50 m (40 m for segments C, D, E, and F plus 10 m for the nick point segment G).

Fish Distribution

Fish distribution was based on two, single pass, contiguous, whole-stream electro-fishing surveys. The first survey was carried out in June of 2004 and the second in November of 2004. Only fish larger than 100 mm in fork length were used in our fish distribution map because triple-pass depletion showed high efficiency of fish this size or greater (between 92% and 100% being captured on the first pass; mean = 98%). Fish position was recorded with a Garmin V GPS unit and 89% of projected UTM coordinate locations for fish were within 10 m of the stream channel. These UTM coordinates were used to construct our GIS fish distribution map, and each fish was given its own "point" location in the map. Pools with multiple fish would have multiple points at the same location. The number of fish per 10 m stream segment was determined by tallying the number of fish "point" locations closest to each 10 m segment using ARC GIS.

Temperature

Thermo-loggers (I-buttons, Dallas Semiconductor) were used throughout the basin to record stream temperatures. Throughout Line and Sage Creeks, one thermo-logger was placed at approximately every stream kilometer. At each major tributary confluence, thermo-loggers were placed in the receiving channel both upstream and downstream of the confluence as well as in the tributary itself. Universal Transverse Mercator (UTM) coordinates were taken for all thermo-logger locations, and all thermo-loggers were calibrated both before placement and after removal. Thermo-loggers were programmed to take hourly temperature readings from June 25 through November 30 of 2004. Water temperatures were also recorded in each fish-occupied habitat unit with hand-held thermometers.

Hyporheic Input

We employed two techniques to determine if hyporheic exchange was occurring within nick-point stream segments. First, we used hand-held thermometers to detect patches of thermal refugia, and thus indirectly detected the vertical and horizontal hyporheic input associated with such areas. During our fish surveys, we occasionally identified areas of possible hyporheic exchange, either through observation of a change in substrate color or through observation of discharge emerging from the substrate or stream bank. In order to determine if hyporheic-influenced thermal refugia occurred in these areas, we used a handheld thermometer to record the temperature both inside the patch and in the surface flow 1 m upstream of the patch. Patches of thermal refugia were defined as patches where water temperature inside the patch differed by more than 2 º C from upstream surface flows. UTM coordinates (Garmin V GPS) were recorded for all such locations of hyporheic influenced thermal refugia.

Second, to directly detect hyporheic exchange, piezometers were used to measure vertical hydraulic gradient. Vertical hydraulic gradient (VHG) is positive where upwelling occurs and negative where downwelling occurs and is calculated as:

$$\mathrm{VHG} = \Delta h/\Delta l$$

Where Δh is the difference between the height of the stream and the height of the water inside the piezometer and Δl is the distance from the top of the substrate to the top of the piezometer screen (see Baxter 2003 for a description of piezometer installation and VHG). In our study, hyporheic upwelling was considered to be occurring in a location if the vertical hydraulic gradient was greater than 0.02. In July of 2005, we installed five piezometers in each of six stream reaches, adjacent to topographic nick-points. The first piezometer was placed in the midpoint of the nick-points segment, and the remaining four piezometers were placed upstream of the first at approximately 10 m intervals. All piezometers were driven into the substrate to a depth of 40 cm. The UTM coordinates (Garmin V GPS) were recorded for all piezometers where hyporheic upwelling was detected. We projected our UTM coordinates for both our patches of thermal refugia and areas of hyporheic input onto our valley confinement map to determine if areas of hyporheic input were occurring within nick-point segments.

The methodology we used to detect hyporheic exchange was not designed to be exhaustive surveys of the sub-basin, but rather to determine if hyporheic input was occurring within at least some nick-point segments and to therefore infer its potential occurrence at other locations.

Valley Confinement and Stream Depth

In this study we also looked at possible relationships between stream depth and valley confinement. We focused on pool and riffle depths, because both can be influenced by valley confinement and the depth to bedrock. In July of 2004, during summer base flows, we recorded the pool depth for every habitat unit and maximum riffle depth for every third riffle. Riffle depth was the average of three "maximum" depths, spaced equidistantly along the length of the riffle. Pool maximum depth was the greatest depth found in the pool. Both pool max depth and riffle depth were measured with the aid of a 2 m stadia rod.

Statistical Analysis

For Sage Creek water temperature data, linear regression was used to examine relationships between stream kilometer and stream temperature (°C) mean value and variance between June and October.

We used linear regression to determine significant relationships between our five topographic metrics and our response variable: the number of fish per 0.5 km stream segment. While longitudinal fish density may be correlated to pool volume or pool surface area, which may in turn co-vary with one of the topographic metrics we analyzed, only linear fish density was used because we wanted to determine if easily collected landscape and topographic features correlated to fish distribution patterns. We also limited this analysis (between fish counts and our five topographic metrics) to those segments of Line and Sage Creeks potentially occupied by LCT. Downstream distribution was limited by temperature (Dunham et al. 1999) while upstream distribution was likely limited by physical barriers. Stream segments analyzed were bounded downstream by a maximum stream temperature of 23º C and the upstream boundary was the first significant barrier (height greater than 0.5 m) above the upper limit of fish distribution. In both Sage and Line Creeks, the contiguous length of the "LCT inhabitable" portion of the stream did not exceed the contiguous length of the occupied portion of the stream by more than 2 km.

To look at the possible relationship between valley confinement and stream depth, we used simple bivariate linear regression. We compared our independent variable, of median valley confinement, to one of two response variables: either the proportion of riffles that were deep or the proportion of pools that were deep within a reach. For this analysis, we divided the inhabitable portion of Sage Creek into 22 reaches, each of which was 250 m in length. Mean valley confinement was the mean percent hillslope of all 10 m buffer segments within the 250 m reach. The proportion of deep pools within a reach was calculated as the number of "deep" pools within a 250 m reach divided by the total number of pools within the reach. Because stream depth can co-vary with stream kilometer, we defined deep pools in one of two ways. We used linear regression to determine if there was a significant relationship between stream kilometer and maximum pool depth. If no significant relationship between stream kilometer and pool max depth was detected, then deep pools were defined as pools with maximum depths that exceeded the mean max depths for all pools across all reaches. In contrast, if a significant relationship between stream kilometer and maximum pool depth was detected, we used an alternate technique, which corrected for the effect of stream kilometer on pool depth. First, we fit a trend line to our stream kilometer versus pool max depth regression data and solved for this line algebraically. We then used this equation to calculate the residuals for our pool max depth data, and pools with positive residuals were considered deep pools. The proportion of deep riffles in a reach was calculated similarly.

We also looked at how the preferential use of BVS and nick-points by trout changed across a longitudinal stream temperature gradient. Because we were looking at habitat preference, we restricted our analysis to stream segments with LCT densities greater than five fish per 500 m. The preferential use of BVS within each 500 m reach was calculated as the expected proportion subtracted from the observed proportion of LCT in BVS. This value was then regressed against stream kilometer for Sage Creek using linear regression. Stream kilometer was used as a proxy for temperature because we did not have temperature data for every reach, and stream kilometer co-varied with both mean stream temperature and daily variation in stream temperature (Figure 4). The expected proportion of fish in BVS within a 500 m reach was equal to:

$$n_{total} * (segments_{BVS} / segments_{total})$$

where "n_{total}" is the total number of trout in a reach, "$segments_{BVS}$" is the number of 10 m bounded valley segments within a 500 m reach, and "$segments_{total}$" equals 50 (the total number of 10 m segments in a 500 m reach). Observed proportion of fish in BVS within a 500 m reach was equal to:

$$n_{BVS} / n_{total}$$

where "n_{BVS}" and "n_{total}" are the number of trout in $segments_{BVS}$ and $segments_{total}$ respectively.

We also examined how patterns in preferential use of nick-point segments changed along the longitudinal temperature profile of Sage Creek (represented as stream kilometer). Once again, the preferential use of nick-points within each 500 m reach was measured as the expected proportion subtracted from the observed proportion of LCT in nick-points. The expected proportions were equal to:

n_{total}* ($segments_{np}$ / $segments_{total}$)

where "$segments_{np}$" is the number of 10 m stream segments within each 500 m stream reach that were downstream nick-points. "$Segments_{total}$" equals 50 (the total number of 10 m segments in a 500 m stream reach). The observed proportions of trout were equal to:

n_{np} / n_{total}

where "n_{np}" and "n_{total}" are the numbers of trout in $segments_{np}$ and $segments_{total}$ respectively. For statistical analysis we used linear regression with the observed minus expected proportion of fish in either BVS or nick-points as the response variable and stream kilometer as the independent variable.

Results

Topographic Data Sets

No data transformation was needed because all our geomorphic variables were normally distributed (Appendix 1). For all linear regression results, *P* values are for Pearson's correlations. In Sage Creek, of the five geomorphic variables we examined only two were significantly correlated with LCT numbers (Table 1): median valley confinement and the number of nick-points per reach ($P<0.01$ for both; Figures 5 and 6). There was no significant relationship between LCT density and the length of BVS, variance in valley confinement, or stream gradient. In contrast, no geomorphic variables examined were significantly correlated with LCT counts in Line Creek (Table 1).

Temperature

In Sage creek both mean temperature ($P<0.001$, $R^2 = 0.95$) and variance in temperature ($P<0.001$, $R^2 = 0.89$) decreased as stream kilometer increased. From June through October, 2004, mean temperature ranged from 14.7° to 10.1° C and its variance ranged from 9.5° to 2.4° C among our five sample sites spread throughout the occupied portion of Sage Creek (Figure 4). Maximum temperature recorded in any occupied portion of Sage or Line Creek was 23° C.

Hyporheic Input

Within nick-point segments of Sage Creek, we detected both hyporheic input and their associated patches of thermal refugia. A total of seven patches of thermal refugia were found within nick-point segments. Horizontal hyporheic input (through the stream bank), appeared to be the source for most (six of seven) of the patches. The difference in temperature between patches and surrounding surface flows was as great as 5° C with a mean temperature difference of 3° C. We also detected hyporheic upwelling at two of the six nick-point reaches we examined. Even within these two reaches hyporheic upwelling was patchy and only two out of the five piezometers installed in each reach had positive vertical hydraulic gradients. Mean vertical hydraulic gradient among the four piezometers where upwelling was detected was 0.024.

Valley Confinement and Stream Depth

We found a positive relationship between pool depth and stream kilometer (R^2 = 0.16, *P* <0.01, slope= 0.022 ± 0.0037, n=213, linear regression). Thus to minimize the effect of stream kilometer on pool depth we defined deep pools as pools with positive residuals using the best fit regression line ($y = 0.0216x + 0.0115$, where y = pool depth in meters and x = stream kilometer). There was no significant relationship between riffle depth and stream kilometer (*P* = 0.81, n=84, Linear regression) hence deep riffles were defined as those riffles with mean depths greater than the mean for all riffles across all reaches.

During our analysis of the relationship between the proportion of deep pools versus the mean valley confinement within a reach, we identified one of our 22 reaches as a potential outlier with a studentized residual of 4.7. This outlier was the first topographically confined stream segment below a major tributary confluence on Sage Creek. Thus pool depths in this area were probably affected by the larger sediment sizes and steeper gradients associated with areas below tributary junctions (Benda et al. 2004). The tributary of Sage Creek also had greater incisement than the main stem. As a result the tributary may have contributed larger sediment loads in portions of Sage Creek below the confluence, which in turn affected pool depths. After removal of the outlier, we found a significant and positive relationship between the proportion of deep pools within a reach and mean valley confinement ($R^2 = 0.63$, $P < 0.001$, n=21, linear regression) (Figure 7). Inclusion of the outlier still revealed a significant, positive relationship between the proportion of deep pools within a reach and mean valley confinement, but did reduce the R^2 from 0.63 to 0.41 ($P < 0.01$, n=22, linear regression). We found no significant relationship between the proportion of all riffles in a reach that were deep riffles and the mean valley confinement ($P = 0.78$, n=22, Linear regression).

Habitat Preference and Stream Temperature

For our analysis of fish habitat preference, we used stream kilometer as a proxy for stream temperature, because stream kilometer co-varied with temperature ($R^2 = 0.92$) and stream temperature data were contiguous while our temperature data were not. Preferential use of nick-point segments, measured as the observed minus expected percentage of LCT found in nick-points, decreased with increasing stream kilometer and this trend was statistically significant (R^2 = 0.92, *P* <0.001, n=9, linear regression)(Figure 8). Nick-point preference varied from 45% more than expected for the stream segment ending at kilometer 12 to 0.5% less than expected for the stream segment ending at kilometer 16 (Figure 8). There was only a weakly significant, negative relationship between BVS preference and stream kilometer (R^2 = 0.45, *P* <0.07, n=9, linear regression) (Figure 9). The preferential use of BVS by all LCT within a reach ranged from 26% more than expected at stream kilometer 13.5 to 15% less than expected at stream kilometer 14.5 (Figure 9). Thus in the occupied headwaters of Sage Creek, LCT showed a high preference for nick-point segments in downstream portions where stream temperatures were warmer but had no preference for nick-point segments in upstream portions where temperatures were cooler.

Discussion

In our study, topographic features explained much of the LCT distribution in Sage Creek. In particular, nick-points and median valley confinement were positively related to LCT abundance. One possible reason for the positive relationship between median valley confinement and LCT abundances may have been the greater mean depths and more persistent surface flows associated with stream segments flowing through confined canyons. In catchments of similar size, streams flowing through bedrock canyons had greater mean depths than streams flowing through alluvial valleys (Hinton et al.1993). Additionally, May (2004) found that pools in areas with thicker alluvial deposits lost connectivity sooner (during summer) than pools in areas with thin alluvial deposits over bedrock (confined canyons generally have thinner alluvial deposits than valley segments). These areas of deeper and more persistent water may be particularly important to salmonids like LCT, which reside in high desert streams where patches of cool perennial water may be limited. First, deeper and more persistent water may allow greater connectivity, and connectivity can affect fish growth rate. A study by Kahler et al. (2001) found that fish which remained in a single habitat unit had lower growth rates than fish which utilized multiple habitat units. Second, desiccation or low water levels may result in increased mortality of LCT. Desiccated pools are obviously lethal to LCT, and fish trapped in isolated, shallow pools may suffer from increased predation. Thus the potential differences in survival rates among the reaches, or selection by LCT of reaches with greater connectivity and stream depth, may have resulted in higher numbers of fish in reaches with greater median valley confinement

The positive correlations between median valley confinement and the number of LCT may also be the result of differences in the depth of habitat units among the reaches. While we found no significant relationship between the mean valley confinement and the proportion of deep riffles in a reach, we did find that the proportion of deep pools increased with mean valley confinement. Pools can be critical habitat for other cutthroat species (Young and Guenther-Gloss 2004, Harig and Fausch 2002, Young 1996) and deep pools in particular may provide ideal habitat for salmonids (McIntosh et al. 1994; Bisson et al. 1997). Thus the positive relationship between LCT numbers and median valley confinement may be the result of the greater proportion of deep pools in stream segments with greater mean valley confinement.

At first it may seem puzzling that confined canyons which generally have limited sediment deposits over underlying bedrock, had the highest proportion of deep pools, because bedrock can limit pool scour and thus pool depth in such areas (Reeves et al. 1995). Although pools in confined canyons segments may have less scour depth than pools in open valley segments where sediments are thicker, differences in surface flow depths between confined and less confined segments also affect pool depths. Confined canyon segments often have a limited hyporheic zone with only a small portion of the total flow occurring in the hyporheic zone. In contrast, less confined valley segments generally have a larger hyporheic zone with a greater portion of total flow moving through alluvial deposits. Because of the increased channel confinement and limited loss of surface flows to the hyporheic zone, confined stream segments can have greater water depths than less confined segments. Thus, while pool scour may be less in canyon versus valley stream segments, actual pool depth may be greater in canyon segments due to greater stream depths in such areas (Figure 10).

There are at least two potential reasons for the positive relationship we observed between the number of nick-points and the number of LCT per reach. First nick-point counts may have been correlated with LCT numbers because nick-points are topographically confined stream segments, similar to areas with high median valley confinement discussed earlier. Thus nick-points, like areas with high median valley confinement may have had greater stream depths or deeper pools. As a result, stream segments with higher numbers of nick-points may have had greater numbers of LCT because these segments had a greater number of deep pools, deepwater patches or persistent water patches.

Second, the greater number of LCT found in stream segments with greater numbers of nick-points could also be due to the hyporheic input associated with nick-points. As the topography surrounding the stream transitions from a broad meadow-like area into a narrow canyon (the nick-points in our study), some of the hyporheic flow is diverted into the stream channel. In our own study, we detected both hyporheic input and their associated cold water patches within stream segments adjacent to nick-points. Although we only found evidence for hyporheic upwelling in two of the six nick-point segments we examined, we did find numerous cold water patches formed by horizontal hyporheic input and this form of input would not have been detected by our piezometers. Numerous other studies have also linked geomorphic features similar to nick-points with hyporheic input (Baxter and Hauer 2000; Stanford and Ward 1993).

Preferential use of nick-points by LCT decreased with stream kilometer (km from mouth) in the occupied headwaters of Sage Creek. This trend was likely related to the reported relationship between stream temperature, elevation and stream kilometer. As stream distance (km) from its mouth increases, so does its altitude and, consequently, mean temperature and temperature variance decrease. In addition to the altitudinal effect, water temperatures in the upper reaches of the LCT-occupied portion of Sage Creek were lowered by abundant springs, which were uncommon in the lower reaches. Thus, in downstream reaches, groundwater inputs associated with nick-points may provide valuable refugia from daily variation in water temperature, high temperatures and reduced water discharge. Such refugia are likely to be less beneficial to trout in the spring-dominated upper reaches. Ebersole et al. (2003) found a similar pattern in multiple tributaries of the Snake River where the proportion of fish in cold water patches increased with stream temperatures. Other studies have reported other species of salmonids using groundwater inputs as refugia from high summer temperatures (Baxter and Hauer 2000; Torgersen et al. 1999; Dunham et al.1999; Nielsen and Lisle 1994; Bilby 1984; Kaya et al. 1977; Gibson 1966; Latta 1965) or ice (Harper and Farag 2004; Brown and Mackay 1995) and cold water during winter (Harper and Farag 2004; Brown and Mackay 1995; Cunjak and Power 1986; Craig and Poulin 1975).

Although we did not look at correlations between temperature and our topographic variables because of our small sample size in temperature data (n=5) and differences in grain size between the data sets (1 km versus 0.5 km respectively), our topographic variables may have co-varied to a limited extent with temperature. Despite this, our two headwater reaches with relatively low LCT densities had correspondingly low numbers of both BVS and nick-points, as well as low values in median valley confinement. We also found a greater number of LCT in nick-point segments than were expected to occupy nick-point segments based on their availability in eight out of our nine reaches. This evidence suggests that positive correlations between LCT density and BVS density, nick-point density, and variance in valley confinement was based on more than just co-occurrence between geomorphic traits and low stream temperature or high elevation.

Although Sage and Line Creeks have been managed under a light grazing regime (three year rotation with no warm season grazing) for at least the last 15 years, historically this was probably not the case (pers. com. Evan Zimmerman). Unconfined valley segments may have seen extensive cattle use due to their close proximity to shade and water, stable flat footing, and abundance of forage. In contrast, confined valley segments may have been avoided by cattle, both presently and historically because of their steep slopes, unstable footing, and minimal forage. Additionally, the current land manager only utilizes these confined valley segments for moving cattle from one pasture to another and hence these segments experience little cattle use at present. Hence correlations between LCT density and geomorphic variables could simply be due to a lack of grazing impacts in these confined valley segments. However, during this study, we did detect the preferential use of nick-points in the majority of reaches. This preferential use of nick-points suggests that the positive relationship between the number of LCT and the number of nick-points was based on more than solely the lack of cattle-related impacts.

Although there were significant correlations between LCT density and two topographic variables for Sage Creek, there were no significant correlations between LCT density and topographic variables for Line Creek. This may be due to small sample size on Line Creek where only 32 adult LCT were captured; whereas, over 200 adult LCT were captured in Sage Creek. It is also possible that the greater bank incisement and stream-bed sedimentation observed in Line Creek account for these differences. Sedimentation has been linked to a reduction in intra-gravel flow and, in turn, hyporheic input associated with nick-points (Schalchli 1992; Bjerklie and LaPerriere 1985). This may explain the lack of correlation between topography and LCT numbers in Line Creek. While nick-points may offer some refugia from thermal stresses and shallow stream depths thus mitigating land use impacts, high sediment levels such as those found in portions of Line Creek may negate these benefits.

Patterns in temperature and geology may have also affected downstream distribution limits. In both Sage Creek and Line Creek, 99% of the LCT were found above an elevation of 1640 m. There are several possible explanations for this. First, below that altitude, stream temperatures may have exceeded LCT preference levels. For example, in both Line and Sage Creeks, summer water temperatures often exceeded 21 °C in stream reaches below 1640 m of elevation. A similar relationship between reach altitude, water temperature and LCT distribution was reported by Dunham et al. (1999), who found that elevation was useful in predicting the downstream distribution limits of this species throughout its range. Second, the topography surrounding each stream changed from confined-canyon segments above 1640 m to open-meadow segments below. Finally, the geology changes from the more consolidated basalt and tuffaceous sedimentary rocks in portions above 1640 m to unconsolidated sediments including lacustrine and fluvial deposits in most of the lower portions of both streams (Walker and MacLeod 1991). Geology and topography can alter stream characteristics such as discharge, and both Sage and Line Creeks experienced reduced surface flows and seasonally desiccated reaches after entering the open valley segments below 1640 m of elevation. It is likely that none of these factors is acting independently but rather in combination to influence water levels and stream temperatures in a manner that precludes LCT summer presence below 1640 m elevation.

Although others have considered scale to be extremely important when examining patterns of cold water refugia use (Ebersole et al. 2003, Torgersen et al. 1999), we found evidence for use of geomorphic features associated with groundwater across a range of scales. In Sage Creek, geomorphology appeared to affect LCT density at multiple scales. At the coarsest grain, LCT abundance was greatest in canyon-confined stream reaches, and increased as median valley confinement augmented. Within reaches with high valley confinement, LCT preferred nick-points, at least in downstream portions of their distribution. One possible reason for these multiple-scale distribution patterns is the relatively high level of association among our geomorphic variables. For example, because nick-points are defined as 5% or 10% changes in mean hill slope, stream segments with high densities of nick-points will also have both high variance in valley confinement and median valley confinement since each of these variables are also based on hill slopes. Despite this possible covariance, when all five variables were analyzed at the same scale only two were significantly related to LCT numbers.

There are important management implications for our study results. We found higher numbers of LCT in more confined valley segments and greater numbers of nick-points. Confined valley segments and nick-points were linked to deeper pool habitat, and areas of thermal refugia, in our own study, and other studies have linked these areas to deeper, more persistent water and thermal refugia. These areas may be particularly important in other high desert streams in eastern Oregon and the Great Basin, which, like McDermitt Creek, often have highly variable stream discharge both among and within years. Patches of deeper, more persistent water and thermal refugia associated with nick-points and confined valley segments may allow LCT to persist during periods of seasonal low-water and low water years. Populations of LCT occupying streams with greater amounts of these confined valley segments and nick-points may be more resistant to the detrimental effects of low-water years and summer-fall low flows. Thus, identification of these areas within a stream may provide information useful for prioritizing streams or stream sections for protection, restoration, reintroduction or translocation efforts.

Previous work has examined links between topography and fish distribution, specifically the relationship between salmonid distribution and areas of cool water maintained by topographic shading. Our study is somewhat unique, however, in that it uses topographic features to identify areas of potential hyporheic input, or increased surface flow, and thus explains patterns in LCT distribution. Geomorphic variables related to hyporheic flow had strong effects on LCT distribution patterns. Managers can potentially use these geomorphic variables to efficiently determine coarse scale LCT distribution patterns and to infer stream quality. Streams with large areas of confined canyon segments, and their associated greater stream depths, and persistent flows or nick-points and their associated thermal refugia may have more stable populations of LCT or greater lengths of stream occupied by LCT. Thus, streams or stream segments with confined canyons or nick-points could be given a higher priority for restoration, translocation and reintroduction efforts. Our findings may become a valuable tool that will allow managers to concentrate monitoring and restoration efforts on streams or stream segments likely to contain important LCT habitat in the form of greater stream depths, more persistent flows or thermal refugia, and thus more efficiently and effectively utilize available resources. Management should protect areas with confined canyons and nick-points from land-use impacts to preserve these important refugia. Exclusion of cattle from such areas could be done with little or no hardship to ranchers since these confined valley segments are largely unsuitable for grazing.

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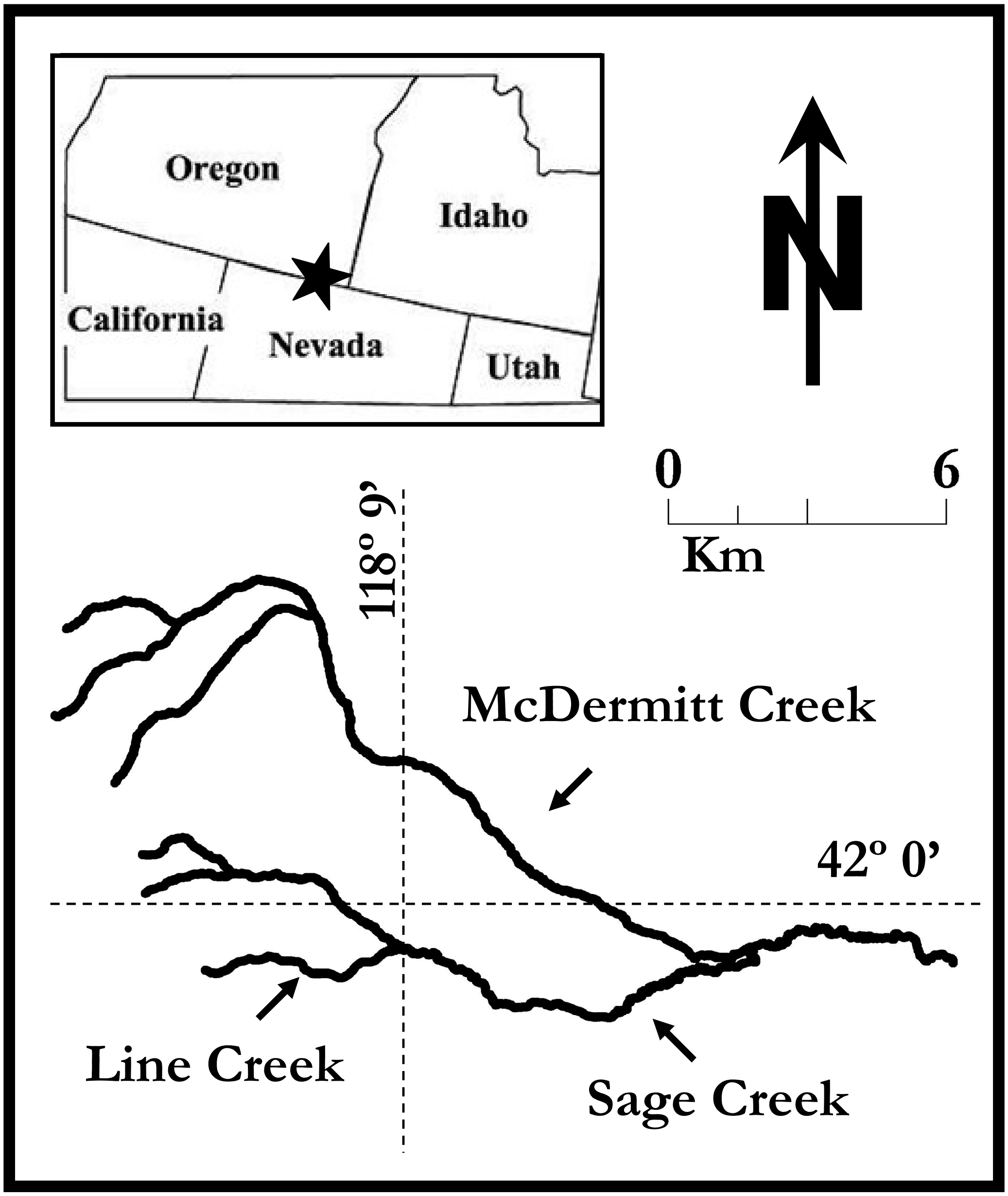

FIGURE 1. Map of the McDermitt Creek Sub-Basin, Malheur County, Oregon and Humboldt County, Nevada.

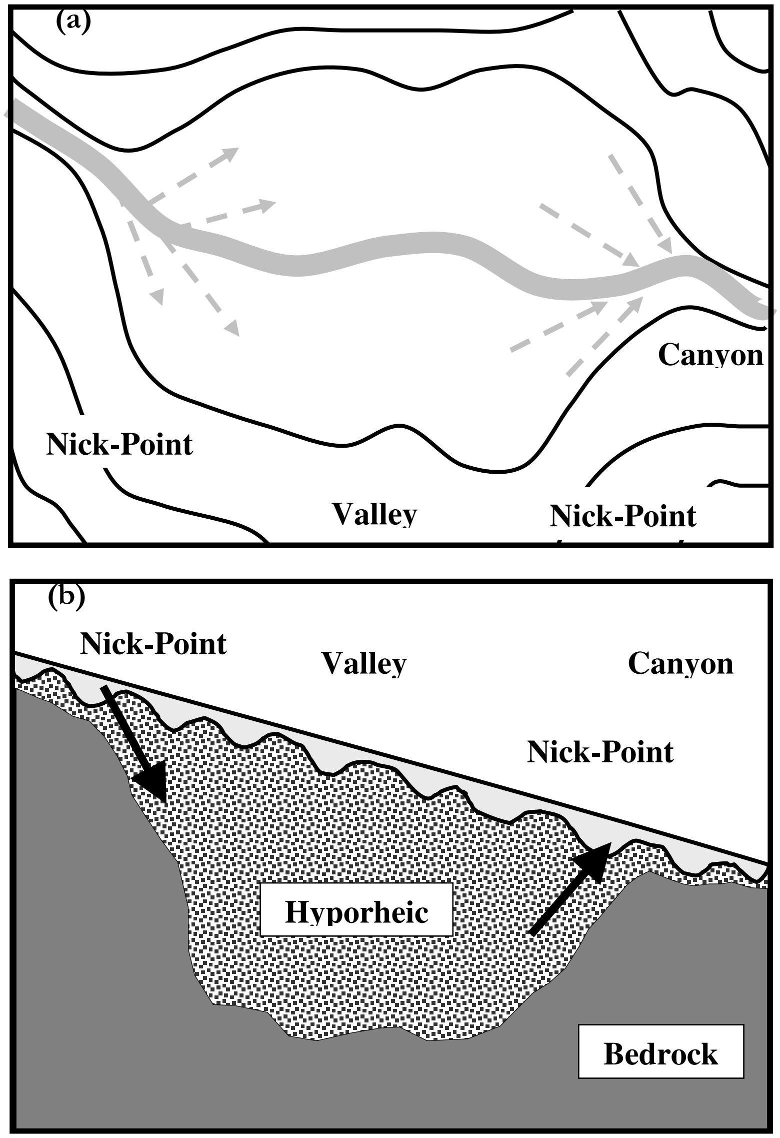

FIGURE 2. Hyporheic exchange patterns for upstream and downstream nick-points. In (a) black lines are topographic contour lines, the solid grey line is surface flow and grey dashed arrows are horizontal hyporheic exchange. Figure (b) is a cross-section of the same stream segment. Arrows are flow paths of vertical hyporheic exchange. Dark grey is bedrock, stippled grey represents alluvial deposits, and light grey is surface flows.

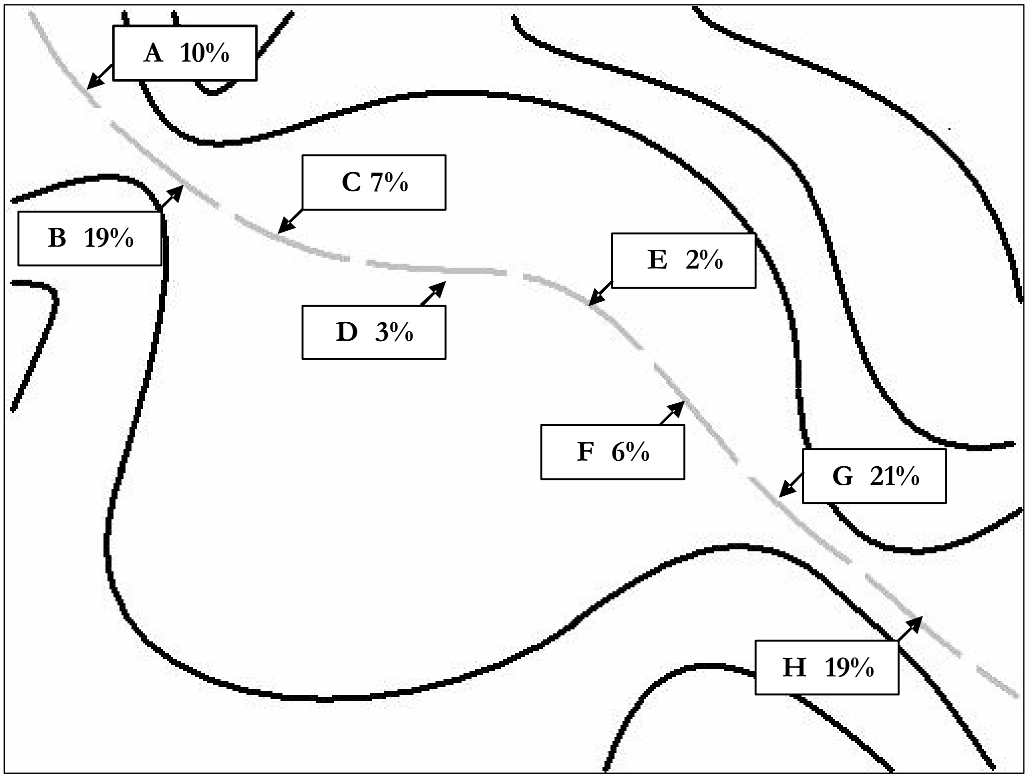

FIGURE 3. Diagram of bounded valley segments (BVS), 10% upstream nick-points and 10% downstream nick points. Black lines are lines of elevation contours, and grey segments A through H are 10 m contiguous stream segments. Segment B would be considered an upstream nick-point because the change in mean hill slope of its 10 m buffer area (not pictured) between stream segments B and C is greater than or equal to 10% (19%-7%=12%). Segment G would be considered a downstream nick-point because the change in mean hill slope of its 10 m buffer area (not pictured) between stream segments F and G is greater than or equal to 10% (6%-21%=15%). Segments C through G are a 10% BVS with a length of 50 m (BVS length = 10 * the number of stream segments between an upstream and downstream nick-point + 10m for the downstream nick-point). Calculations are the same for 5% nick-points and BVS.

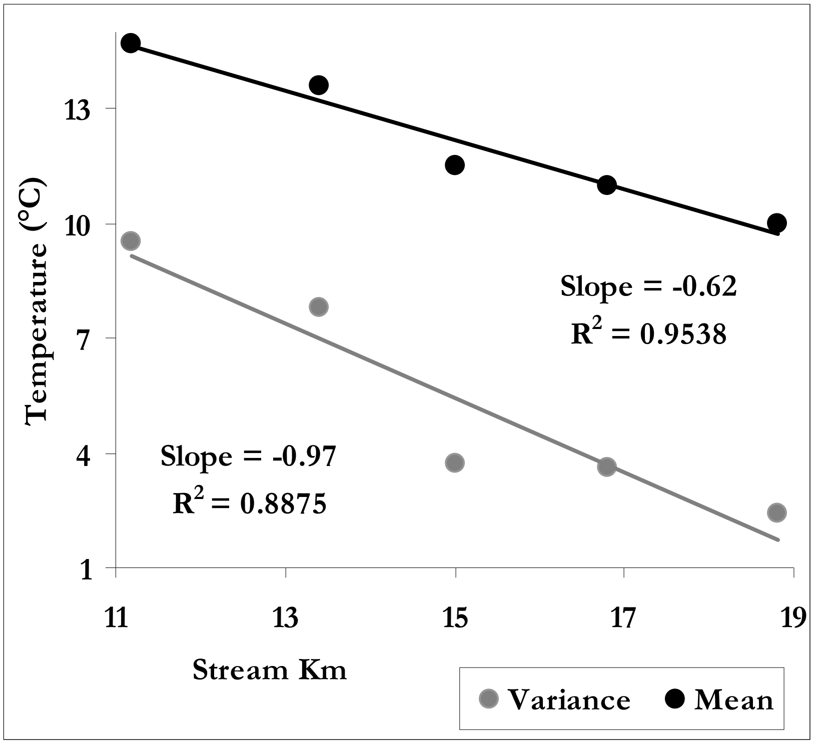

FIGURE 4. Stream kilometer (km from mouth) versus mean stream temperature (ºC) and variance in temperature (ºC) during June through October 2004 for Sage Creek.

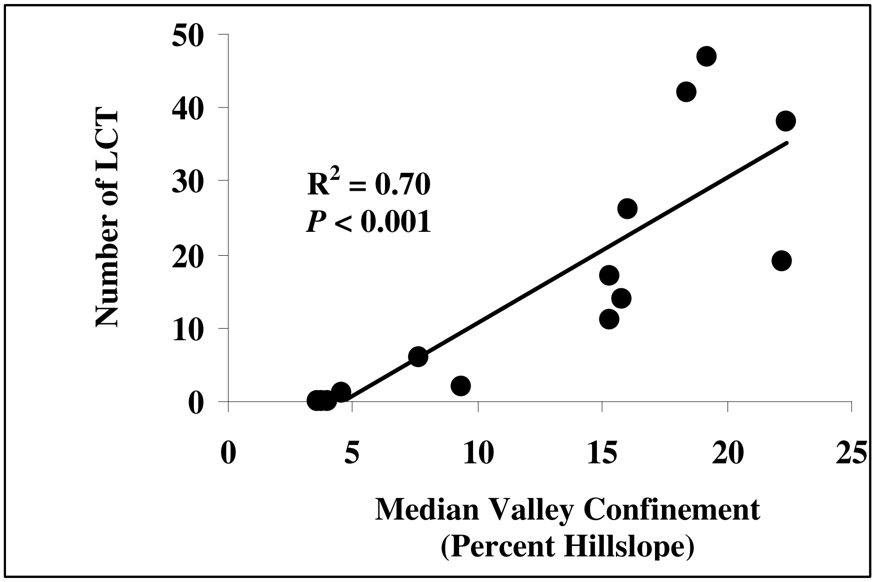

FIGURE 5. Median valley confinement (measured as percent hillslope) versus the number of LCT per 500 m stream segment for Sage Creek.

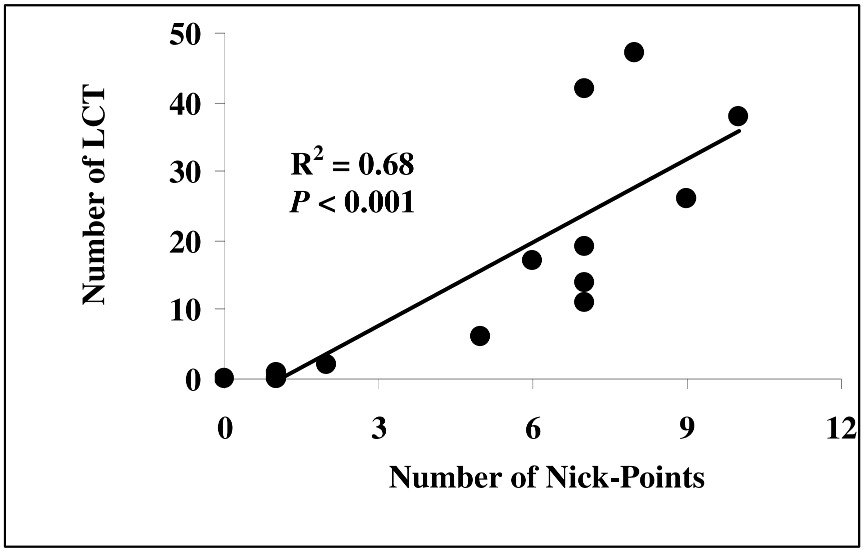

FIGURE 6. Number of nick-points versus the number of LCT per 500 m stream segment for Sage Creek.

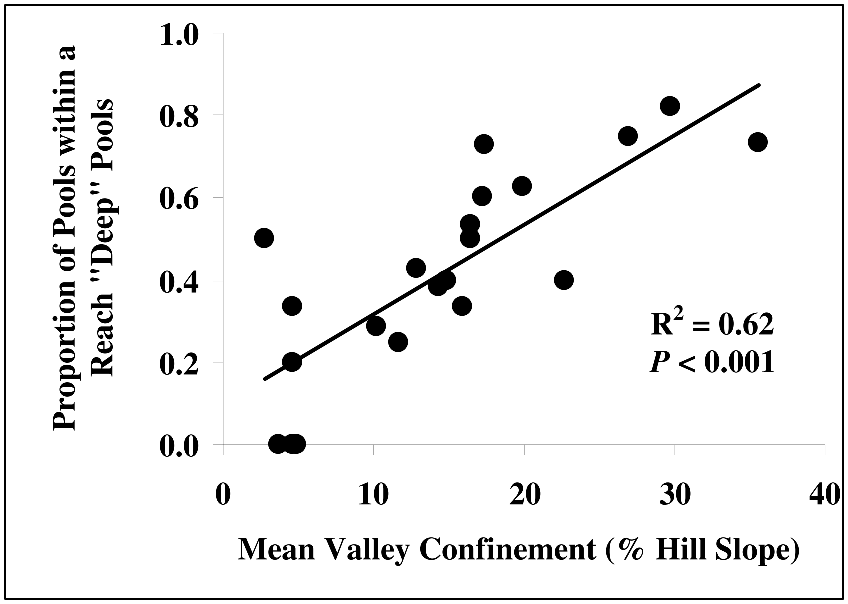

FIGURE 7. Mean valley confinement (measured as percent hillslope) versus the proportion of all pools within a reach that were "deep" pools for Sage Creek.

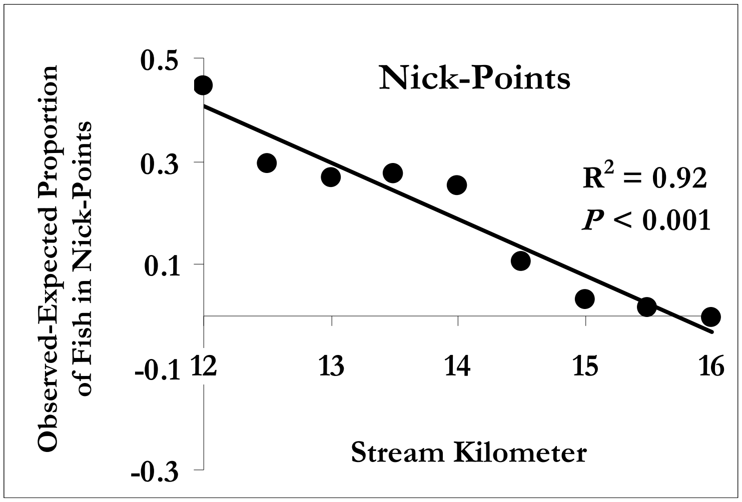

FIGURE 8. Changes in habitat preference patterns along a longitudinal stream gradient for nick-points for Sage Creek. The x-axis is kilometers from mouth.

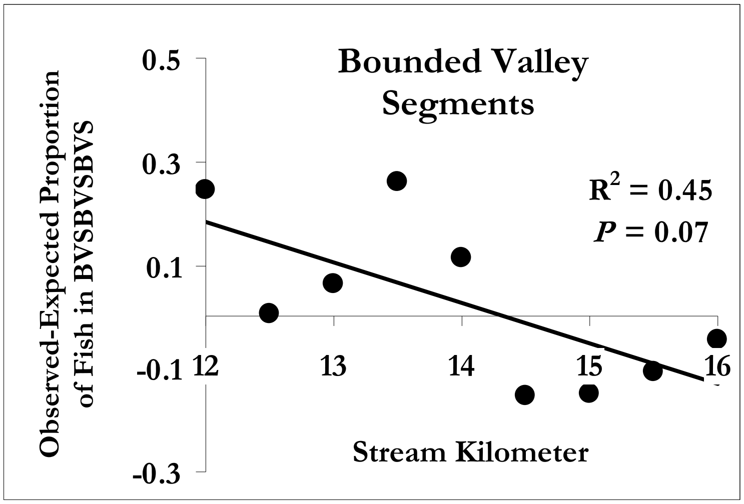

FIGURE 9. Changes in habitat preference patterns along a longitudinal stream gradient for bounded valley segments for Sage Creek. The x-axis is kilometers from mouth.

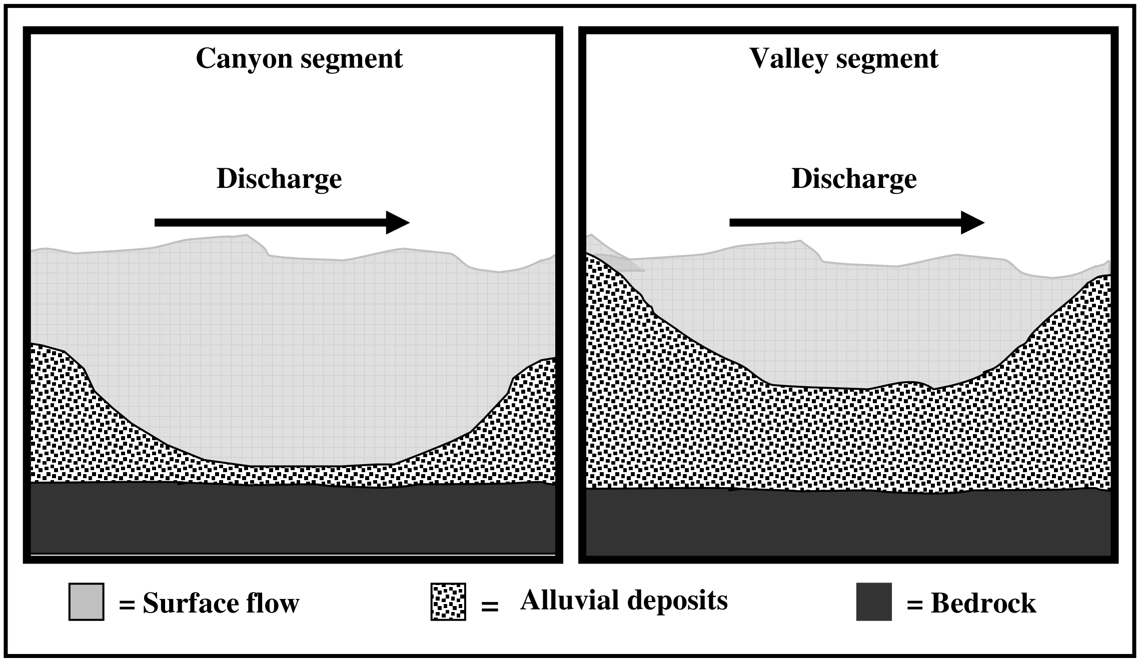

FIGURE 10. The effect of the differences in depth to bedrock or hyporheic zone depth between topographically confined canyon segments versus less confined valley segments on pool depths.

TABLE 1. Results of bivariate linear regression between topographic variables and the number of fish per 500 m stream segments. Analysis was limited to segments accessible to fish based on temperature and upstream barrier distribution.

Variables	Number of fish			
	Sage Creek		Line Creek	
	R^2	*P* value	R^2	*P* value
Stream Gradient	0.25	ns	0.17	ns
Median valley confinement	0.70	$P < 0.01$	0.32	ns
Variance of valley confinement	0.37	ns	0.11	ns
Length of BVS	0.27	ns	0.07	ns
Number of nick-points	0.68	$P < 0.01$	0.28	ns

P values are for correlation coefficients. Alpha was 0.05

Appendix 1: Geomorphic characteristics of Sage and Line Creeks, McDermitt Basin NV and OR

	Sage Creek 0.5 km reaches		
Variables	Mean	Range	Transformation
Average gradient (% slope)	1.8	6.8	*none*
Variation in valley confinement (% hillslope)	146.9	140.2	*none*
Median valley confiment (% hillslope)	13.9	17.7	*none*
Total length of BVS (m)	197.5	370.0	*none*
Number of nickpoints	11.9	21.0	*none*

CHAPTER 3:

Using Lahontan Cutthroat Trout (*Oncorhynchus clarki henshawi)* Movement, Survival and Growth As Indicators of Habitat Quality In A High Desert Watershed

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Key Words: movement, survival, growth, Lahontan, cutthroat, trout, habitat selection, habitat quality.

Abstract

After almost 30 years of conservation effort, Lahontan cutthroat trout (LCT) *(Oncorhynchus clarki henshawi)* populations remain in peril throughout the Great Basin region of southeastern Oregon and northern Nevada. This is not surprising since very little research has been done on the ecology of LCT, and management has been carried out without essential information on this sub-species. The objectives of our study were to determine whether there are inter-stream or inter-reach differences in LCT habitat selection, and if those differences corresponded to differences in fish survival and growth. We relied upon contiguous whole stream surveys to look at fish distribution and in-stream habitat. The use of half duplex PIT tags allowed us to determine the growth, movement patterns, and survival rates of most adult (>100 mm) LCT within the system. We found greater trout growth (median daily change in biomass 0.46% vs. 0.07%), but lower survival (35% vs. 61% between July and November), in relatively warmer and more open reaches than in cooler reaches. Additionally, undercut banks (predation shelter) were more important to trout in cooler stream reaches than in warmer ones, where habitat choice responded first to cold water input (which was influenced by topography). Our results will be useful in identifying and describing areas of high quality LCT habitat in low order streams throughout the Great Basin, thus allowing informed management decisions to facilitate the recovery of the sub-species.

Introduction

Lahontan cutthroat trout (*Oncorhynchus clarki henshawi)* (LCT) have been listed as a threatened sub-species for over thirty years (Office of Federal Register 40:29864). Their distribution is currently reduced to a patchwork of small isolated populations, the likely result of the interaction among land type, habitat degradation, stream temperatures (Nelson et al. 1992) and the presence of non-native salmonids (Coffin and Cowan 1995). Fluvial populations in particular have been reduced to less than 11% of their historic distribution (Coffin and Cowan 1995, Gerstung 1986), and there is little information on their basic habitat requirements (Nelson et al. 1992). Although understanding their patterns of habitat selection and how habitat affects survival and growth may be critical to the recovery of this sub-species, obtaining the necessary information has proven challenging.

It is impossible to separate LCT habitat selection from stream temperature patterns. Like other trout living in high desert environments, LCT are subjected to high temperatures during summer as well as large diel and seasonal thermal fluctuations (Dunham et al. 1999, Ebersole et al. 2000, Zoellick 1999). High temperatures may become barriers to fish movement and thus reduce the quantity and quality of available habitat. Earlier studies have shown that the distribution of salmonids is limited by temperature both in neighboring catchments (Jones et al. 1998) and in other high desert systems (Torgersen et al. 1999, Dunham et al. 1999). High temperatures can also have sub-lethal effects on fish by reducing habitat quality while increasing metabolic rates

(Brett 1979, Brett and Groves 1979). Therefore, during summer trout may select habitats with the lowest water temperature they can find because this allows them to reduce their metabolic costs. Large diel thermal fluctuations also make habitats less desirable to fish because the acclimation to ever changing conditions is metabolically costly (Cunjak 1988). In the case of LCT, Meeuwig et al. (2004) demonstrated that growth is negatively impacted by both relatively warm temperatures (above 12° C) and greater diel temperature variation.

Although numerous studies have looked at both habitat selection and the influence of habitat on survival and growth of trout, they have failed to identify clear patterns. Other researchers have used data from censuses of unmarked individuals to correlate fish numbers or biomass densities to habitat variables. However, these methods have serious limitations. First, a census is a snapshot in time and the behavior of individuals is not taken into consideration. Therefore, census data cannot distinguish between habitats that have equal densities but different turnover rates (frequency at which newcomers replace residents); where habitats with low turnover rates are those with such conditions that retain the same individuals—most often dominant ones—over time (see Belanger et al. 2002; Winker et al. 1995; and Van Horne 1983 for a full discussion). Second, density tells us nothing about survival and growth of individuals within a habitat. Clearly, habitats with similar densities but very different growth or survival rates are not of equal quality. Only by tracking and recapturing marked fish can one distinguish between the two habitats. We were able to do this by using passive integrated transponder (PIT) tags and mobile antennas that allowed reliable fish tracking with a minimum of disturbance until the end of the study period when recapture was necessary.

Our objectives were: first, to detect inter- and intra-reach differences in LCT habitat selection patterns; and, second, to determine whether LCT movement, survival and growth can be used as indicators of habitat quality. We distinguished between habitats of different quality by combining contiguous whole stream surveys, tagging methods that allowed for fish tracking with minimal disturbance, and end-of-season recaptures that provided growth related data. The results of this study not only contribute to improving our understanding of LCT habitat requirements, but provide key information towards the identification of stream reaches that may still offer adequate conditions for the re-establishment of viable populations of this sub-species.

Methods

Study Site

Our study was conducted in Sage and Line Creeks, two first- and second-order headwater tributaries of McDermitt Creek, which is part of the Quinn River Basin. McDermitt Creek straddles the border between Oregon (Malheur and Harney Counties) and Nevada (Humboldt County) as it drains the eastern slopes of the Trout Creek Mountains (Figure 1). These mountains range in elevation from 1200 to 2600 meters (Orr et al. 1992). Sage and Line Creeks are spring fed, and both flow through a variety of geology types, including canyons and hills of basalt, welded tuffs, and tuffaceous sedimentary rocks, as well as valleys dominated by lacustrine and fluvial deposits. Air temperatures in this area range from -34° C to over 40° C, with a winter mean of – 2° C and a summer mean of 18.8° C. The majority of the limited precipitation (mean annual of 22.6 cm) accumulates during winter and spring, and desiccated pools occur in the downstream reaches during summer low flows (Climate Data from WRCC). Discharge is highly variable both within and between years. Annual mean discharge between 1948 and 2004 in McDermitt Creek was 0.92 m^3/s, and ranged between 2.65 m^3/s and 0.09 m^3/s with a standard deviation of 0.62 m^3/s (USGS Gauging Station). Monthly mean discharge values between 1948 and 2004 were generally low from July through January with medians ranging from 0.07 m^3/s in September to 0.27 m^3/s in January and were greatest during March, April, and May with medians of 1.84 m^3/s, 1.89 m^3/s, and 1.68 m^3/s respectively.

Riparian vegetation consists mainly of alders *(Alnus spp.)* in the upstream reaches, with willows *(Salix spp.)* becoming increasingly common in lower portions and roses *(Rosa woodsii)* predominately in downstream canyon areas. Beyond the riparian corridor, the vegetation is dominated by a sage brush *(Artemisia spp.)* complex, which includes bitterbrush (*Purshia tridentate)* and gray rabbitbrush (*Chrysothamnus nauseosus)* among other species.

Physical barriers to fish movement are common in both streams, and include plunges, debris jams, and push-up dams. The main land-use activity in the area is cattle grazing. The entire catchment area for both Sage and Line Creeks is managed by a single ranch, which owns approximately 10% of those lands and leases the rest from the

Bureau of Land Management (BLM). The current grazing regime is planned for minimal impact with most allotments receiving two or more years of rest between periods of light use. While Sage Creek shows limited signs of land-use impacts, Line Creek has reaches with marked incision (up to 3 meters), head-cutting and sedimentation. McDermitt Creek is the only stream open to fishing in the system, and we only observed anglers on one occasion during the two years of our study.

Geomorphology and Land Use

Geographical information systems (GIS) were used to construct topographic and stream data sets. The stream layer was digitized using 1 to 24,000 digital ortho quad (DOQs) maps (United State Geological Survey; USGS) and air photos rectified to DOQ control points (ERDAS Imagine). Each stream was then divided into 10 m longitudinal segments using ARC GIS 9 software. For the topographic data set, 10 m Digital Elevation Models (USGS, DEMs) were used to create a percent hill slope map using Spatial Analyst (ARC GIS 9). A 10 m latitudinal buffer was created for each 10 m stream segment and the mean percent hill slope within each buffer polygon was calculated using Spatial Analyst (ARC GIS 9). This map was used to examine patterns in valley confinement and to identify downstream nick-points. Nick-points are constrictions in valley width caused by changes in the zone's topography. Downstream nick-points are those marking stream channel transition from relatively unconfined valleys to narrow canyon segments. Conversely, upstream nick-points correspond to stream segments that transition from narrow canyons into relatively wide and open valleys. In our study, we characterized nick-points as changes of 10% or more between the mean hill slopes of any pair of consecutive 10 m stream segments (Figure 2).

Three contiguous reaches were delineated in the upper half of Sage Creek based on topography, vegetation, and discharge. The reaches ranged from 1.7km to 0.7km in length and will hereafter be referred to as upper, middle and lower Sage reach. The upper Sage reach was in a moderately confined valley and had relatively low discharge with a dense alder-dominated riparian zone (median pool canopy cover 95%). Middle Sage reach followed immediately downstream, and had higher discharge (due to a major tributary) and greater valley confinement than the upper reach. It also had a dense alder-dominated riparian community (median pool canopy cover 95%). Finally, lower Sage reach was in a highly confined valley with a less dense mixed-canopy of willow, alder and rose (median pool canopy cover 75%). Its discharge was relatively lower than the two previous reaches.

Temperature

Thermo-loggers (I-buttons, Dallas Semiconductor) were deployed throughout our study sub-basins. One thermo-logger was placed approximately every stream kilometer. At each major tributary, thermo-loggers were placed in the main stem both upstream and downstream of the confluence and in the tributary itself. Universal Tranverse Mercator (UTM) coordinates were taken for all thermo-logger locations, and all thermo-loggers were calibrated both before placement and after removal. Thermo-loggers were programmed to take hourly readings from approximately June 25th through

November 30th of 2004. Temperatures were also taken using hand thermometers for each fish location.

LCT Habitat Selection

Other fish habitat selection studies have relied on radio tags to track fish. However, due to the cost and size of those tags, normally only a few relatively large-size individuals are used. The small body size of fish in most high desert streams would restrict radio tagging to only the largest members of the population, who will not accurately describe the habitat selection patterns of the entire population. Passive integrated transponder (PIT) tags are a solution to this problem. There are two main types of PIT tags, Duplex and Half-duplex tags. The former are available in the smallest size, 11 mm, but have a relatively limited detection range (up to 30 cm). In contrast, Half-duplex PIT tags are about twice as large (23 mm), but can be detected by either stationary or portable antennas from distances of up to 70 cm. This allows fish detection and individual identification with no need for recapture and minimal disturbance.

To locate LCT and monitor their movement we carried out five contiguous, whole stream surveys. Two of them used single-pass electro-fishing, and the other three used portable antennas to detect PIT tags. The first electro-fishing survey was conducted between June and July of 2004, and the second in November of 2004. Because pools were small and fish numbers low, we managed to "herd" fish into our dip-nets by using a low voltage setting. Hence, we did not have any electro-fishing-related mortalities. All captured fish were measured to the nearest 1 mm to determine their standard length, and they were weighed to the nearest 0.1 gram. During the first survey, all fish greater than 100 mm in standard length were implanted with one 23 mm Half Duplex PIT tags (Texas Instruments 23mm RFID) each. For every fish located during any of our surveys, we recorded the pool identification number (see habitat survey) and UTM coordinates using a Garmin V GPS. Ninety one percent of projected UTM coordinate locations for fish were within 5 m of the stream channel. Only fish greater than 100 mm in standard length were used to construct our fish distribution map because triple pass depletion showed high efficiency of fish this size or greater (between 92% and 100% being captured on the first pass; mean = 98%).

During September and October of 2004 we conducted three surveys on Sage and Line Creek using portable RFID antennas to track the tagged fish. Our antenna surveys were restricted to portions of Line and Sage Creeks above 1,500 m elevation because low water, desiccated reaches, and high temperatures caused LCT to be scarce below that elevation (only three LCT were captured below 1,500 m during both the fall and early summer electro-fishing surveys). Portable antennas were used to "sweep" the stream in a back and forth motion.

To determine antenna efficiency, we used block nets to isolate a 1 km section of stream, and then proceeded to survey the reach with our portable antenna noting the location of all detected fish. After completing the first survey, a second operator with no knowledge of the number or location of fish in the previous survey (to avoid operator bias) conducted a second survey. These calibrations were conducted on three different reaches, and more than 99% of all fish detected were found in both surveys. This means that antenna surveys were highly efficient at detecting PIT tagged LCT. Additionally, during our calibration surveys, all LCT detected in our second pass were found in the same pool in which they were located during our initial pass, which suggests that antenna surveys did not displace fish permanently from the pools in which they were first detected.

Habitat

Habitat surveys were conducted concurrently with fish surveys in June and July during base flows. During subsequent fish surveys, data were collected on all pools which formed as the result of seasonal changes in discharge. These newly formed pools however, were very rare on both Sage Creek (n= 4) and Line Creek (n= 3).

We examined two types of overhead cover: undercut banks and canopy cover. In measuring undercut banks, we recorded both the undercut width and the percent overhang for all habitat units. Undercut banks could be formed by any physical object including wood, soil, boulders or vegetation but had to meet two criteria in order to be classified as undercut. First, the lowest portion of the undercut bank could be no higher than 15 cm above the pool's water level, and second, its width had to be greater than 7.5 cm. Undercut width was defined as the greatest length from the streamside edge of the bank to the "back end" of the undercut, as measured by a ruler held perpendicular to the thalweg and placed under the overhanging portion of the bank. Percent overhang was visually estimated as the percent (by length) of all banks within a pool that were undercut. We visually estimated pool canopy cover. An observer standing in the middle of the pool would determine what percentage of the surface area of the pool had canopy cover directly overhead. Our estimates of canopy cover and percent overhang were highly correlated among observers when multiple observers estimated these values for the same pool (Pearson's $r > 0.9$).

We examined three variables related to substrate: dominant substrate, sub-dominant substrate and percent surface fines. We visually estimated dominant and subdominant substrate based on a pool's surface substrate composition using five categories (silt, sand, gravel, cobble, and boulder/bedrock) from a Wentworth particle scale. Percent surface fines were also measured in the tail of each pool near the thalweg. A 17.5 cm by 17.5 cm, 49-point grid was dropped into the tail of the pool from a height of approximately 1.2 m to select a sampling site. Percent fines were calculated as the percentage of points with fine substrate underneath them.

The number of pieces of large wood (LW) was also recorded for each pool. Only those structures that had some portion of their length wetted at the time of the survey, provided in-stream fish cover, and were larger than 0.1m in diameter and 1.5m in length were classified as LW. Our size requirements for LW were small when compared to other studies; however, they were appropriate for small high desert streams with relatively low discharge. Pieces of this size were likely to provide at least seasonally permanent fish cover. Both the number of individual pieces and aggregates (two or more pieces combined) of LW were recorded for each pool.

We also recorded riffle and pool characteristics. We focused on riffle variables related to connectivity, and used both mean riffle depth and riffle length. Riffle depth was the average of three recordings of maximum depths, spaced equidistantly along the length of the riffle. Riffle length was collected using the protocol outlined by Hankin and Reeves (1988). Maximum depths and widths of pools were measured with the aid of a two meter stadia rod.

Data Analyses

Because we were looking at habitat selection patterns, analysis was limited to those segments of Line and Sage Creeks inhabited by Lahontan Cutthroat Trout (LCT). Stream segments analyzed were bounded downstream by a maximum stream temperature of 23° C; the upstream boundary was the first significant barrier (height greater than 0.5 m) above the upper limit of fish distribution. In both Sage and Line Creeks, the contiguous length of the "inhabitable" portion of the stream never exceeded the contiguous length of the occupied portion by more than 1 km.

Survival and Growth: We examined survival and growth of LCT to determine if the observed differences in habitat selection patterns corresponded to reach-specific differences in survival and growth.

Survival rates were based on recaptures of marked adult (> 100mm SL) fish. Fish were PIT tagged in June and July of 2004 and recaptured in November of 2004. All fish not recaptured were assumed to be mortalities for two reasons. First, capture efficiencies were high, with a mean of 98% of fish (> 100mm SL) being captured on the first of three electro-fishing passes during triple pass depletion work. Second, not only were our mobile antenna surveys extremely effective at detecting tags within the system (> 99% detection rate), but they were also capable of detecting tags buried up to 30 cm into the substrate. Most (> 90%) of the tagged fish that were not recaptured during fall electro-fishing were also not detected in the previous antenna survey. Finally, only three fish confirmed to be alive through detection of inter- or intra-pool movement during our last antenna survey were not recaptured during the November electro-fishing survey. Thus, most of the tagged fish that we did not recapture were likely to have been removed from the system by predators or scavengers. Statistical analysis was conducted using a X^2 test with Yates' correction for a 2 x 2 table to compare survival rates in middle and upper Sage reaches (which we combined in our analyses due to their similarities) to lower Sage reaches.

We used data from our electro-fishing and relocation surveys to look at relationships between undercut selection and survival. Survival rates were based on recaptures of marked adult (> 100mm SL) fish as described previously. Undercut use was based on the locations of PIT tagged fish during five fish location surveys between June and December. All fish were divided into two groups based on whether they were detected more often in pools with or without undercuts. Seven fish were detected an equal number of times in pools with and pools without undercuts. Therefore, they were not used for the analysis. Statistical analysis was conducted using a X^2 test with Yates' correction for a 2 x 2 table.

We analyzed mark-recapture data to determine if there were reach-specific differences in LCT growth. We compared fish occupying lower Sage reach to fish occupying the upper and middle Sage reaches combined. Our recapture efforts were highly successful in Sage Creek with 47% of LCT that were PIT tagged in the spring being recaptured in the fall. We calculated the percent daily (or instantaneous) growth rate for each fish as:

$$GR = (\log_e W_2 - \log_e W_1) / t_2 - t_1 * 100;$$

where W_1 is the initial weight (in grams) when captured in June-July, and W_2 is the final weight at the time of recapture in November. The formula denominator, $t_2 - t_1$, is the number of days between the first capture and the recapture of fish (Ricker 1975). The Mann-Whitney test for medians was used for statistical comparison because it does not require normal distribution of the data. In Line Creek, neither survival nor growth data were analyzed because the majority of LCT were found in only one, relatively homogeneous and short section; thus inter-reach analysis was not possible.

Turnover Rates and Densities: We also examined the effect of downstream topographic nick-points on pool turnover rates and habitat selection. For all analyses, pools were considered to be in a nick-point if they were within a 10 m downstream nick-point segment or either 10 m segment immediately adjacent to a nick-point segment. Pools in segments adjacent to nick-point segments were still considered to be affected by the nick-point for two reasons. First, an adjacent 10 m segment would often be nearly as close to the actual topographic nick-point as the nick point segment. Second, the benefits associated with nick-points such as hyporheic input and pool formation may have extended easily into adjacent 10 m stream segments.

To look at reach-specific differences regarding the effects of nick-points on the proportion of fish emigrating from pools we conducted two separate analyses: one with the combined data from the middle and upper Sage reaches and a second with data from lower Sage reach only. During our 2004 study period, middle and upper Sage reaches had cooler and less variable summer temperatures. Thermal refugia associated with nick-points were probably of less importance in these reaches than in the lower Sage reach, where temperatures were higher and more variable and, therefore, likely to be stressful to LCT. We compared LCT emigration rates between pools in nick-points and pools out of nick-points. Emigration rate was calculated as: emigrated biomass / total biomass. Whereby, emigrated biomass was the total biomass of LCT leaving a pool between any of our five sampling surveys. Fish removed from the pool as a result of predation or other sources of mortality were included in the biomass emigrated. Total biomass was the sum of the biomass of all LCT found in a pool during all five surveys. For fish that were detected during a mobile antenna survey and later recaptured, biomass was adjusted based on their daily growth rate and number of days since their initial capture. Growth was assumed to be constant across the entire study period. For fish that were not recaptured, their initial capture weight was used in calculating the biomass emigrating or total biomass for any pool they occupied. Although fish that were not recaptured may have grown, and we could have estimated their change in biomass using the mean growth for fish within the reach, we ultimately decided against this for two reasons.

First, fish that weren't recaptured were assumed to be mortalities and thus the habitats they occupied were of lower quality than habitats where fish survived; and second, there was considerable variation in growth rates among individuals. Statistical analysis was conducted using the Mann-Whitney test for medians because it is more robust than other tests comparing central tendencies, and does not require a normal distribution of the data.

We looked at the relationship between nick-points and LCT turnover rates in 40 pools in lower Sage reach, and 44 pools in middle and upper Sage reaches combined. We used the pool biomass data from our pool score calculations to determine the turnover rate of pools. Turnover was calculated as: Biomass E/Biomass T, where Biomass E is the mass of all fish which emigrated from a pool between times "t1" and "t2", and Biomass T is the mass of all fish in a pool at time "t1". Time "t1" corresponds to that of the initial fish survey (either electro-fishing or antenna), and "t2" is the time of the subsequent fish survey. Data were used from all five surveys.

To rule out density-dependence as the potential cause of differences in habitat selection, survival and growth, we looked for differences in adult LCT (>100 mm TL) density between the reaches. We calculated fish density four ways: as the number of LCT per pool, LCT biomass per pool, number of LCT per meter, and LCT biomass per meter. Fish linear density (number or biomass per meter) was calculated as the number or weight of fish in a pool divided by the combined lengths of that pool and its upstream riffle. We did not look at surface area or volumetric density because riffles were generally shallow, narrow and relatively homogeneous across all reaches; thus, the potential effects of surface area or volumetric densities were unlikely to be different from linear density.

Pool Scores: We used logistic regression for our analyses because we had contiguous whole stream habitat surveys, highly patchy habitat, and only a small fraction (30%-40%) of pools with year 1+ LCT. Other studies with similar data sets also used this statistical method (Rieman and McIntyre 1995, Wiley et al. 1997, and Torgersen et al.1999). Regression analysis allowed us to determine relationships between selected habitat variables and pool score values. These scores were our response variable, and incorporated both LCT movement and pool-specific LCT production. We used the following formula:

$$\text{Pool Score} = S + I + G - E$$

where S was the biomass of LCT that continued to occupy a pool between consecutive surveys; I was the biomass of LCT that immigrated into the pool between surveys; G was the biomass gained by LCT growth between surveys; and E was the biomass of LCT that emigrated from the pool-either voluntarily or removed by predators-between surveys. Values for S, I, and E were back-calculated to the survey dates using the estimated daily growth rates of individual fish that were tagged in spring and recaptured in fall. The equation we used was:

$$\Delta\text{Biomass t2-t1} = \text{biomass t1} + \text{G}$$

where ΔBiomass t2-t1 is the change in biomass of individual fish between the time of initial fish tagging and measuring (t1) and the time of fish detection or recapture (t2). The value of G was calculated as the number of days an individual spent in a pool * its daily growth rate. Individuals who moved pools between surveys were assumed to have spent equal amount of time between “origin” pool and “destination” pool. Growth could not be calculated for fish that were not recaptured in fall; therefore, neither S, I, nor E were adjusted for daily growth rates, and no estimation of their "unmeasured" growth was added to the pool score. For our final survey’s pool score, data were pooled from our four re-sampling events. Pools for which E was greater than or equal to “$S + I + G$” were given a score of “1” to differentiate them from pools where LCT were never detected. In the regression analyses, pools with a score greater than 2 were assigned a "1" for presence, and all other pools were assigned a "0" for absence.

All habitat variables used in our regression models were transformed into categorical data by assigning "1" to values above each variable’s median and "0" to values equal to or less than the median (Table 1).

We conducted a total of five separate analyses at two different spatial scales. The first two "stream-scale" analyses consisted of the entire portion of Sage and Line Creeks respectively that were inhabitable by LCT. Whereas, the final three "reach-scale" analyses only considered the lower, middle, and upper reaches of Sage Creek. For each analysis, we ran both bivariate and stepwise logistic regression models. Bivariate models were useful in determining simple relationships between pool habitat characteristics and LCT distribution, while forward stepwise models were helpful in examining hierarchical relationships between habitat variables and LCT pool scores. Stepwise logistic regression models are especially valuable in analyzing the relationship between fish presence/absence patterns and multiple habitat metrics, since they make no assumptions regarding either covariance or normality (Hosmer and Lemeshow 1989, Trexler and Travis 1993). Furthermore, fish habitat relationships may be better explained as environmental thresholds and not linear relationships between habitat variables and our pool scores. For example, pools with values in undercut width above a certain value may be attractive to LCT, and thus selected by fish. In contrast, there is no reason to expect that an undercut that is twice as wide should contain twice the amount of fish especially in streams with low fish densities such as ours.

Results

Temperature

Both mean temperature and variance in temperature (Figure 3) decreased as stream kilometer increased (kilometers from mouth). From June through November 2004, mean temperature ranged from 14.6 °C to 11.3 °C and variance in temperature ranged from 9.5 °C to 3.4 °C among our four sample sites spread throughout the study area (Figure 3). Upper Sage reach had cooler and less variable temperatures than lower Sage reach. Middle Sage reach was a transition zone, with intermediate values in both temperature mean and variance. The maximum temperature recorded in any occupied portion of Sage or Line Creek was 23 °C.

LCT Habitat Selection

In order to examine the possible effects of temperature and areas of potential thermal refugia on habitat selection, we used the stepwise logistic regression model from upper and middle Sage creek (where stream temperatures were cooler and less variable) to predict which pools should be occupied in lower Sage creek (where stream temperatures were warmer and more variable). Our regression model from upper and middle Sage Creek predicted that pools with undercuts wider than 7 cm should contain LCT. The proportion of pools predicted to be occupied that were actually occupied by LCT was greater for pools located within nick-point segments (9/9 or 100%) than in pools located outside of nick-points (5/14 or 36%) (Figure 4). This difference in the proportion of occupied pools was significant ($P = 0.008$, X^2 test using Yates' correction for a 2 x 2 table).

Survival and Growth

For our survival, growth and turnover rate analyses, fish from upper and middle Sage reaches were pooled because they had similar habitat selection patterns. Survival rates of LCT were significantly greater in upper and middle Sage reaches than in lower Sage reach ($P = 0.027$, X^2 test using Yates' correction) (Figure 5). Only 35% (16 out of 45) of the LCT survived the summer and fall in lower Sage reach, while 61% (28 out of 46) of the LCT survived in upper and middle Sage reaches (Figure 5).

Use of pools with undercuts may have also affected LCT survival rates in Sage Creek. During our five relocation surveys, 53 fish were found most often in pools with undercut banks, while 31 fish were detected most often in pools without undercuts. Only seven of those 31 LCT in pools without undercuts survived, while 35 of the 53 LCT in pools with undercuts survived the six month study period. This difference in LCT survival rates between pools with and without undercuts was significant ($P = 0.002$, X^2 test using Yates' correction) (Figure 6).

In spring of 2004, there was no significant difference in the mean weight of LCT between the lower Sage reach (36.2 g) and the upper and middle reaches combined (35.6 g) (P=0.92, t-test). However, the June through November daily growth rates of LCT differed between the lower Sage reach and the middle and upper Sage reaches combined. Median daily growth was significantly greater in the lower reach (0.46%; n=16) than in the other two reaches combined (0.07%; n=28) ($P = 0.001$, Mann Whitney U-test) (Figure 7).

Turnover Rates and Densities

Movement of LCT between lower Sage reach and middle and upper Sage reaches was extremely limited during the 2004 field season; only one fish moved from middle or upper Sage reach to lower Sage reach during 2004. LCT densities were low across all reaches of Sage Creek with an average of only one adult LCT (> 100mm) for every 2.5 pools or one LCT for every 21 meters of stream. In spring of 2004 there was no significant difference between any of our density measurements in lower Sage reach versus upper and middle Sage reach (Table 2) Mean fish densities were low in both lower Sage reach and the combined upper and middle Sage reaches (Table 2). In the fall of 2004, only fish per pool was significantly greater in upper and middle Sage reach than in lower Sage reach (*P* = 0.036, Mann-Whitney U Test) (Table 2). There was no significant difference between the reaches for any other density metric, including: grams per pool, grams per meter and number of fish per meter. Mean fish densities in any of the reaches differ significantly between spring and fall (*P* > 0.10 for all tests, Mann-Whitney U Test,)

We looked at the effect of topographic nick-points on the proportion of LCT (by biomass) emigrating from pools in all three reaches of Sage Creek. In lower Sage reach, the proportion of LCT emigrating was greater in pools located outside of nick-point segments (median = 1.0; n=23) than in pools located within nick-point segments (median = 0.21; n=19). This difference in proportion of fish emigrating was statistically significant (*P* = 0.006, Mann Whitney U-test) (Figure 8). A similar but weaker pattern was observed when analyzing the combined data from upper and middle Sage reaches. Although for these reaches the proportion of LCT emigrating from pools outside nick-point segments (median = 0.20; n=10) was also greater than from pools within nick-point segments (median = 0.07; n=33), this difference was not statistically significant. (*P* = 0.29, Mann Whitney U-test) (Figure 8). Finally, turnover rates of "nick-point" pools in lower Sage reach were similar to turnover rates of pools inside and outside of nick-points in upper and middle Sage reaches with medians of 0.21, 0.07, and 0.20 respectively.

Pool Scores

Lahontan Cutthroat Trout were the only fish detected in our study section. Both

Sage and Line Creeks consisted exclusively of pool and riffle habitat units, and more than 99% of all adult LCT (>100mm) were found in pools. Fish density was low in all reaches with an average of one adult LCT for every 24 stream meters or one fish every 2.4 pools. There was no significant spatial autocorrelation in the pool score response variable used in the logistic regression (Pearson's correlation coefficient = 0.07 for adjacent pools).

Movement was rare during the study period. Total mean distance moved by a trout was 65 m, and most individuals moved considerably less. For example, we detected that 90% of the fish moved less than 91 m, 70% moved less than 16 m, and 48% did not move.

Sage Creek: In the bivariate logistic regression analysis for the whole stream undercut width (undercut), pool maximum depth, and percentage overhang were all significantly and positively related to pool production (i.e., pool scores). All three variables were positively associated with peaks in LCT pool score and their individual regression models had relatively high prediction abilities (~ 70%) (Table 3). A stepwise logistic model selected undercut, followed by pool maximum depth as positively associated with peaks in LCT pool score with both variables adding significant ($P <$ 0.001) explanatory power to the model. The combined model using both habitat variables accurately predicted 80% of the presence/absence of pools with positive pool scores in Sage Creek (Table 4).

Line Creek: A stream-level bivariate regression analysis revealed that peaks in pool score were significantly associated with peak values in percent overhang, overhead cover, undercut, and percent fines (P = 0.001, 0.01, 0.001, and 0.02 respectively). Percent overhang most accurately predicted patterns in pool score with a model accuracy of 72%, overhead cover had a model accuracy of 67% and both undercut and percent fines had model accuracies of 65%. Percent overhang, overhead cover, and undercut, were positively associated with positive pool scores while percent fines were negatively associated with pool scores (Table 3). A stepwise logistic regression analysis of Line Creek revealed that percent overhang was significantly and positively associated with peaks in pool production (pool score). After adding percent overhang to the model, no other variables added significant explanatory power and this final model accurately predicted 72% of the distribution pattern of pool score in Line Creek (Table 4).

Lower Sage Reach: Bivariate logistic regressions for this reach revealed significant relationships between two pool habitat variables (pool maximum depth and overhead cover) and our LCT pool score. Pool maximum depth was positively associated with pool score, explaining 82% of variability in pool trout production. In contrast, high values in overhead cover were negatively associated with pool score, explaining 75% of pool production (Table 5). In our stepwise regression analysis for lower Sage reach, once pool maximum depth was considered, only overhead cover added any additional explanatory power to the model ($P < 0.001$ for both), which ended up with an accuracy of 93% in predicting LCT pool scores. As in the bivariate regression, overhead cover showed a negative relationship with pool score (Table 4).

Middle Sage Reach: Both undercut and percent overhang were significantly associated with pool score ($P < 0.001$ and $P = 0.004$, respectively). Undercut predicted

74% while percentage overhang predicted 70% of the positive and negative values in pool production. Peaks in both variables were positively associated with peaks in pool production (Table 5). In our stepwise analysis of middle Sage reach, only undercut was significantly related to patterns in pool scores ($P < 0.001$). Peaks in undercut width were significantly and positively associated with peaks in pool production and no other variable added significant explanatory power to the model. Our final model explained 74% of patterns of peaks and troughs in LCT pool production in middle Sage Creek (Table 4).

Upper Sage Reach: Bivariate logistic regression showed that undercut, overhead cover, and percentage overhang had highly significant ($P < 0.001$, 0.005, and 0.008 respectively) positive relationships with LCT pool score. Undercut predicted 82%, overhead cover predicted 76%, and percent overhang predicted 74% of LCT pool score (Table 5). After selecting undercut ($P < 0.001$), our stepwise logistic regression model selected only overhead cover ($P = 0.01$) as providing significant additional explanatory power. Our model showed with an 87% prediction accuracy that high values for both undercut and overhead cover were positively related to LCT pool scores. (Table 4).

Discussion

We found differences in the survival, growth, and habitat preference of LCT in warmer versus cooler reaches in Sage Creek. In warmer reaches, LCT preferred deeper pools, with lower densities of overhead cover and near topographic nick-points. In contrast, LCT occupying cooler reaches preferred pools with undercuts and denser overhead cover. Pool proximity to nick-points did not seem to influence LCT pool choice in reaches with lower water temperature. Besides these reach-specific differences in habitat selection, there were reach-specific differences in trout survival and growth. Access to hyporheic input in stream segments influenced by nick-points may have allowed LCT not only to persist in the warmer reaches but also grow at high rates. LCT in warmer reaches experienced almost twice the mortality rates and over six times the growth rates of LCT in cooler reaches.

The use of immigration, emigration (including mortality) and growth rates in our habitat preference analyses allowed us to distinguish the habitats that provided the highest returns in terms of LCT survival and growth (i.e., production) from those habitats that fish were merely moving through at the time of one of our surveys. Although reach-specific differences in habitat selection, survival and growth were large and—in some respects—clear, the underlying mechanisms responsible for these patterns seem controlled by complex interactions of multiple environmental factors. Reach-specific differences in temperature, thermal refugia and overhead cover probably contributed to the observed differences in growth between the reaches, whereas differences in trout survival were the likely result of pool turnover rates, undercut use, and temperature related shifts in habitat selection. In turn, fish growth and survival rates likely affected habitat selection as individuals could have moved among habitats to compensate potential trade offs between potential gains in body mass and survival. Thus several of the habitat factors we examined may have acted synergistically to affect survival, growth, or both.

In our study, temperature seemed to influence habitat selection directly and, through this process, indirectly affect LCT growth and survival. Although our analyses of data for all study reaches in Sage Creek suggested that undercut and pool maximum depth were both important in explaining LCT pool score patterns, our reach by reach analyses revealed that this larger-scale pattern could be explained by two smaller-scale, temperature-related patterns. In both upper and middle Sage reaches (the cooler reaches), only undercut was directly related to LCT pool scores, pool maximum depth was not. However, in lower Sage reach (the warmer reach) our analyses showed that LCT pool scores were directly associated with pool maximum depth, and did not respond to presence of undercuts. These differences in habitat selection between reaches were likely caused by differences in stream temperatures. The cooler and less variable water temperatures that characterized the upper and middle reaches of Sage Creek allowed fish to choose from all available habitats without having to avoid areas with either high or highly variable temperatures. As a result, fish were able to utilize a broad variety of habitats, including those which provide refugia from predation, such as undercuts. This is the type of habitat feature that is also preferred by Golden Trout *(Oncorhynchus mykiss aguabonit)* in similar conditions to those in Sage Creek (Matthews 1996), and by cutthroat trout *(Oncorhynchus clarki)* in larger streams (Brown and Mackay 1995). In contrast, habitat selection in the warmer and more thermally variable lower reach of Sage Creek gave priority to habitats with thermal refugia, such as pools receiving hyporheic upwelling caused by nick-points (Baxter and Hauer 2000), over those that provided better cover.

What seemed like a contradiction between the results of our stepwise regression analysis of LCT distribution in lower Sage reach, which selected overhead cover and pool depth as key explanatory variables, and the results of turn-over rate analysis, which identified nick-points as the main factor, can be explained at closer examination. Pools adjacent to nick-points may attract LCT for at least two reasons. The first is the presence of pockets of colder water formed by hyporheic input. This process has also been reported by Baxter and Hauer (2000) in their study of bull trout *(Salvelinus confluentus)* in the Swan Basin. Hyporheic input has been observed to provide thermal refugia both from elevated as well as from highly variable water temperatures **(**Ebersole et al. 2003, Cunjak and Power 1988, Lowry 1993**)**. Second, the topography associated with nick-points may facilitate deeper pools, less prone to desiccation. Topographically confined segments like nick-points are generally erosional zones with limited alluvial deposits. May and Lee (2004) found that pools in areas with thin alluvial deposits were less likely to desiccate during summer low flows than pools in areas with thicker alluvial deposits over bedrock. Therefore, LCT seem to select pools in the vicinity of nick-points because they are larger, more persistent, and receive hyporheic input of relatively cooler water.

Numerous studies have shown that temperature strongly affects the growth rates of fish. In the case of salmonids, there is evidence of greater growth in warmer rather than in cooler stream reaches (Adams 1999), and in downstream rather than in upstream portions of watersheds (Harvey et al 2005). LCT growth rates in the upper and middle reaches of Sage Creek may have been reduced by low water temperatures. While laboratory studies have found that multiple strains of rainbow trout (*Oncorhynchus mykiss*) had greater growth at 15° C than at 7° C (Wangila and Dick 1988, Mckay et al. 1984), there is conflicting evidence for such a pattern in LCT. For example, in controlled studies, Dickerson and Vinyard (1999) found no difference in growth rates of LCT across a range of temperatures between 13° C and 22° C, while Meeuwig et al (2004) found optimal LCT growth rates at 12° C. In contrast, field studies have found greater LCT growth in warmer versus cooler systems (Cowan *cited by* Coffin and Cowan 1995). One possible explanation for this discrepancy is that temperature depressed growth rates may only occur at temperatures below 12° C. In a laboratory study, Bear (2005) found that growth rates were significantly lower for both West Slope Cutthroat and rainbow trout held at 8° C compared to fish held at 13° C. Mean water temperatures in lower Sage reach were above 13° C and, thus, favorable to trout growth. In contrast, mean water temperatures for both upper and middle Sage reaches were between 8° C and 13° C, which is within the range of temperatures reported to reduce cutthroat and rainbow trout growth rates. Therefore, LCT in upper and middle Sage reaches may have spent more time in temperatures that were suboptimal for growth, compared to LCT in lower Sage reach.

The higher growth rates LCT exhibited in the lower reach of Sage Creek compared to the middle and upper reaches suggest that either food was abundant throughout the study period or that fish were able to behaviorally thermo-regulate to optimize growth in response to changes in both prey availability and water temperature. High water temperatures boost fish metabolic rates, and unless they increase food intake proportionately and prey are not in limited supply they will experience reduced growth rates and even death by starvation (Hughes and Grand 2000). In rainbow trout, Linton et al. (1998) found that even a slight increase in water temperature augmented feeding rates. By utilizing pools with a range of water temperatures resulting from the mixing of surface and hyporheic flows, LCT in lower Sage reach may have been able to select temperatures which maximized growth during seasonal changes in temperature and prey availability better than fish in upper and middle Sage reaches. This type of behavioral thermo-regulation can facilitate optimal growth in salmonids by allowing them to maximize food intake in warmer areas and then retreating to cooler areas to minimize metabolic cost (Hughes and Grand 2000, Berman and Quinn 1991, Kaya et al. 1977, Brett 1971, Crowder and Magnuson 1983). Controlled laboratory studies have demonstrated that even when salmonids are fed in excess, they select temperatures which optimize growth efficiency and not maximum growth (Larsson 2005).

Large diel temperature fluctuations have been shown to both reduce growth (Meeuwig 2004) and be metabolically costly (Cunjak 1988) to trout. Therefore, our finding that the highest LCT growth rates were realized in the reach with the greatest daily temperature fluctuation provides support to the notion that these trout are able to obtain shelter from such extreme conditions in the pools that receive relatively cool and more stable hyporheic water input.

Daily growth rates of LCT in the warmer reach (lower Sage) were not only significantly greater than daily growth rates in the cooler reaches (upper and Middle sage) but also greater than growth rates of LCT in other systems in the Sierra Nevada mountains (Gerstung, 1986) and comparable to growth rates in another Trout Creek Mountain system (Talabere, 2002). The higher growth rates of LCT in lower Sage reach is surprising because LCT, like other inland cutthroat species, are generally found only in headwater portions of streams (Shepard 2004, Dunham et al. 1999, Behnke 1992).

LCT survival rates may have also been affected by temperature. Temperature patterns influenced movement rates and undercut use resulting in poorer survival in lower Sage reach than in upper and middle Sage reaches. While undercut banks, which have been shown to provide predation shelter (Boss and Richardson 2002), were preferred by LCT in cooler stream reaches (i.e., upper and middle Sage reaches), it was primarily the cooler groundwater input associated with nick-points that LCT sought above other habitat features in reaches with warmer and more variable temperatures (i.e., lower Sage reach). Ebersole et al. (2003) found a similar distribution pattern in his study of multiple tributaries of the Snake River where the proportion of rainbow trout found in cold water patches within a reach increased with stream temperature. Our results show that the warmer low reach pools that combined both thermal refugia (nick-points) and predation shelter (undercuts) were always occupied by trout; whereas, pools with only thermal refugia were occupied 67% of the time, and pools offering only undercuts were generally vacant. This coincides with the findings of Brown and Mackay (1995) who reported that cutthroat trout can occupy exposed habitats, such as very shallow pools (<8cm), if these receive groundwater inputs. Individuals found in pools outside nick-point stream segments seem to be "transient" because they were not found in the same pool during two consecutive surveys (which gave these pools their high turnover rates). In contrast, pools associated with nick-points had very low LCT turnover rates, and these were similar to those in the cooler upper and middle reaches of upper Sage creek. Thus, in lower Sage reach, pools with undercut banks but outside of nick-points may have been initially attractive to LCT, but, eventually, warmer and more variable temperatures may have driven LCT from these pools to pools near nick-points, with or without undercut banks. In upper and middle Sage reaches, where thermal patterns probably did not affect habitat selection, LCT selected pools with undercuts. Many of these nick-point pools were largely devoid of escape cover which may have left LCT vulnerable to predation. Other studies have demonstrated that undercut banks can provide significant cover from predation (Boss and Richardson 2002), and, in our own study, LCT utilizing pools with undercut banks had significantly higher survival rates than LCT utilizing pools without undercuts. Thus temperature may have caused LCT in lower Sage reach to select pools near nick-points over pools with undercuts and as a result left LCT more vulnerable to predation.

Predation was probably the major source of LCT mortality in our study. We observed not only evidence of predators in the area (tracks and scat), but also the predators themselves including Green heron *(Butorides virescens),* American White Pelican (*Pelecanus erythrorhynchos),* Snowy egret *(Egretta thula),* Great blue heron *(Ardea herodias),* terrestrial garter snake *(Thamnophis elegans)*, and common garter snake *(Thamnophis sirtalis)* and witnessed multiple predation events. Tagged fish (or tags only) that were not relocated were assumed to have been taken by predators for three reasons. First, we found very few shed tags during our relocation surveys of either Line or Sage Creeks and it was unlikely that we could miss a shed tag because we conducted multiple, highly efficient, contiguous relocation surveys. Second, because there was no flooding during our study, and Sage Creek had many desiccated reaches below the intensively surveyed section, it was impossible for tagged fish to leave the channel and bypass the isolated pools in the downstream section. Third, fixed antennas were positioned at all confluences to detect any fish leaving our study reaches. Consequently, we concluded that in-stream mortality from other sources was rare, and that the tagged fish which we did not recapture must have been removed from the system by predators.

The search by LCT for pools with suitable water temperatures may have ultimately affected their vulnerability to predators. Although LCT in our study showed rather restricted movement patterns, comparable to those reported for other cutthroat trout (Miller 1957, Heggenes et al. 1991) and for golden trout (Matthews 1996), pools away from the influence of nick-points in the lower Sage reach had significantly higher turnover rates than any other pools in the surveyed reaches. Thus, higher fish movement and habitat shifts may have resulted in greater risk of predation (Aarestrup et al. 2005, Milinski 1993) for LCT occupying the warmer pools with no groundwater input than for trout in either the groundwater fed pools of this reach or in any of the pools of the cooler middle and upper reaches.

While temperature was probably the main causal factor for reach-specific differences in both LCT habitat selection and somatic growth rates, overhead cover may have also contributed to these patterns. The selection of areas with lower levels of canopy cover by LCT in lower Sage reach may be explained by the feeding behavior of LCT and other salmonids. In low order stream channels, terrestrial prey are an important part of the diet of rainbow trout (Nakano et al. 1999, Kawaguchi et al. 2003), brown trout *(Salmo trutta),* brook trout *(Salvelinus fontinalis)* (Cada et al. 1987), cutthroat trout (Hilderbrand and Kershner 2004, Wipfli 1997), and even coho salmon (Chapman 1965). Terrestrial input is positively correlated with the density of canopy cover (Kawaguchi and Nakano 2001, Wipfli 1997, Cloe and Garman 1996) and, therefore, habitats with greater overhead cover should be more attractive to trout because of increased foraging opportunities. Nevertheless, excessive amounts of cover limit light intensity, and eventually affect the ability of visual predators like trout to detect prey. It has been demonstrated that the feeding efficiency of salmonids on terrestrial prey items **(**Angradi and Griffith 1990, Bisson 1978) and invertebrates in general (Henderson and Northcote 1985, Robinson and Tash 1979) is positively correlated to light intensity. Wilzbach et al. (1986) reported that cutthroat trout feeding efficiency is negatively correlated with overhead cover, probably as a result of low solar input in areas of dense riparian canopy (Ward 1985, Beschta 1997). Furthermore, other studies found that cutthroat trout rarely occupy areas near overhead cover (Young 1996), especially when feeding (Nakano et al. 1992) or when food was scarce (Wilzbach et al 1986). This suggests that an intermediate density of overhead cover may be the most desirable for

LCT because it may provide abundant terrestrial input while allowing enough light through for fish to detect their prey.

Individuals in upper Sage reach occupied pools with the densest overhead cover (> 95%) available, and avoided pools with even a slight reduction in overhanging vegetation density (< 95%). In contrast, fish in lower Sage reach selected pools with moderate to high levels of overhead cover (between 25% and 80%), but avoided areas of very dense cover (> 80%). These reach-specific differences in habitat selection may have played some role in the differences in growth rates between fish in lower Sage reach versus middle and upper Sage reaches. In lower Sage reach, where fish used pools with more open overhead cover, LCT may have had higher feeding efficiency than in upper Sage reach where fish selected pools with dense overhead cover. Because fish density was low in all reaches, even pools with relatively low overhead cover may have had terrestrial invertebrate inputs that were far in excess of consumption. Thus by utilizing pools with intermediate values in overhead cover, LCT in lower Sage reach may have had higher feeding efficiency than fish in upper and middle Sage reaches, and daily growth rates of LCT were greatest in lower Sage reach.

This apparently contradictory pattern in overhead cover use between fish in upper and middle Sage reach versus lower Sage reach may be the result of differences in life strategies. Fish may have adopted one strategy emphasizing growth in less stable environments and a second strategy emphasizing survival in more stable environments. Thus LCT in the thermally more stable upper and middle Sage reach selected pools with denser overhead cover in order to avoid predation, thereby maximizing survival.

Alternatively, LCT in less thermally stable lower Sage reach, selected pools with moderate levels of canopy cover to increase feeding efficiency, thereby maximizing growth. Still the mechanisms behind this seemingly contradictory pattern in pool overhead cover use remain unclear.

Variation in fish density between the warmer and the cooler reaches of Sage Creek were probably insufficient to explain the observed differences in survival and growth. Although upper Sage reach had slightly lower median riffle length than lower or middle Sage reaches, this probably had little effect on food availability because LCT densities were low across all reaches and seasons at approximately one adult LCT (>100mm) for every 2.7 pools. There was no significant difference between fish densities in lower Sage reach versus upper and middle Sage reach in spring. However, in the fall only fish numbers per pool were significantly greater in upper and middle Sage reaches than in lower Sage reach. This difference was not significant when density was expressed as fish biomass per pool, fish per meter, or fish biomass per meter. The lack of spatial autocorrelation in our pool scores for adjacent pools indicates that LCT occupancy of one pool did not affect occupancy of adjacent pools. We also found no significant difference in fish size between the warmer lower reach and the cooler reaches above in the spring. Thus, it is highly unlikely that the observed differences in growth rates were the result of density-dependent factors or reach-specific differences in fish size, but rather growth rates can more easily be explained by differences in habitat selection patterns and stream temperatures.

Because both Sage and Line Creeks are small, high desert streams, water depth and temperature are the main factors restricting fish distribution. Most adult LCT (>100mm) were found in pools, which is the same pattern reported for other cutthroat sub-species (Young and Guenther-Gloss 2004, Harig and Fausch 2002, Young 1996). Riffles were probably not utilized by adult LCT because they contained little cover. Not only was in-stream cover such as boulders and large wood rare in riffles, but riffles were also typically both shallow and narrow (in average less than 5 cm deep and less than 1 m wide). We did not find LCT in stream segments with water temperatures higher than 23 ° C. This matches the temperature-restricted distribution patterns reported by Dunham et al. (1999), which can be attributed to reduced LCT growth and survival rates at temperatures over that limit (Dickerson and Vinyard 1999).

The relatively high mortality rates of LCT in lower Sage reach could initially suggest that this part of the creek may act as an ecological sink, especially because intermountain cutthroat trout are usually found in headwater portions of streams (Shepard 2004, Dunham et al. 1999). However, a closer examination of the data reveals that this lower and warmer reach may, in fact, be a population source. While fish in lower Sage reach had nearly twice the mortality rate of fish in upper and middle Sage reaches, the individuals that managed to survive in the lower and warmer reach experienced nearly seven times the growth rate of fish in upper and middle reaches. Considering that trout fecundity and egg size is directly related to female body mass (Sigler et al. 1983) and that larger trout reach sexual maturity earlier than small ones (Bigelow, J. public presentation, 2006), it is evident that the benefits derived from the elevated growth rates in the lowermost of the three study reaches (almost 0.5% per day higher than in the other reaches) more than compensated for the higher risks fish faced in it. It is advantageous for female trout in small headwater streams to reach a threshold size for sexual maturity early, because once sexually mature the female can divert energy that would have been used for growth into egg production. The energy that becomes available in this manner for egg production is critical to fluvial populations of LCT, which generally produce low numbers of eggs (between 100 and 300 eggs per individual; Coffin 1981). Moreover, the benefits to recruitment associated with "high growth" habitats such as the lower reach in our study section of Sage Creek is likely to be even more important to fish like LCT that—at least in adfluvial populations—rarely survive to spawn multiple years (Cowan 1982 *in* Coffin and Cowan 1995; King 1982).

Our study suggests that while temperatures remain low LCT choose pools with undercut banks and overhead cover. However, once temperatures increase and become more variable they abandon those pools in favor of pools that offer some amount of thermal refugia through groundwater input (which in the upper reaches of systems like ours tend to be associated with topographic nick-points). Thus, in the summer, water temperature controls LCT habitat selection, and groundwater fed pools in the vicinity of nick-points allows this sub-species of trout to occupy highly productive habitats in reaches that otherwise would be too warm for them. Therefore, special management strategies designed to protect stream reaches that are adjacent to nick-points need to be implemented to ensure the persistence of LCT throughout the area.

Finally, one important difference between our study and more traditional habitat selection or habitat quality studies is that we used our pool score, or pool-specific production, as our dependent variable instead of fish biomass or density. By using a "pool score", we avoided some of the pitfalls associated with habitat selection models which compare fish density to habitat metrics. First, density (i.e., number of fish per pool) may not accurately represent habitat selection because both large and small fish count equally in such models. Therefore, studies often incorporate fish size (biomass) into habitat selection models. While this avoids the problem of giving equal values to large and to small fish, it does not incorporate individual behavioral information (e.g., turnover rates) that may reveal important differences in quality among pools that have the same fish biomass. If we assume fish are free to distribute themselves among multiple habitats and have information about pool characteristics within a reach, the pools that are continuously occupied by the same fish (i.e., low turnover rate pools) are in effect being preferred by those fish over other pools in the vicinity. In contrast, pools with high turnover rates may sustain a relatively constant biomass over time but do not keep the same individual fish for long. Fish that move into these pools either move out or are taken by predators, and are replaced by new immigrants. Pools with low turnover rates are arguably “preferred” habitats over pools with similar biomass but higher turnover rates. Fish continue to "select" and/or survive in pools with low turnover rates, while fish do not continue to "select" and/or survive in pools with high turnover rates. Because we were able to mark most adult LCT in our study reaches we could incorporate pool-specific biomass, immigration, emigration, and mortality and growth data into our pool habitat selection models. Thus, areas with positive pool scores could be thought of as population sources and areas with low pool scores (in our analysis pool scores ≤ 1) as population sinks. As a result, we were able to look for relationships between source pools and habitat metrics and, therefore, separate habitats which function as population sinks from habitats which function as population sources. By linking production to specific habitats, we enable managers to identify and protect areas associated with LCT production instead of merely occupancy. This may be critical for the recovery and persistence of the sub-species.

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TABLE 1. Median values of pool habitat variables for Sage Creek, Line Creek and three contiguous reaches on Sage Creek. Numbers in parentheses are standard deviations.

	Sage Creek				Line Creek
	All Reaches	**Lower Reach**	**Middle Reach**	**Upper Reach**	**All Reaches**
Variable					
Pool Max Depth(m)	0.30 (0.08)	0.28 (0.08)	0.32 (0.10)	0.30 (0.07)	0.20 (0.10)
Overhead Cover(%)	90.0 (21.0)	80.0 (22.4)	95.0 (18.1)	95.0 (21.2)	30.0 (35.9)
Pool Width(m)	1.1 (0.5)	1.2 (0.5)	1.3 (0.6)	1.2 (0.3)	1.1 (0.5)
Undercut(m)	0.07 (0.24)	0.06 (0.17)	0.07 (0.19)	0.08 (0.26)	0.05 (0.20)
Percent Fines(%)	42.0 (28.7)	80.0 (23.3)	30.0 (21.9)	40.0 (16.7)	70.0 (19.9)
Wood(no.)*	0.35 (0.53)	0.22 (0.23)	0.52 (0.67)	0.41 (0.52)	0.38 (0.51)
Percent Overhang(%)	5.0 (20.4)	5.0 (18.9)	7.0 (22.0)	5.0 (22.0)	20.0 (31.4)
Riffle Length(m)	5.5 (8.7)	8.0 (8.5)	4.5 (10.0)	6.0 (7.9)	17.0 (17.8)

* Categorical variable

TABLE 2. Results of Mann-Whitney U-test comparing four metrics of LCT density in lower versus upper and middle reaches of Sage Creek, McDermitt, NV.

	Reach Means		U-test
Density Metric	Upper and Middle	Lower	*P* value
Spring 2004			
grams/meter	1.68	1.49	0.95
grams/pool	14.7	12.1	0.59
fish/meter	0.050	0.046	0.99
fish/pool	0.50	0.43	0.61
Fall 2004			
grams/meter	1.89	1.66	0.24
grams/pool	16.0	12.5	0.25
fish/meter	0.043	0.032	0.18
fish/pool	0.50	0.30	0.04*

Medians for all metrics in all reaches were "0". *Significant at the 0.05 level

TABLE 3. Results of bivariate logistic regression models using pool habitat variables to explain pool-specific fish production for Sage and Line Creeks.

Variable	**Estimated Regression Coefficient**		**Wald X^2**	**P**		**95% Confidence Limit**		**Model Prediction Accuracy**
					Odds Ratio	**Lower**	**Upper**	
Sage Creek *(n=278)*								
*Pool Max Depth***	1.51	±0.55	29.1	<0.001	0.22	0.12	0.39	70%
*Undercut***	1.22	±0.55	19.1	<0.001	0.29	0.16	0.51	70%
*Percent Overhang***	0.85	±0.55	9.4	0.002	0.43	0.25	0.74	69%
Percent Fines	-0.34	±0.54	0.3	0.55	1.17	0.68	2.00	
Riffle Length	0.3	±0.55	1.2	0.28	0.74	0.43	1.27	
Overhead Cover	0.23	±0.55	0.8	0.38	1.27	0.74	2.17	
Pool Width	0.31	±0.53	1.4	0.24	0.73	0.43	1.24	
Wood	-0.11	±0.55	0.1	0.71	1.12	0.63	1.98	
Line Creek *(n=79)*								
*Percent Overhang***	1.98	±1.1	14.6	<0.001	0.14	0.05	0.41	72%
*Undercut***	1.58	±1.04	9.8	0.001	0.21	0.07	0.58	67%
*Overhead Cover**	1.23	±1.01	6.1	0.01	0.29	0.11	0.81	65%
*Percent Fines**	-1.29	±1.14	5.9	0.02	0.27	0.09	0.85	65%
Wood	0.8	±1.01	2.6	0.11	0.44	0.16	1.20	
Pool Max Depth	0.32	±0.98	1.1	0.51	1.39	0.51	3.77	
Pool Width	0.37	±0.98	0.6	0.44	0.69	0.26	1.84	
Riffle Length	0.04	±1.01	0.0	0.92	0.95	0.35	2.60	

Habitat variables were always entered into the model as "1" for peaks above the median and "0" for values equal to or less than the median value (see table 1) The response variable of LCT pool score assigned a "1" for pools with positive pool production and "0" for negative or no pool production. Regression coefficients are shown ± 1 standard error. Model prediction accuracy was calculated by using the stepwise equation to predict fish presence or absence (fish were predicted to occur in pools were $y \geq 0.5$) and compared to field data.

TABLE 4. The results from five stepwise multivariate regression models using pool habitat variables to explain pool-specific fish production.

Variable	**Estimated Regression Coefficient**		**Wald X^2**	**P**	**95% Confidence Limit**			**Model Prediction Accuracy**
					Odds Ratio	**Lower**	**Upper**	
Sage Creek (All Reaches) ***(n=278)***								
Undercut	1.38	±0.59	21.2	<0.001	0.25	0.13	0.46	80%
Pool Max Depth	1.65	±0.58	31.2	<0.001	0.19	0.10	0.35	
Lower Sage Reach ***(n=89)***								
Pool Max Depth	3.19	±1.34	38.1	<0.001	6.86	2.20	20.66	93%
Overhead Cover	-1.92	±1.46	13.6	<0.001	0.04	0.02	0.14	
Middle Sage Reach ***(n=95)***								
Undercut**	2.25	±1.17	16.7	<0.001	0.1	0.03	0.35	74%
Upper Sage Reach ***(n=94)***								
Undercut	3.15	±1.59	21.6	<0.001	0.14	0.03	0.77	87%
Overhead Cover	1.93	±1.67	6.3	0.01	0.04	0.01	0.21	
Line Creek ***(n=79)***								
Percent Overhang	1.98	±1.1	14.6	<0.001	0.14	0.05	0.41	72%

All habitat variables were transformed into categorical data for stepwise regression models using "1" for values above the median and "0" for values equal to or less than the median.. (see table 1 The response variable of LCT pool score assigned a "1" for pools with positive pool production and "0" for negative or no pool production. Regression coefficients are shown ± 1 standard error. Model prediction accuracy was calculated by using the stepwise equation to predict fish presence or absence (fish were predicted to occur in pools were $y \geq 0.5$) and comparing to field data.

TABLE 5. Results of bivariate logistic regression models using pool habitat variables to explain pool-specific fish production for three contiguous reaches on Sage Creek.

Variable	**Estimated Regression Coefficient**		**Wald X^2**	***P***	**Odds Ratio**	**95% Confidence Limit**		**Model Prediction Accuracy**
						Lower	**Upper**	
Lower Sage Reach ***(n=89)***								
*Pool Max Depth***	3.1	±1.01	45.4	<0.001	0.041	0.01	0.13	82%
*Overhead Cover***	-1.92	±0.92	20.2	<0.001	6.83	2.74	16.99	75%
Undercut	0.38	±0.98	0.7	0.39	1.47	0.59	3.67	
Percent Overhang	0.21	±0.86	0.2	0.63	0.55	0.11	2.72	
Wood	0.88	±0.97	0.2	0.68	2.4	0.49	11.00	
Percent Fines	-0.16	±0.81	0.2	0.69	1.18	0.52	2.68	
Pool Width	0.133	±0.81	0.1	0.74	0.88	0.39	1.90	
Riffle Length	0	±0.76	0.0	1	1	0.21	4.70	
Middle Sage Reach ***(n=95)***								
Undercut**	2.25	±1.17	16.7	<0.001	0.1	0.03	0.35	74%
Percent Overhang**	1.5	±1.07	8.3	0.004	0.21	0.07	0.65	70%
Overhead Cover	0.62	±1.13	1.3	0.25	0.54	0.20	1.60	
Riffle Length	-0.47	±1.10	0.7	0.4	1.6	0.50	5.40	
Percent Fines	0.13	±1.04	0.7	0.78	0.87	0.31	2.39	
Pool Width	0..37	±1.03	0.6	0.45	1.7	0.47	6.70	
Pool Max Depth	0.39	±1.01	0.6	0.43	0.67	0.25	1.05	
Wood	0.01	±1.00	0.0	0.98	1.01	0.36	2.70	
Upper Sage Reach ***(n=94)***								
Undercut**	3.05	±1.44	23.2	<0.001	0.047	0.01	0.20	82%
Overhead Cover**	1.78	±1.39	8.1	0.005	0.17	0.04	0.68	76%
Percent Overhang**	1.58	±1.27	7.0	0.008	0.21	0.06	0.74	74%
Riffle Length	1.01	±1.16	3.1	0.08	0.36	0.11	1.17	
Wood	1.01	±1.24	2.8	0.1	2.77	0.77	9.90	
Pool Max Depth	0.59	±1.13	1.1	0.29	0.55	0.17	1.70	
Percent Fines	-0.36	±1.18	0.4	0.53	1.44	0.45	4.60	
Pool Width	0.038	±1.05	0.0	0.94	1.04	0.34	3.19	

All habitat variables were transformed into categorical data for stepwise regression models using "1" for values above the median and "0" for values equal to or less than the median (see table 1) The response variable of LCT pool score assigned a "1" for pools with positive pool production and "0" for negative or no pool production. Regression coefficients are shown ± 1 standard error

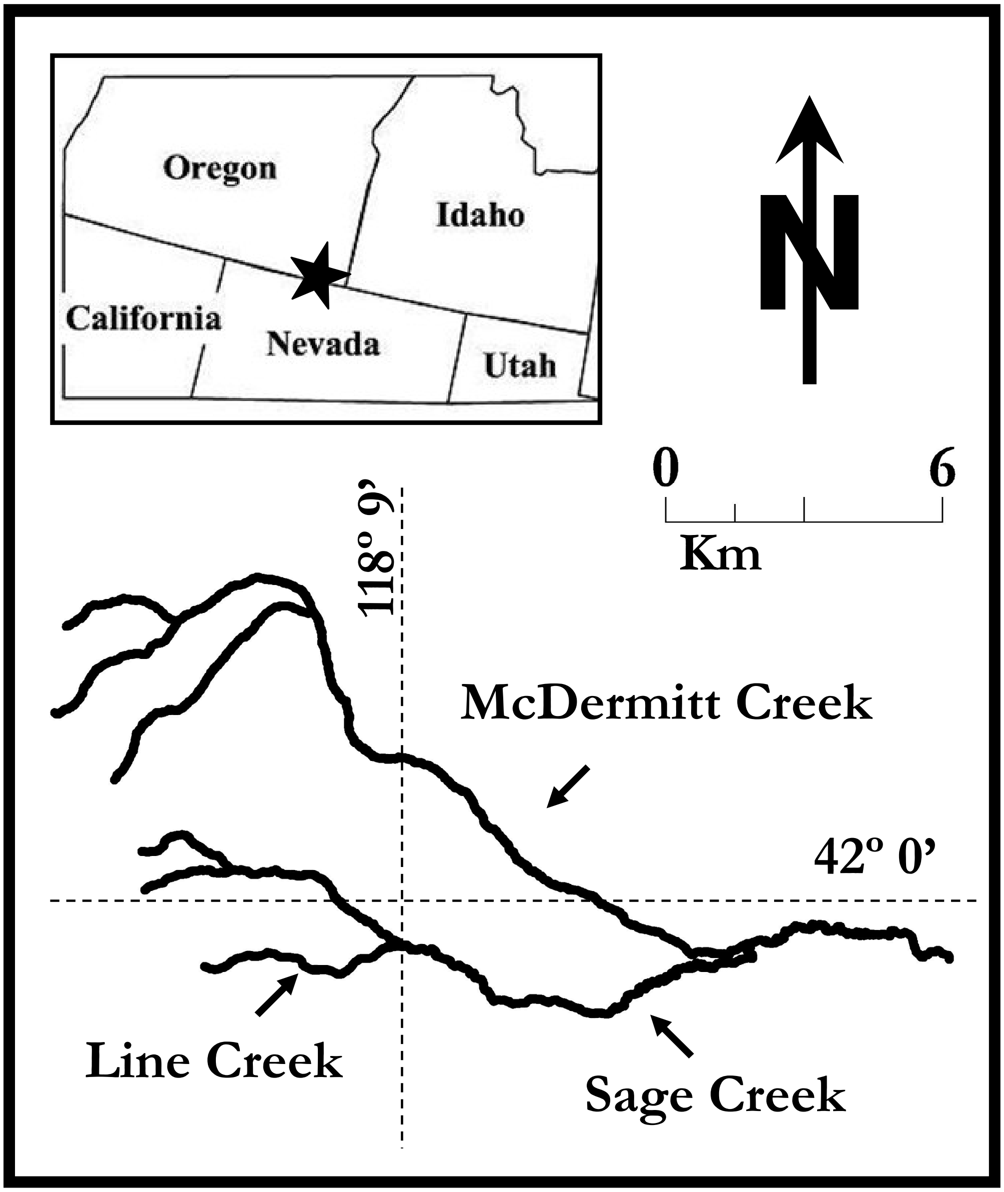

FIGURE 1. Map of the McDermitt Creek Sub-Basin, Malheur County Oregon and Humboldt County, Nevada

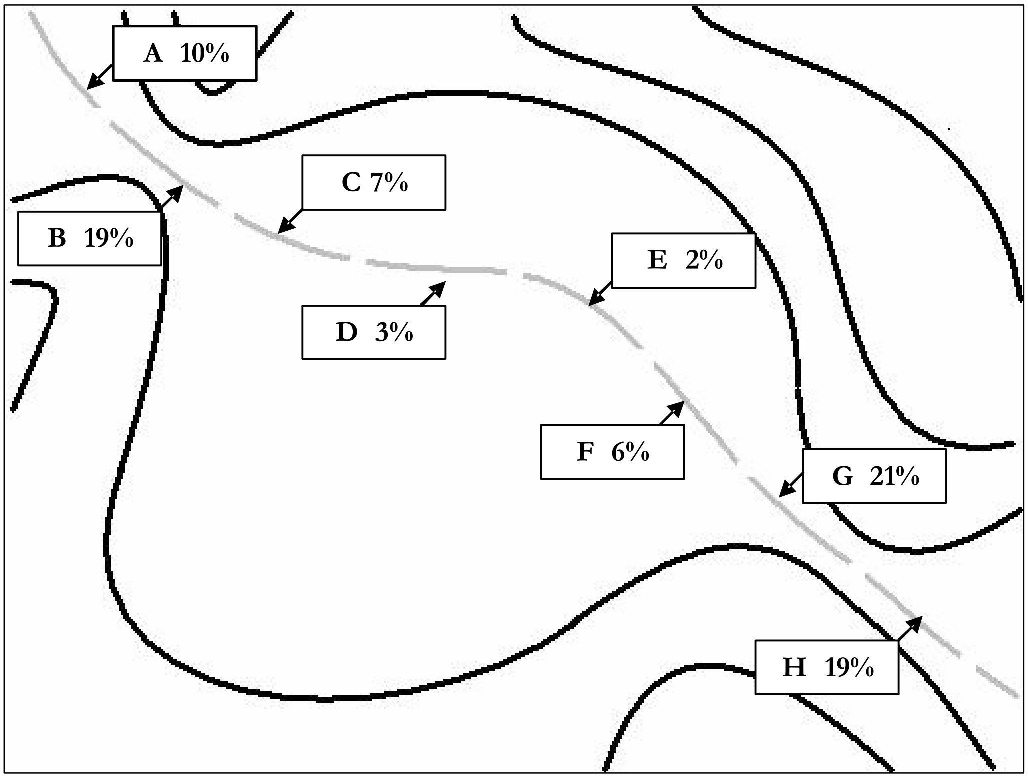

FIGURE 2. Diagram of nick-points. Black lines represent elevation contours and grey lines labeled with letters represent 10 m long stream segments. Segment G would be considered a nick-point because the absolute change in mean hill slope of the 10 m buffer area (not pictured) between stream segments F and G is greater than or equal to 10% (6%-21%=15%).

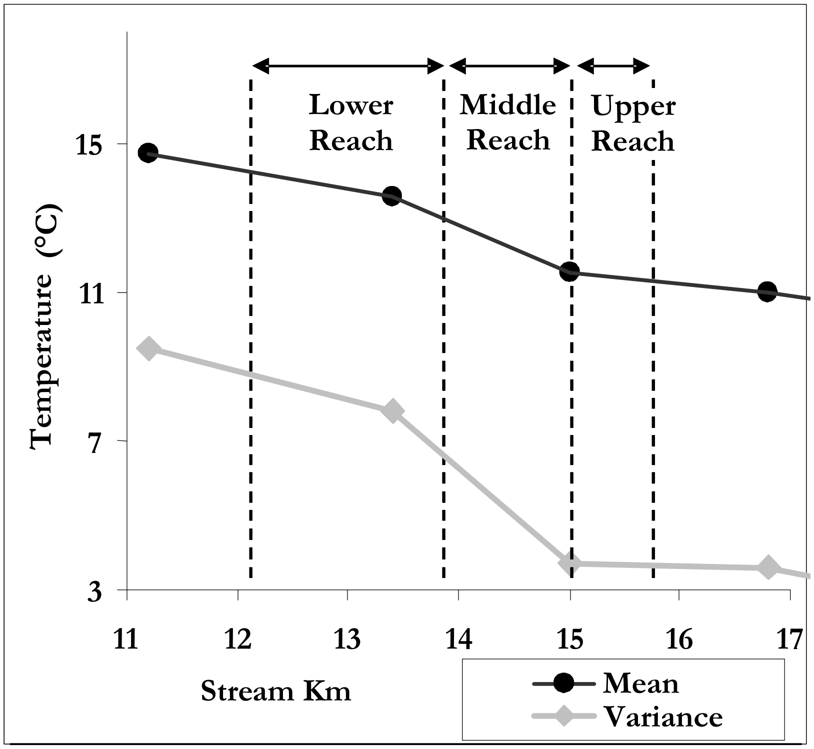

FIGURE 3. Stream kilometer versus mean stream temperature (° C) and variance in temperature (° C) during June through October 2004 for our upper, middle, and lower reaches on Sage Creek.

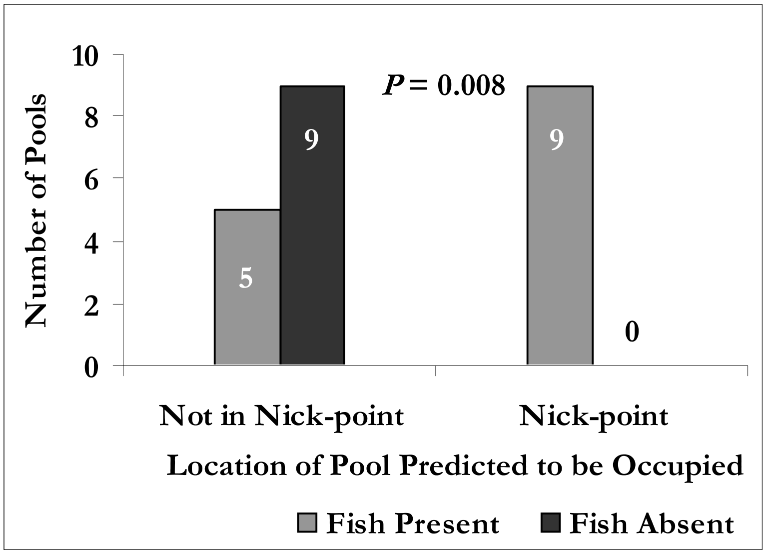

FIGURE 4. The effect of nick-points on LCT occupancy of pools with undercut banks. Pools were located in the lower reach of Sage Creek. Pools with an undercut bank wider than 0.07m were predicted to be occupied. *P* value shown was from a X^2 test using Yates' correction for a 2 x 2 table.

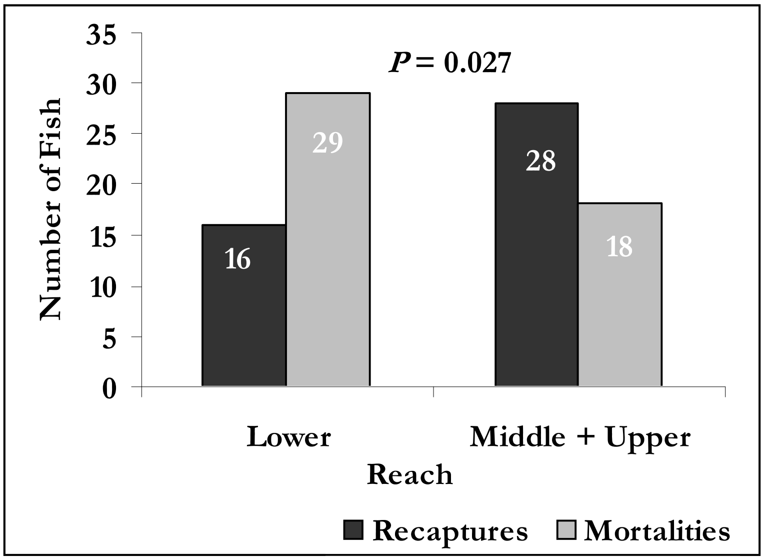

FIGURE 5. Survival rates of LCT in three reaches in upper Sage Creek (above 1640 m elevation). Fish were PIT tagged in June and July and recaptured in November of 2004. All fish not recaptured were assumed to be mortalities because capture efficiencies were high (with a mean in excess of 98% based on triple pass depletion work). *P* value shown was from a X^2 test using Yates' correction for a 2 x 2 table.

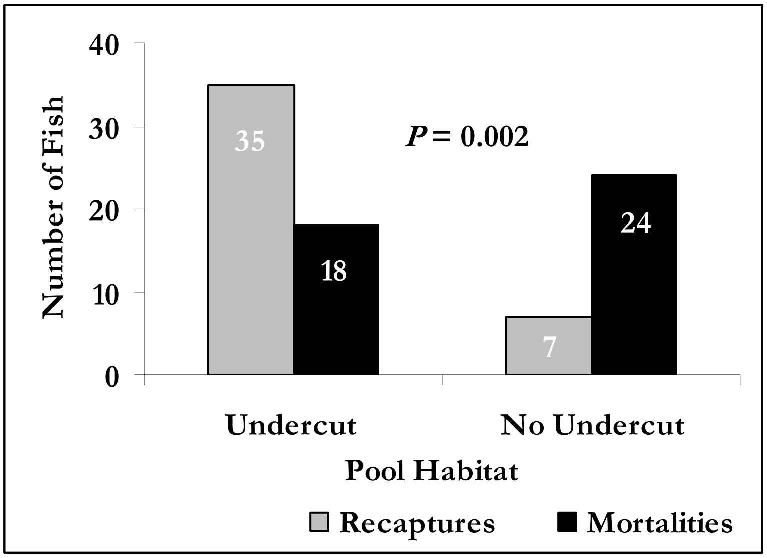

FIGURE 6. Survival rates of LCT detected most often in pools with undercut banks versus pools without undercuts for three reaches in upper Sage Creek. Fish were PIT tagged in June and July and recaptured in November of 2004. *P* value reported was for a X^2 test using Yates' correction for a 2 x 2 table.

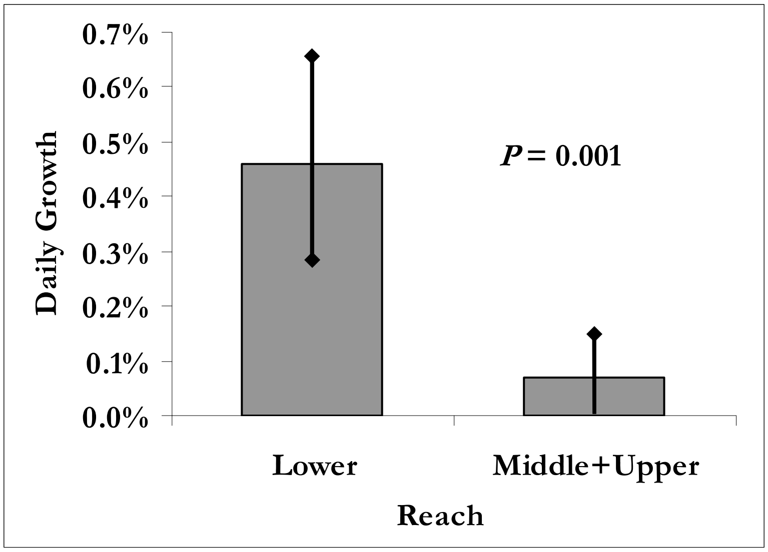

FIGURE 7. Percent daily growth for LCT in three reaches in upper Sage Creek. Values are the median daily increase in biomass between June and November. *P* value shown was from a Mann Whitney U-test of medians. Error bars represent 95% confidence intervals for means.

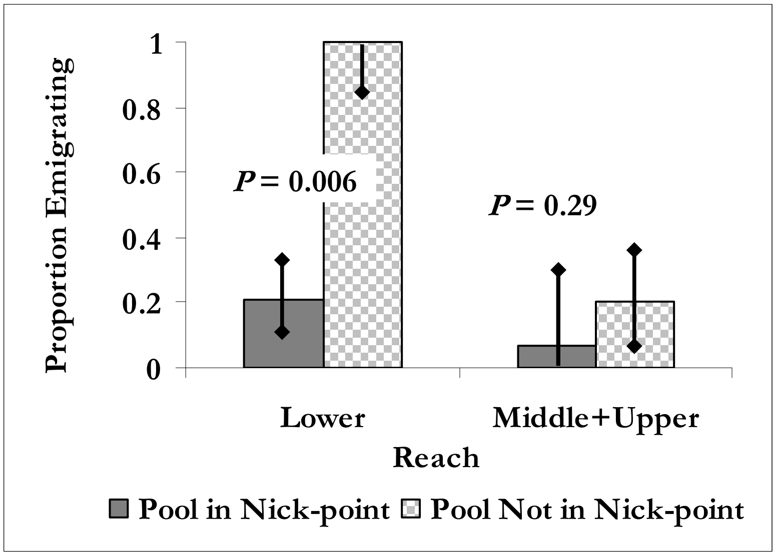

FIGURE 8. The effect of topographic nick-points on the proportion of fish emigrating from pools in three reaches of Sage Creek. *P* value shown was from a Mann Whitney U-test of medians. Error bars represent 95% confidence intervals for means.

DISCUSSION

In this study, I linked LCT distribution to landscape topography, and LCT production to in-stream habitat. At the landscape level, I observed strong relationships between topographic variables related to hyporheic input, deeper, more persistent pools, and LCT distribution patterns. In particular, I found that confined canyon segments with topographic nick-points had greater numbers of LCT than other stream segments. These refugia of cooler, deeper, and more persistent water may be particularly important for LCT during seasonal low water periods or during low precipitation years. Streams with large areas of confined canyon segments punctuated by nick-points, and/or large numbers of nick-points may have more stable populations of LCT or greater lengths of stream occupied by LCT.

At the habitat unit level, I used pool production to link in-stream habitat to areas of LCT production. In relatively warmer reaches most of the LCT production (positive pool scores) occurred in deeper pools with more open canopy cover, while in cooler reaches production occurred (positive pool scores) in pools with greater canopy cover and undercut banks. Temperature also had a strong effect on habitat selection, and nick-point segments, which provided hyporheic input, allowed LCT to extend their distribution into highly productive downstream habitats. While my results offer an increased understanding of LCT behavior, habitat requirements, and the complex relationship between landscape topography, stream flow and temperature, they will also benefit the restoration of LCT in a number of ways.

The recovery of LCT, like the recovery of other threatened and endangered species, faces a number of challenges including: maximizing the benefit from limited human and financial resources, balancing various land-uses with the conservation and restoration of the species, and accurately identifying high quality habitats.

Finite funding restricts both the extent and intensity of restoration efforts. By applying the landscape analysis techniques used in my study to other systems, stakeholders could identify areas with nick-points and confined canyons. Stream systems can then be ranked based on the quantity of these important refugia, enabling managers to prioritize restoration, translocation, reintroduction, and preservation efforts. Such an approach may be especially valuable as a management tool because Digital Elevation Models are widely available, and, as a result, using them to quantify high quality LCT habitat is both more efficient and less expensive than traditional methods such as stream surveys.

My findings can also help integrate various land-uses with the conservation and restoration of LCT. Most of the remaining populations of LCT are located on federal lands. In the interest of developing a successful and cooperative recovery effort, and to fulfill the multiple-use mandates of most federal agencies, managers must balance the interests of land-users with the habitat requirements of LCT. The techniques I presented in my thesis will allow managers to identify important LCT habitats. By providing additional protection to stream segments flowing through these areas, while implementing less restrictive land-use policies elsewhere, one can minimize land-use impacts on LCT populations. For example, cattle can be excluded from confined canyon and nick-point stream segments with little or no hardship to ranchers because steep slopes in these areas make them largely unsuitable for grazing. In turn, water gaps can be located in areas outside of nick-points and confined canyons with little impact on LCT populations.

Finally, by using a metric of pool-specific production to measure habitat quality, I was able to link key habitat features to LCT production and not just to occupancy. While analyses using density to determine habitat quality can fail to differentiate between habitats which have similar densities but different turnover, growth, or survival rates, my analyses avoided this problem by using a response variable incorporating immigration, emigration, mortality, and growth rates. Through the use of these biologically meaningful measurements, I identified habitats that are important for LCT and avoided many of the pitfalls associated with other methods of determining habitat quality. By linking habitat to production, I not only measured habitat quality more accurately, but also linked key habitat features to LCT production, hopefully providing useful guidance for future LCT restoration and monitoring efforts.

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