LIVESTOCK AND ELK GRAZING EFFECTS ON STREAM MORPHOLOGY, BROWN TROUT POPULATION DYNAMICS, MOVEMENT, AND GROWTH RATE, VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

BY

MICHAEL C. ANDERSON, B.S.

A thesis submitted to the Graduate School
in partial fulfillment of the requirements
for the degree
Master of Science

Major Subject: Wildlife Science

New Mexico State University
Las Cruces, New Mexico
May 2009

"Livestock and elk grazing effects on stream morphology, brown trout populations, movement, and growth rate, Valles Caldera National Preserve, New Mexico," a thesis prepared by Michael C. Anderson in partial fulfillment of the requirements for the degree, Master of Science, has been approved and accepted by the following:

____
Linda Lacey
Dean of the Graduate School

____
Colleen A. Caldwell
Chair of the Examining Committee

____
Date

Committee in charge:
Dr. Colleen A. Caldwell, Chair
Dr. Terrell T. Baker
Dr. Robert J. DuBey

VITA

November 15, 1980	Born in Fort Collins, Colorado
May 1999	Graduated from Paradise Valley High School, Phoenix, Arizona
December 2003	B.S. in Zoology, Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona
2005	Fisheries Technician, Montana Fish, Wildlife, & Parks
2006-present	Research Assistant, Department of Fisheries and Wildlife Sciences, New Mexico State University, Las Cruces, New Mexico

Acknowledgments

I would like to thank Dr. Colleen Caldwell for providing me the opportunity to pursue this degree. Your support and enthusiasm throughout my time here has made this experience great. I would also like to recognize my committee members Dr. Robert DuBey and Dr. Terrell Baker, with whom I have had many stimulating conversations over the past three years. I would also like to thank Dr. William Gould for his help analyzing and interpreting the results of this study. The benefit of having such a wealth of experience from a diverse group of mentors was invaluable, and will be a strong base which I can build upon in the future.

Funding for this project was provided by Valles Caldera National Preserve, U.S. Forest Service Rocky Mountain Research Station, T&E Inc., and Trout Unlimited. Support was also provided by the USGS New Mexico Cooperative Fish and Wildlife Research Unit, New Mexico State University, and the Agricultural Experiment Station at New Mexico State University.

I would also like to thank Jesse Berryhill and Rene Galindo who spent many long days in the field under less than ideal conditions–frozen boots and waders, ice dams, the list could go on and on–you guys were a blast to work with. To everyone who has helped me out in the field and in the lab I cannot thank you enough, I would not have been able to get this project done without you. D. Myers, M. Moses, M. Zeigler, H. Halbritter, Z. Tiemann, D. James, K. Romig, J. Schroeder, L. Svejcar, J. Runnels, and J. Garcia, have all been to the Caldera or helped out in the lab at some point and your help was much appreciated.

There are also a number of people I owe special thanks to for making grad school the experience it was. SungJin, Marty, Roger, Darren, and Matt-thanks for keeping things in perspective.

Finally and most importantly, I would not be in this position without the unending support and encouragement of my family. Whether it be one kind of fish bum or another (or sitting on a boat twiddling my thumbs), you have stood behind me and supported me in everything I have done, no matter how crazy it seemed at the time. Anything I have or will accomplish has been a result of what I have learned from you.

Abstract

LIVESTOCK AND ELK GRAZING EFFECTS ON STREAM MORPHOLOGY, BROWN TROUT POPULATION DYNAMICS, MOVEMENT, AND GROWTH RATE, VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

BY

MICHAEL C. ANDERSON, B.S.

Master of Science
New Mexico State University
Las Cruces, New Mexico, 2009
Dr. Colleen A. Caldwell, Chair

Ungulate grazing in riparian areas has been shown to detrimentally impact stream morphology and fish populations. Goals of this research were to assess changes in stream morphology and responses of a brown trout (*Salmo trutta*) population to exclusion of cattle (*Bos taurus*) and elk (*Cervus elaphus*) from riparian areas, and to monitor spatial variability among individual and population level characteristics in brown trout in response to changing biotic and abiotic conditions.

Cattle stocking rates and elk presence inside grazing sites were variable during this study (160-6400 AUM). Riparian forage utilization estimates at stocking rates observed in 2007 and 2008 were below VCNP riparian forage utilization objectives (6-26%). Riparian vegetation communities benefitted from grazing exclosures, with elk exclosures exhibiting greater stubble heights than cattle exclosures and grazed reference sites. Baseline stream morphological data indicated grazing sites with similar cross-sectional measurements prior to exclusion of livestock and elk in 2004. Minimal changes in stream morphology were noted among grazing sites closed to livestock and elk grazing in the five years following the construction of grazing exclosures. Brown trout populations exhibited no response to grazing exclosures between 2004 and 2008. Analysis of marked brown trout showed a population composed largely of resident individuals (65%) with a smaller mobile component (35%). Median displacement distance in all grazing sites was 0 m, which, in combination with similar turnover rates and the proportion of mobile individuals, suggests that grazing exclosures had no effect on trout movement. Growth rates were also similar among grazing sites (range; $\Delta TL=0.061-0.068$, $\Delta W=0.19-0.21$). Brown trout density, biomass, mean total length, and recruitment were similar among grazing sites

Conservative livestock grazing management within VCNP has resulted in forage utilization rates lower than grazing standards, minimizing potential impacts on streams. Livestock and elk grazing in VCNP had no impact on stream morphology or brown trout population and individual level characteristics from 2004 to 2008. Characterization of stream morphological changes and fish population responses in the first five years of grazing exclosures imply that the grazing treatment applied was too minor to observe significant changes among stream habitat and fish population characteristics monitored.

Table of Contents

List of Tables

List of Figures

Introduction

Riparian areas in the southwestern United States have been identified as critical management areas by natural resource agencies. These areas provide integral habitat to many species that evolved in the Southwest, and as such should be assessed for functionality and managed to maintain and restore streamside communities. Historic land use throughout much of the western United States such as timber harvest, mining, road construction, agriculture, and livestock grazing has resulted in degradation of many areas, making the conservation of healthy, functioning riparian systems of even greater importance.

Riparian areas vary greatly depending on watershed basin characteristics and vegetation communities present within different stream systems, making generalized definition `of these areas difficult (Gregory et al. 1991). Riparian zones are broadly defined as the transitional zone between the aquatic and terrestrial systems (Baker et al. 2001). Among the many functions provided by the riparian zone are increased infiltration, filtering of sediment run-off (Lusby 1970), stream shading (Beschta 1997), fish and macroinvertebrate habitat diversity (Kauffman et al. 1983a; Platts and Rinne 1985; Myers and Resh 2000; Bengeyfield 2006) and reduction of fine sediments in the water column (Elmore and Beschta 1987). Connectivity between aquatic and terrestrial systems maintains productivity in the riparian interface, as decreased terrestrial productivity can often be offset by increased aquatic productivity (Baxter et al. 2005). Terrestrial vertebrate species rely on seasonally available emergent aquatic macroinvertebrates for large proportions of their diets (Baxter et al.

2005). Fish species and macroinvertebrate assemblages are also heavily reliant on terrestrial subsidies in the form of terrestrial invertebrates and organic matter from surrounding riparian vegetation (Nakano and Murikami 2001; Allan et al. 2003; Kawaguchi et al. 2003; Baxter et al. 2005). Productivity and stability of aquatic systems are a function of associated riparian vegetation communities, which buffer stream environments from surrounding upland areas.

Impacts of land management practices on riparian and aquatic systems have been widely documented across the western United States in the past 100 years. Livestock grazing has been the focus of many studies, and as such has become the center of great debate. Previous research evaluated stream habitat alterations, fish population dynamics, and riparian disturbances (Rinne 1999). To date, little research regarding individual level fish responses to riparian grazing has been undertaken, and as such a gap in the knowledge base is present. Individual movement and growth rate among brown trout can impact the spatial distribution and abundance in the overall population. Much of this literature is comprised of studies with little baseline data reflecting local scale variation in fish and macroinvertebrate assemblages and stream morphology (Rinne 1988; Li et al. 1994). The absence of baseline data disregards inherent variation in aquatic biota and stream morphology which may be due to watershed characteristics and not land use practices. Research lacking in description of baseline conditions can lead to inaccurate conclusions regarding grazing effects on aquatic systems (Rinne 1988).

Understanding the inherent variability among grazing sites allows a robust comparison of changes in morphology and fish populations that are specifically related to riparian grazing. Spatial variability in the response of stream morphology and fish populations were also assessed using replicated grazing sites across multiple stream reaches within one watershed. In addition, long-term monitoring of fish populations can reveal temporal variation in brown trout populations. The combination of baseline conditions as well as accounting for spatial and temporal variability in stream morphology and trout populations provides accurate identification of the impacts of livestock and elk on aquatic systems.

Goal and Objectives

The overall goal of my research was to evaluate the responses of stream morphology and a brown trout population to riparian grazing exclosure as well as to assess the current state of the brown trout population within the Rio San Antonio, Valles Caldera National Preserve, New Mexico. In accordance with the multiple use mandate of the Valles Caldera Preservation Act, VCNP is required to maintain livestock grazing, as well as provide recreational angling and elk hunting opportunities. Determination of the impacts of cattle and elk on the aquatic systems was necessary to identify specific management objectives for livestock grazing as well as elk population levels. The objectives of this research were to:

1) Assess the impact of livestock and elk grazing on stream morphology;
2) Determine the response of brown trout populations to riparian grazing; and
3) Evaluate the influence of biotic and abiotic factors on the spatial distribution of brown trout within Rio San Antonio.

Literature Review

State of Riparian Communities

Riparian areas in the western United States comprise approximately 2% of the total land area (Chaney et al. 1993). Due to the diversity of vegetation in riparian zones, these areas account for a large portion of the productivity of southwestern landscapes. Natural resource agencies have identified these communities as critical management areas, as many are in poor or degraded condition (Armour et al. 1994).

Countless land use activities contribute to the degradation of these systems including logging, mining, road construction, agriculture, and livestock grazing. Previous work has identified livestock grazing as the single most influential human caused disturbance altering riparian habitat (Kauffman and Krueger 1984; Armour et al. 1994; Elmore and Kauffman 1994; Li et al. 1994). However, while several land use practices have been implicated in the degradation of streamside habitat, other studies have identified the risk of classifying specific cause and effect relationships without regard to larger scale watershed characteristics which may intrinsically make specific lotic systems more susceptible to human caused disturbance (Nelson et al. 1992; Long and Medina 2006).

Functions of Riparian Areas

Streamside communities perform integral processes that stabilize, buffer and sustain aquatic systems. High resilience and resistance to disturbance is a characteristic of healthy riparian zones and is a function of compositional, structural, and functional diversity (Elmore and Kauffman 1994; Kauffman et al. 1997).

Vegetation communities along waterbodies have adapted to rapidly shifting conditions associated with seasonal flooding and other naturally occurring events (Naiman et al. 1993). In the presence of healthy riparian vegetation, these events play a dynamic role in the formation and alteration of stream morphology (Kauffman et al. 1997). Riparian zones increase microhabitat biodiversity, maintain water quality and quantity, provide habitat for fish and macroinvertebrates by increasing niche availability, and link the aquatic and terrestrial systems within food webs.

Stream morphology is determined initially on the watershed scale, influenced by basin morphology, geology, and land use. These factors determine major stream characteristics such as substrate size, gradient, and sinuosity. Local scale variables that impact stream morphology are stabilized by streamside vegetation, which functions not only to strengthen streambanks but also to maintain both habitat and biotic diversity within the system. Vegetation anchors streambanks decreasing erosive potential of flood events and allowing the creation of habitat such as undercut banks which are important to fish species (Platts and Rinne 1985; Bengeyfield 2006) and aquatic macroinvertebrates (Myers and Resh 2000). Overhanging vegetation and root structure extending into the water column also provides critical rearing habitat for larval and juvenile fish (Casselman and Lewis 1996), organic matter consumed by aquatic invertebrates (Flory and Milner 1999), and reduction in the amount of fine sediments in the water column (Elmore and Beschta 1987). Vegetation stem and root structure allows aggradation of streambanks, increasing habitat complexity and maintaining the natural biodiversity of the system (Gregory et al. 1991). Flow initiated erosion removes substrate from the outside bank of meanders and deposits substrates downstream in areas of low stream flow. Accumulation of sediments in these areas renews streams as vegetation rapidly makes use of newly available habitat. Continuous habitat turnover results in the presence of several seral stages, increasing the resilience and recovery of streamside communities during disturbance events (Gregory et al. 1991). Over time, stable streambanks allow channels to narrow and deepen, reducing solar radiation input thereby maintaining lower water temperatures (Schulz and Leininger 1990; Gregory et al. 1991; Naiman et al. 1993; Platts and Rinne 1985; Beschta 1997). Habitat complexity increases niche availability in aquatic systems, and thereby increases biodiversity of both fish and aquatic macroinvertebrate assemblages.

Water quality and quantity are also under the influence of streamside vegetation, both above and below surface biomass. Above-ground vegetation slows runoff from surrounding upland areas allowing increased infiltration, resulting in shallow water tables, sustaining streamflow during low flow periods while also providing constant water supply for streamside vegetation (Lusby 1970). Streamside vegetation and root structure extending into the water column filters fine sediments decreasing turbidity and reducing embeddedness (Elmore and Beschta 1987; Platts 1990). Insulation of lotic systems by riparian vegetation buffers streams during elevated summer temperatures and low winter temperatures (Beschta 1997). By ameliorating minimum and maximum temperatures, aquatic systems are stabilized providing favorable conditions for aquatic biota.

Connectivity between the aquatic and terrestrial systems may be the most important function of riparian zones in maintaining productivity of both systems.

Organic inputs from streamside vegetation provide nutrients and cover for aquatic invertebrates (Flory and Milner 1999) and some fish species. Terrestrial invertebrates make up a significant portion of the annual diet for many fish species with consumption rates between 44 and 86% of their total diet (Nakano and Murikami 2001; Allan et al. 2003; Kawaguchi et al. 2003; Baxter et al. 2005). Emergent aquatic macroinvertebrates provide an important seasonal food source for many terrestrial species including birds, bats, amphibians, and reptiles (Baxter et al. 2005). Nakano and Murikami (2001) determined that utilization of aquatic macroinvertebrates accounted for between 50 and 90% of the annual diet among riparian bird species.

Riparian Grazing Effects

Various livestock grazing strategies are currently employed to control utilization rates, stocking density, and to decrease disproportionate use of preferred vegetation types. Each grazing strategy leads to differential use of vegetation communities and changes in vegetation productivity. Cattle have exhibited seasonal preference for streamside vegetation which may be due to range management practices, favorable abiotic conditions, and type of cattle grazed. Gillen et al. (1984) demonstrated that 47% of the total forage utilization occurred on only 5% of the pasture, and that during certain time periods cattle remained within 200 m of water at all times. Roath and Krueger (1982) observed a disproportionately high use in riparian areas soon after cattle were turned onto pasture with gates that opened directly into the riparian zone. Cattle soon dispersed occupying most vegetation types within the pasture, suggesting that early preference for riparian areas was due to cattle being put onto the pasture in the riparian areas rather than preference for riparian vegetation. In a study comparing utilization rates among cow-calf pairs and yearling steers, Bryant (1982) observed streamside areas were occupied at higher rates by cow-calf pairs than by yearlings due to increased energetic requirements and favorable temperatures. Pasture topography and slope have also influenced utilization rates. Cattle grazed less in areas with increased slope (>35%), resulting in the concentration of grazing activities in the riparian zone (Bryant 1982; Kie and Boroski 1996).

Availability of water and forage appears to be the greatest driving force in cattle utilization rates. Improvement in cattle distribution can be accomplished through the addition of off-stream water (Stillings et al. 2003), nutrient supplements (Bailey 2004), and fencing riparian corridors within larger pastures (Platts and Wagstaff 1984). Off-stream water has shown potential benefits for livestock producers, streamside vegetation communities, and aquatic habitat conditions. Development of water availability in upland areas had a positive influence on distribution and forage utilization in upland pasture (Platts and Nelson 1985; McInnis 2001; Stillings et al. 2003). Streambank cover and increased bank stability decreased erosion, which were positively influenced by alternative water sources (McInnis and McIver 2001). Increased utilization of upland areas allowed livestock producers to leave cattle in pastures for longer periods of time while still maintaining utilization rates less than 35% (prescribed levels) for streamside vegetation (Stillings et al. 2003). Fencing pasture into homogenous areas such as upland and streamside vegetation communities was also proposed (Kauffman et al. 1983a; Platts and

Wagstaff 1984). This tactic shows potential for success, however, high initial costs of erecting long sections of fence combined with yearly maintenance and loss of pasture may make the implementation of this strategy unfeasible for many livestock producers (Platts and Wagstaff 1984).

Rest-rotation systems provide longer periods of rest between grazing events, allowing significant regeneration of plant material during each rest cycle. Infiltration rates were reported to be similar to those found in ungrazed controls due to increased amounts of ground cover (Bohn and Buckhouse 1985). Evaluation of stocking rates based on goals for utilization rates under this system resulted in better use of all forage types, however, overuse can nullify improvements in forage availability and aquatic habitat rapidly (Platts and Nelson 1985).

Early season grazing (spring or early summer) provides regeneration time after grazing has ceased. Regenerated vegetation buffers stream systems during low winter temperatures and high spring flow events. Forage quality during early grazing promotes even distribution of cattle across all vegetation types, increasing cattle productivity while decreasing grazing pressure on streamside communities (Clary and Webster 1989). Decreased utilization of streamside vegetation was driven by increased palatability of upland vegetation and favorable climatic conditions such as lower temperatures in both upland and riparian pasture (Clary and Booth 1993; Parsons et al. 2003). Proportional distribution and utilization rates can benefit both livestock producers and aquatic systems, as indicated by longer periods of grazing in each pasture and stream channel narrowing and deepening and increased substrate size (Clary 1999).

Late season (late summer or fall) grazing has shown potential benefits for both aquatic systems and livestock producers through proportional distribution between upland and riparian areas. Management of forage utilization during this period requires that minimum residual stubble heights be maintained, allowing vegetation to stabilize streambanks during spring high flow events (Clary and Webster 1989). Cattle distribution during this time may be a function of abiotic conditions such as temperature (Roath and Krueger 1982) and decreased forage quality and quantity of riparian vegetation (Bryant 1982; Kauffman et al. 1983b). Streamside vegetation was not negatively impacted during this time as cattle distribution and forage utilization were associated with both upland and streamside vegetation communities. Late season grazing also resulted in less trampling which reduced soil compaction, increasing infiltration (Sedgwick et al. 1991).

Season-long and continuous grazing leads to the heaviest use of streamside vegetation communities due to cattle preference for these areas. The result is inadequate forage use in upland areas, disproportionate use of forage types, and potential degradation of aquatic systems due to heavy utilization of streamside vegetation (Meehan and Platts 1978). Vegetation removal in combination with trampling throughout the growing season resulted in decreased infiltration and increased sediment transport into aquatic systems (Lusby 1970; McEldowney 2002; Bohn and Buckhouse 1985; Flenniken et al. 2001). Vegetation community structure was altered by high utilization rates, with preferred forage being replaced by less utilized species (Leege et al. 1981). This shift in species composition can result in the destabilization of aquatic systems, as riparian species may be replaced with vegetation adapted to xeric areas. Depaupered streamside vegetation can result in loss of streambanks due to erosion, which leads to channels becoming wider and water depth decreasing, both of which may lead to increased water temperatures and negative impacts on fish assemblages (Platts and Rinne 1985).

Deferred rotation grazing has been shown to have similar cattle utilization as season-long continuous grazing (Bohn and Buckhouse 1985; Gillen et al. 1984), but does provide periodic rest for portions of pastures which may allow recovery of plant species after grazing. Providing time for vegetation to recover between grazing events has the potential to maintain and improve aquatic habitat conditions. High quality pools and some bank recovery were noted within aquatic systems in pastures under deferred rotation grazing after a long period of continuous grazing (Myers and Swanson 1995).

Vegetation species such as sedges (*Carex* sp.) can be obligate riparian species requiring access to permanent water. These species have adapted to withstand disturbance events more readily than are species with shallow root systems (*Poa* sp.), which are facultative riparian species (Case and Kauffman 1997). Presence of resilient vegetation provides stability within the system, leading to streambank recovery and dynamic stream functions such as bank aggradation. Evaluation of aquatic and streamside habitat regeneration after exclusion has shown recovery and improvement in many cases allowing increased habitat complexity to maintain ecological stream processes (Schulz and Leininger 1990; Myers and Swanson 1995).

High resilience of riparian vegetation and the ability to recover rapidly after disturbance events facilitates regeneration of vegetation in the riparian zone when additional human-caused disturbances are removed. Under exclusion of livestock, riparian vegetation communities stabilize streambanks over long periods of time, leading to decreases in channel and wetted width, and width to depth ratio (Myers and Swanson 1995; Magilligan and McDowell 1997). Kondolf (1993) cautioned, however, that narrowing channels may be a function of increased vegetation cover and that stream channel improvement may take many years depending on watershed characteristics. Research on livestock grazing exclosures has noted shifts in riparian vegetation after cessation of grazing in northern Colorado. Inside grazing exclosures, riparian communities were dominated by sedges, while shallow rooted grasses dominated pastures outside the exclosures (Schulz and Leininger 1990). Similar research concluded that width–depth ratios within grazing exclosures were lower, bank stability increased by 40%, and overall substrate size increased by 15%, compared to the grazed reaches (Myers and Swanson 1995). Dobkin et al. (1998) determined that ground cover was positively related to grazing exclosures with 73% ground cover provided by shrubs inside exclosures, while bare ground and litter made up 89% of the cover in grazed areas.

Vegetation communities have been shown to be positively impacted by grazing through the removal of excess biomass, litter, (Clary and Webster 1989), and increased species richness under light and moderate grazing intensity management (Courtois et al. 2004; Holechek et al. 2006). Evaluation of proper stocking rate, forage utilization, timing of grazing, and proper management of livestock can positively impact range conditions leading to increased production of forage (Holechek et al. 2006).

Although elk and cattle utilize similar vegetation communities, the species occupy spatially distinct habitat types. During summer grazing periods, elk utilize areas with higher slopes than those occupied by cattle. This spatial separation provides a period of recovery for heavily used forage (Torstenson et al. 2006). Complex interactions such as time of use by livestock had positive impacts on elk populations. Elk utilization during winter increased in areas grazed by cattle the previous summer and fall (Torstenson et al. 2006). Specialized grazing systems were developed in Arizona allowing simultaneous use by elk and cattle using a system similar to deferred rotation with alternatively grazed and rested pastures. Pastures containing only elk had forage utilization rates of 20-24%, while pastures with both cattle and elk had utilization rates nearing 46% (Halstead et al. 2002) exceeding suggested forage utilization rates of 30-40% (Holechek et al. 1998). While forage utilization exceeded suggested levels, residual stubble height remained above minimum levels, demonstrating the importance of assessing several range characteristics when determining proper stocking rates (Halstead et al. 2002). Livestock exclosure studies exhibited high utilization by deer and elk which retarded the regeneration of forage species such as willow and aspen (Kay 1994; Case and Kauffman 1997; Opperman and Merenlender 2000; Ripple et al. 2000), nullifying any positive effects of livestock exclusion.

Livestock-Fishery Interactions Research Design Problems

Research regarding the interaction between livestock grazing and aquatic systems has commonly been based on author observation and opinion (Platts 1982), poor data collection, little pretreatment data (Rinne 1988), unidentified stocking rates (Li et al. 1994), scale considerations (Li et al. 1994; Clarkson and Wilson 1995), and improper statistical analysis (Clarkson and Wilson 1995; Larsen et al. 1998). Drawing comparisons among systems is inappropriate due to the complex nature of aquatic systems and variation among stream systems throughout different regions. Drawing conclusions based on effects of grazing without baseline data comprises one of the most common faults of fisheries professionals to date. Careful thought and planning should be applied using studies designed to account for these local variations in habitat quality and complexity. Watershed scale variables were not considered when Clarkson and Wilson (1995) concluded that the influential factors determining trout biomass was ungulate-caused bank damage and channel width. In their review of model components and statistical analysis performed by Clarkson and Wilson (1995), Long and Medina (2006) determined that ungulate caused bank damage had minimal effect on trout biomass. In addition, modified statistical analysis including geologic variation among sampled watersheds accounted for the majority of differences among biomass from sampled trout populations. Studies failing to account for large scale watershed effects on fish assemblages often mislead future research considerations, and may also alienate livestock producers and private landowners (Long and Medina 2006).

In Li et al. (1994), scale and baseline conditions were not considered in research design, land uses other than cattle grazing were ignored, and large areas (21,000 km^2), which encompassed several streams were compared. Variation among streams was described extensively in the methods, but was largely ignored when conclusions stated that livestock grazing was the most influential factor effecting trout abundance (Li et al. 1994). Unknown factors such as historic salmonid distribution and different land use practices were not discussed with relation to observed conditions.

Livestock Grazing Effects on Riparian Vegetation and Stream Morphology

Disproportionate use of riparian areas in relation to their availability often occurs in the southwest due to the productivity of riparian areas as well as perennial sources of water. Much of the riparian habitat in the western United States has been altered, degraded, or fragmented by a host of human-caused factors (National Research Council 2002), making preservation and restoration of these ecosystem components an immediate priority. Livestock grazing impacts can be excessive in riparian ecosystems due to the aridity of many western rangelands (see Kauffman and Krueger 1984; Platts 1991; Larsen et al. 1998; Belsky et al. 1999 for reviews).

Streamside communities perform integral processes that stabilize, buffer and sustain aquatic systems. Riparian vegetation is adapted to rapidly shifting conditions associated with seasonal flooding and other naturally occurring events (Naiman et al. 1993). In the presence of healthy riparian vegetation, high streamflow events perform a dynamic role in the formation and alteration of stream morphology, creating instream fish habitat, moderating detrimental effects of high discharge, and providing allochthonous organic input to lotic systems (Naiman and Decamps 1997; Kauffman et al. 1997; Baxter et al. 2005).

Deep-rooted riparian species such as sedges (*Carex* spp.) and rushes (*Juncus* spp.) armor streambanks allowing creation of instream habitat such as undercut banks which are important to fish species (Platts and Rinne 1985; Simon and Collison 2002; Bengeyfield 2006). Overhanging vegetation and root structure extending into the water column also provides critical rearing habitat for larval and juvenile fish (Casselman and Lewis 1996), organic matter for aquatic invertebrates (Flory and Milner 1999), and reduction in the amount of fine sediments (Elmore and Beschta 1987). Vegetation stem and root structure allows aggradation of streambanks, increasing habitat complexity and maintaining the natural biodiversity of the system (Gregory et al. 1991). Flow-initiated erosion mobilizes substrate from the outside bank of meanders and deposits substrates downstream in areas of low stream flow. Downstream deposition of sediments creates new habitat for riparian vegetation, creating a dynamic equilibrium between erosion and deposition, further stabilizing lotic systems (Leopold et al. 1964). Habitat turnover results in the presence of several seral stages, increasing the resilience of riparian communities during disturbance events (Gregory et al. 1991). Over time, stable streambanks allow channels to narrow and deepen, reducing solar radiation input, thereby maintaining lower water temperatures (Schulz and Leininger 1990; Gregory et al. 1991; Naiman et al. 1993; Platts and Rinne 1985; Beschta 1997; Summers et al. 2005).

Livestock grazing has been shown to cause shifts in riparian vegetation from sedge and rush dominated communities to more xeric grass and shrub species (Belsky et al. 1999). Shifts in riparian vegetation to shallow-rooted grass species such as Kentucky bluegrass (*Poa pratensis*), may have significant implications to streambank stability in meadow streams. Livestock grazing may increase (van der Maarel and Tityanova 1989), decrease (Biondini et al. 1998), or have no effect (McNaughton et al 1998) on root biomass, however, physiological differences in overall root characteristics among vegetation species may result in decreased streambank shear strength (Micheli and Kirchner 2002). Removal of vegetation and compaction of soils by large herbivores has been determined to decrease infiltration, resulting in increased runoff in heavily and moderately grazed pastures (Kauffman and Krueger 1984). Increased runoff due to watershed disturbance has potential to significantly alter channel morphology (Minshall et al. 1997), resulting in stream habitat conditions which may adversely impact aquatic biota.

Physical breakdown of streambanks as a result of livestock trampling has also been shown to detrimentally impact channel morphology. Comparisons of ungrazed and grazed sections of a stream in eastern Oregon showed loss of undercuts, greater amounts of sloughing streambanks and bank collapse all contributing to loss of fish and aquatic macroinvertebrate habitat (Kauffman et al. 1983a). In studies performed on the same river in southern Montana, Gunderson (1968) and Marcuson (1977) determined that livestock grazing resulted in increased channel width as a combined result of streambank sloughing and loss of streamside vegetation which resulted in increased erosion during high flow events. Knapp and Matthews (1996) noted significant differences in channel width and channel depth when comparing channel morphology inside and outside grazing exclosures in California. Similar findings were documented by Magilligan and McDowell (1997) in 14 year-old grazing exclosures, as channel width decreased 10-20% in ungrazed areas. Channel response to livestock exclosure varies, as several studies noted minimal changes in stream habitat conditions in exclosures which had been functioning for 4 to 24 years (Rinne 1988; Kondolf 1993; Overton et al. 1994). Factors other than livestock grazing may have been limiting channel recovery including continued disturbance in the watershed upstream from grazing exclosures and lack of fine sediment delivery necessary for streambank aggradation (Kondolf 1993). Species most heavily impacted by increased sediment loads included benthic feeding and spawning species such as cyprinids and salmonids (Jones et al. 1999).

Erosion caused by streambank trampling can lead to increases in fine sediments resulting in degradation of water quality, a decrease in the proportion of coarse stream substrate, and a decrease in streambank stability. Increasing fine sediment loads can alter fish assemblage structure as fish species adapt to changing conditions or migrate to find suitable habitat (Platts 1981; Platts and Nelson 1984). Embeddedness (the degree to which coarse substrate is surrounded by fine sediments) was negatively impacted by increased fine sediment loads, with reductions in habitat for aquatic macroinvertebrates, entrapment of substrate distributed eggs, and decreased rearing habitat for larval and juvenile fish (Platts 1981). Personal observations described by Platts (1981) were supported by Jones et al. (1999) during which increased fine sediments due to streamside forest removal altered fish assemblages.

Exclusion of livestock from streamside areas may result in improved vegetation communities, leading to recovery and regeneration of streambank stability and gradual improvement of fish habitat. In a comparison of grazed and ungrazed stream reaches increased erosion outside exclosures decreased aquatic macroinvertebrate density (Wohl and Carline 1996), resulted in the loss of undercut banks (Kauffman et al. 1983a), and decreased salmonid biomass and abundance (Keller and Burnham 1982; Platts and Nelson 1985). Under heavy utilization, aquatic conditions can be altered through the loss of streambanks which decreases the number of undercut banks. Comparisons of ungrazed and grazed sections of a stream in eastern Oregon showed loss of undercuts, greater amounts of sloughing streambanks and bank collapse all contributing to the loss of fish and aquatic macroinvertebrate habitat (Kauffman et al. 1983a).

Research evaluating the influences of wild ungulates on riparian ecosystems has generally focused on the impacts on woody vegetation communities. Deer (*Odocoileus* spp.) and elk have been shown to retard regeneration of woody browse species inside cattle exclosures (Opperman and Merenlender 2000) nullifying any potential effects of livestock exclusion. Elk have also been shown to have negative impacts on cottonwood (*Populus* spp.) recruitment (Beschta 2005) and willow (*Salix* spp.) regeneration (Singer et al. 1994) when disproportionate use of riparian areas occurs. Though little research has focused on the direct effect of wild ungulates on stream morphology inference can be drawn from literature regarding the impact of large herbivores on riparian vegetation, and the negative influence of degraded riparian conditions on stream habitat.

Livestock and elk grazing may also have differential effects on stream morphology based on the channel type as well as the dominant substrate found within each system (Rosgen 1994). Meadow streams with smaller substrate are more vulnerable to detrimental impacts of livestock grazing, as the fine substrate dominated systems typically erode at a higher rate than do streambanks armored by larger substrates (Myers and Swanson 1992). Understanding variability among systems prior to assessment of land-use practices is integral to the success of any management objective.

Stream Fish Response to Livestock Grazing

Salmonid responses to management of riparian grazing is best described as an interaction between the pressure imposed on riparian vegetation by grazing and the stabilizing functions provided to lotic systems by riparian vegetation. Current management is focused on controlling the impact of grazing on streams by managing the season, intensity, and duration of grazing plans (Clary and Kruse 2004). By managing riparian grazing in this manner, negative impacts of livestock may be minimized over time. Reduction or elimination of grazing, or construction of grazing exclosures may be necessary under severely degraded conditions.

Research regarding population level changes in stream fish due to livestock grazing has focused on stream habitat characteristics and game fish, with few of these studies having any data concerning spatial variability among study reaches prior to exclosure (see Rinne 1999 for review). Among this research, positive responses of stream fish have been widely reported following the removal of grazing or construction of exclosures. Higher adult density and biomass in ungrazed sites in comparison to grazed reaches has been shown (Gunderson 1968; Marcuson 1977; Summers et a. 2008). Increased fish length due to higher growth rates or emigration of large individuals into ungrazed areas has been noted in several studies (Marcuson 1977; Keller and Burnham 1982; Saunders and Fausch 2007; Summers et al. 2008). Knapp and Matthews (1996) reported an increase in juvenile trout inside grazing exclosures.

While increased populations have been noted, other studies have reported no change in trout populations following livestock exclosure. Chapman and Knudsen (1980) compared grazed and ungrazed sites and found no difference among young-of-year and adult salmonids. Platts and Nelson (1985) noted improvements in stream habitat within grazing exclosures, however, no change in trout density was observed. Variability in the recovery of trout populations following the elimination of grazing suggests that factors other than riparian vegetation communities or instream habitat may be influencing salmonid populations.

Relationships between healthy riparian vegetation and increased terrestrial input exhibit the importance of the aquatic-terrestrial food web link (see Baxter et al. 2005 for review). Terrestrial invertebrates make up a significant portion of the annual diet for many fish species with consumption rates between 44-86% of their total diet (Nakano and Murikami 2001; Allan et al. 2003; Kawaguchi et al. 2003). Increases in terrestrial invertebrate abundance inside grazing exclosures and among well managed allotments has been shown (Allan et al. 2003; Wipfli and Musslewhite 2004; Saunders and Fausch 2007). The abundance of terrestrial invertebrates in streams may result in increased growth among salmonids, which would be a function of improved grazing management. Increased fish size has been noted in several studies suggesting that availability of resources may be greater inside exclosures and less variable over a temporal scale (Marcuson 1977; Keller and Burnham 1982; Summers et al. 2008). Increased fish size may be a function of increased growth rate among juvenile fish which can lead to later onset of maturity due to fitness benefits gained by increased reproductive potential (Hutchings 1993). Kawaguchi et al. (2003) showed that reduction of terrestrial input resulted in a 50% decline in biomass in a trout population.

Spatially variable food resources may lead to differential growth rates and movement among individual fish in an attempt to locate foraging areas where food can be obtained at a rate which maximizes growth. Growth rates among trout vary with respect to temperature (Elliott et al. 1995), food availability (Cada et al. 1987), and fish abundance (Bohlin et al. 2002). Growth rate research for brown trout is based on work of Elliott (1975a, 1975b), evaluating optimal growth temperature among brown trout under laboratory conditions. Further research has validated the findings of laboratory experiments under natural conditions, concluding that optimal growth generally occurs around 13°C, with some variability among populations at lower (6-8°C; Jensen et al. 2000) and higher temperatures (14-16°C; Allen 1985; 15-16°C; Jensen and Berg 1995).

Movement

Research evaluating movement behavior among stream fish typically follows one of two hypotheses. Restricted movement, proposed by Gerking (1959), suggests that stream fish are relatively sessile, occupying small home ranges. Results of many studies have supported this hypothesis (Bachman 1984; Hesthagen 1988; Burrell et al.

2000). Opponents of the restricted movement hypothesis suggest that previous research regarding movement patterns were inaccurate due to limitations in study design (Gowan et al. 1994). Rodriguez (2002) suggested that current understanding of movement patterns may be incomplete. Inclusion of parameters such as population turnover rate decreases the reliance on physical relocation of marked individuals. Assessment of the proportion of the population that immigrates over a given time provides additional information accounting for local movement into study areas (Rodriguez 2002). Movement behavior exhibited by individual fish was shown to follow similar patterns across species, with leptokurtic frequency distributions commonly reported (Harcup et al. 1984; Heggenes et al. 1991; Gowan and Fausch 1996). Leptokurtic distributions are characterized by a higher central peak and longer tails representative of individuals exhibiting exploratory behavior, or boldness which is defined as the propensity to move through and explore unfamiliar areas (Russell 1983; Wilson et al. 1993). Fraser et al. (2001) proposed exploratory behavior as the explanation for leptokurtosis as similar distributions have been noted after controlling for variable effects of age, size, and social status. Increased movement may benefit individuals by increasing the probability of encountering spatially and temporally variable resources (Gowan and Fausch 2002; Hilderbrand and Kershner 2004).

Study Area

Valles Caldera National Preserve

Valles Caldera National Preserve (VCNP) initially existed as the Baca Location Number 1 land grant ranch. The land grant covered 100,000 acres in the

Jemez Mountains, northern New Mexico, and was officially recognized in 1876 by the United States government. During the next 120 years, the ranch passed through the ownership of several private entities prior to federal acquisition. While in private possession, the ranch was grazed by cattle and sheep, mineral and geothermal exploration occurred, as well as extensive timber harvest.

Valles Caldera National Preserve (VCNP) was acquired by the federal government in 2000 through the Valles Caldera Preservation Act. VCNP encompasses approximately 36,000 ha (89,000 acres) with elevations ranging from 2600 m on the valley floors to 3400 m at the summit of Redondo Peak (Figure 1). Approximately 25,000 acres of the preserve are highly productive grassland meadows which formed in the remnant volcanic caldera. Dominant soils in Valle San Antonio and Valle Toledo are composed of Cosey-Jarmillo association, which are deep, well drained, and moderately permeable soils (USDA 2008). Riparian vegetation communities are composed of sedges (*Carex* spp.), bunchgrasses (*Fescuta* and *Phleum* spp.), sod-forming grasses (*Poa* spp.), and forbs.

Rio San Antonio

Two major drainages within VCNP are the East Fork Jemez River and Rio San Antonio, which are the major tributaries to the Jemez River in the middle Rio Grande watershed. Rio San Antonio is a second order stream draining approximately 120 km^2 flowing east to west across the northern boundary of VCNP, with headwaters in the Sierra de los Valles near the east boundary of the preserve (Figure 1). The stream is characterized according to the Rosgen (1994) scale as a C-4 type stream, characterized by well developed floodplain, moderate width/depth ratios (5.6-8.9), high sinuosity (1.7-2.4), low gradient (1-1.5%), and gravel substrate. Throughout VCNP, Rio San Antonio is bordered by 2-3 km wide grassland meadows surrounded by mixed conifer forests. Channel width increases progressively downstream ranging from 9.5 to 16.5 m, while wetted width ranges from 3.4 to 5.4 m.

Study Design

Grazing exclosures (2.56 ha) were constructed in upper (SAUR), middle (SAMR), and lower (SALR) reaches of the Rio San Antonio watershed during fall 2003 (Figure 1). References sites open to all grazing were present at each reach to assess the combined impacts of cattle and elk on aquatic systems. Cattle exclosures were constructed of four strand fencing approximately 1 m in height, with smooth top and bottom strands, allowing elk grazing. Elk and cattle exclosures were constructed of woven wire mesh (0.10 cm^2 opening) 2 m in height and were anchored into the ground preventing access to any large herbivores. Within each stream reach on Rio San Antonio (lower, middle, upper), one grazed reference and two grazing exclosures were present; 1) grazing by both elk and cattle (OPEN), 2) cattle exclosure, elk grazing (CATTLE), and 3) cattle and elk exclosure, no grazing (ELK) (Figure 1).

Exclosures vary in longitudinal placement from upstream to downstream due to logistical constraints which required that CATTLE and ELK sites be constructed adjacent to each other. On Rio San Antonio Creek, grazing exclosures are arranged in the following order from upstream to downstream; ELK, CATTLE, OPEN (upper reach), OPEN, CATTLE, ELK (middle reach), and OPEN, CATTLE, ELK (lower reach). The middle Rio San Antonio stream reach differs from both upper and lower sites in that the ELK exclosure is separated from the OPEN and CATTLE sites by approximately 500 m downstream.

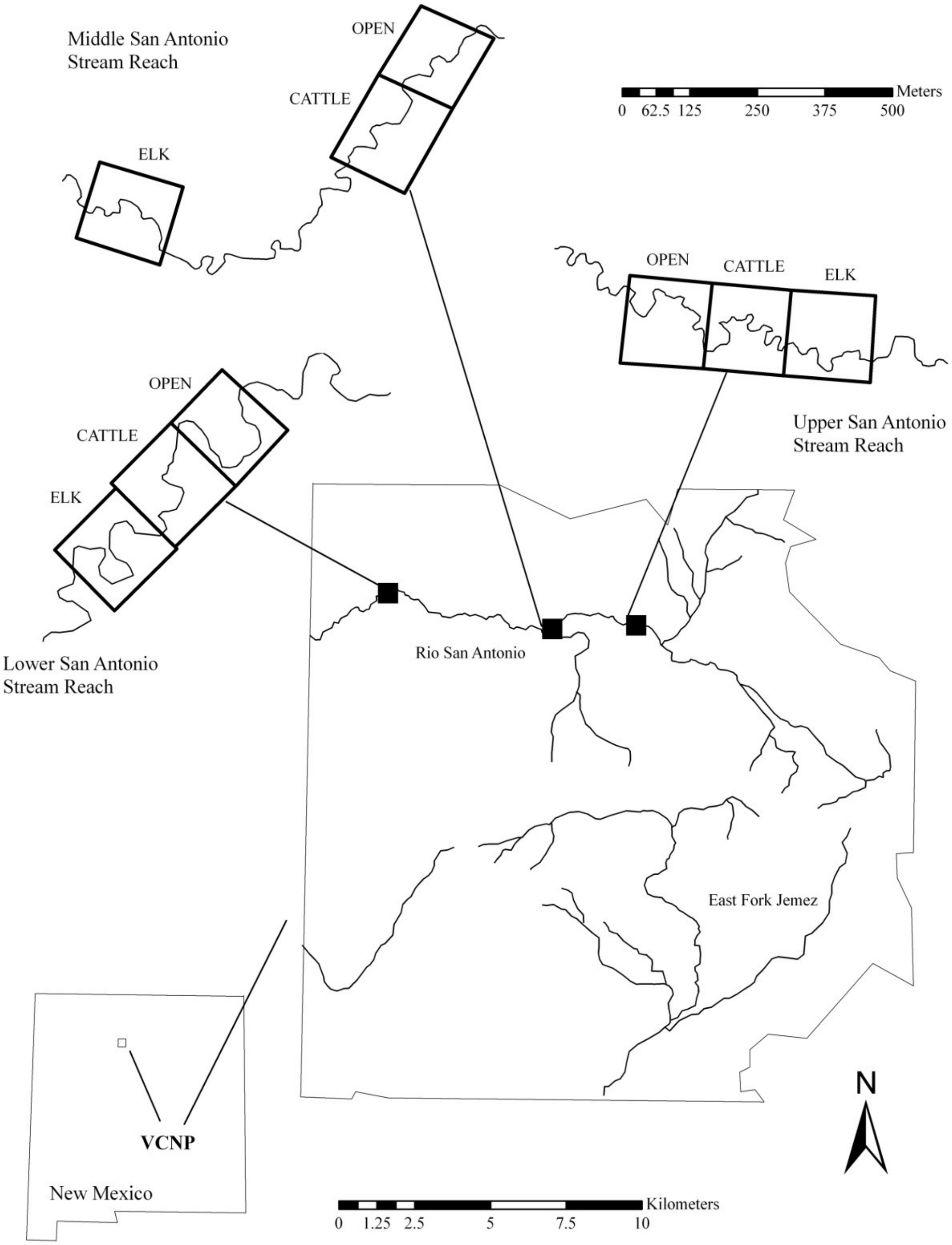


Figure 1: Location of Lower, Middle, and Upper stream reaches along Rio San Antonio, Valles Caldera National Preserve, New Mexico. Grazing sites (■) within the drainage were established to capture longitudinal variation along Rio San Antonio. Grazing exclosures (□) were established to monitor livestock and elk grazing impacts.

Literature Cited

Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60:309-320

Allen, K. R. 1985. Comparison of growth rate of brown trout (*Salmo trutta*) in a New Zealand stream with experimental fish in Britain. Journal of Animal Ecology 54:487–495.

Armour, C., D. Duff, and W. Elmore. 1994. The effects of livestock grazing on western riparian and stream ecosystems. Fisheries 19(9):9-12

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1–32.

Bailey, D.W. 2004. Management strategies for optimal grazing distribution and use of arid rangelands. Journal of Animal Science 82:147–153.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54: 419–431.

Bengeyfield, P. 2006. Managing cows with streams in mind. Rangelands 28:3–6.

Beschta, R.L. 1997. Riparian shade and stream temperature: An alternative perspective. Rangelands 19:25–28

Beschta, R. L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. Ecology 86:391–403.

Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecological Applications 8: 469–479.

Bohlin, T., L. F. Sundstron, J. I. Johnsson, J. Hojesjo, and J. Pettersson. 2002. Density–dependent growth in brown trout: effects of introducing wild and hatchery fish. Journal of Animal Ecology 71:683–692.

Bohn, C.C., and J.C. Buckhouse. 1985. Some responses of riparian soils to grazing management in northeastern Oregon. Journal of Range Management 38:378-381

Bryant, L.D. 1982. Response of livestock to riparian zone exclusion. Journal of Range Management 35:780–785.

Burrell, K. H., J. J. Isely, D. B. Bunnell Jr., D. H. Van Lear, and C. A. Dolloff. 2000. Seasonal movement of brown trout in a southern Appalachian River. Transactions of the American Fisheries Society 129:1373–1379.

Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. Transactions of the American Fisheries Society 116:692–702.

Case, R.L., and J.B. Kauffman. 1997. Wild ungulate influences on the recovery of willows, black cottonwood and thin- leafed alder following cessation of cattle grazing in northeastern Oregon. Northwest Science 71:115–126

Casselman, J.M., and C.A. Lewis. 1996. Habitat requirements of northern pike (*Esox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53:161-174.

Chaney, E, W. Elmore, and W.S. Platts. 1993. Managing change: Livestock grazing on western riparian areas. Report prepared for the Enviornmental Protection Agency. Denver, CO.

Chapman, D. W., and E. Knudsen. 1980. Channelization and livestock impacts on salmonid habitat and biomass in western Washington. Transactions of the American Fisheries Society 109:357–363.

Clarkson, R.W., and J.R. Wilson. 1995. Trout biomass and stream habitat relationships in the White Mountains area, east-central Arizona. Transactions of the American Fisheries Society 124:599-612.

Clary, W.P. 1999. Stream channel and vegetation responses to late spring cattle grazing. Journal of Range Management. 52(3): 218-227

Clary, W. P., and G.D. Booth. 1993. Early season utilization of mountain meadow riparian pastures. Journal of Range Management 43:493–497.

Clary, W. P., and W. H. Kruse. 2004. Livestock grazing in riparian areas: environmental impacts, management practices, and management implications. Pages 237-258 In: Riparian areas of the southwestern United States: hydrology, ecology, and management. Lewis Publishers.

Clary, W.P., and B.F. Webster. 1989. Managing grazing of riparian areas in the intermountain region. General Technical Report INT-263. Ogden, UT. U.S. Department of Agriculture, Forest Service, Inotermountain Research Station. 11p.

Courtois, D.R., B.L. Perryman, H.S. Hussein. 2004. Vegetation change after 65 years of grazing and grazing exclusion. Journal of Range Management 57:574-582.

Dobkin, D.S., A.C. Rich, W.H. Pyle. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. Conservation Biology 12:209–221.

Elliott, J. M. 1975a. The growth rate of brown trout (*Salmo trutta*) fed on maximum rations. Journal of Animal Ecology 44:805–821.

Elliott, J. M. 1975b. The growth rate of brown trout (*Salmo trutta*) fed on reduced rations. Journal of Animal Ecology 44:823–842.

Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Functional Ecology 9:290–298.

Elmore, W., and R.L. Beschta. 1987. Riparian areas: Perceptions in management. Rangelands 9:260-265.

Elmore, W., and J.B. Kauffman. 1994. Riparian and watershed systems: Degradation and restoration. p 212-231 in: M. Vavra, W.A. Laycock, and R.D. Pieper (eds.), Ecological implications of livestock herbivory in the west. Society of Range Management. Denver, CO.

Flenniken, M., R.R. McEldowney, W.C. Leininger, G.W. Frasier, and M.J. Trlica. 2001. Hydrologic responses of a montane riparian ecosystem following cattle use. Journal of Range Management 54:567–574.

Flory, E.A., and A.M. Milner. 1999. Influence of riparian vegetation of invertebrate assemblages in a recently formed stream in Glacier Bay National Park, Alaska. Journal of the North American Benthological Society 18:261–273.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. The American Naturalist 158:124–135.

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

Gillen, R.L., W.C. Krueger, and R.F. Miller. 1984. Cattle distribution on mountain rangeland in northeastern Oregon. Journal of Range Management 37:549–553.

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

Gowan, C. M., and K. D. Fausch. 1996. Mobile brook trout in two high–elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370–1381.

Gowan, C. M. and K. D. Fausch. 2002. Why do foraging stream salmonids move in summer? Environmental Biology of Fishes 64:139–153.

Gregory, S.V., F. J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

Gunderson, D. R., 1968. Floodplain use related to stream morphology and fish populations. Journal of Wildlife Management 32:507–514.

Halsted, L.E., L.D. Howery, G.B. Ruyle, P.R. Krausman, and R.J. Steidl. 2002. Elk and cattle forage use under a specialized grazing system. Journal of Range Management 55:360-366.

Harcup, M. F., R. Williams, and D. M. Ellis. 1984. Movements of brown trout, *Salmo trutta* L., in the River Gwyddon, South Wales. Journal of Fish Biology 24: 415–426.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhyncus clarki*) in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48:757–762.

Hesthagen, T. 1988. Movements of brown trout, *Salmo trutta*, and juvenile Atlantic salmon, *Salmo salar*, in a coastal stream in northern Norway. Journal of Fish Biology 32:639–653.

Hilderbrand, R. H, and J. L. Kershner. 2004. Are there differences in growth and condition between mobile and resident cutthroat trout? Transactions of the American Fisheries Society 133:1042–1046.

Holechek, J., R. D. Pieper, and C. H. Herbel. 1998. Range management, principles and practices. 3rd ed. Prentice Hall, Upper Saddle River, N.J.

Holechek, J.L., T.T. Baker, J.C. Boren, and D. Galt. 2006. Grazing impacts on rangeland vegetation: What we have learned. Rangelands 28:7-13

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth. Ecology 74:673–684.

Jensen, A. J., T. Forseth, and B. O. Johnsen. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69:1010–1020.

Jensen, J. W., and T. Berg. 1995. The annual growth rate cycle of brown trout. The Progressive Fish-Culturist 57:231–237.

Jones III, E.B.D., G.S. Helfman, J.O. Harper, and P.V. Bolstad. 1999. Effects of forest removal on fish assemblages in southern Appalachian streams. Conservation Biology 13:1454-1465.

Kauffman, J.B., W.C. Krueger, and M. Vavra. 1983a. Impacts of cattle on streambanks in north-eastern Oregon. Journal of Range Management 36:683-685.

Kauffman, J.B., W.C. Krueger, and M. Vavra. 1983b. Effects of late season cattle grazing on riparian plant communities. Journal of Range Management 36:685-691.

Kauffman, J.B., andW.C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: A review. Journal of Range Management 37:430–438.

Kauffman, J.B., R.L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. Fisheries 22(5):12–24.

Kawaguchi, Y., Y. Taniguchi, and S. Nakano. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology 84:701–708.

Kay, C.E. 1994. The impact of native ungulates and beaver on riparian communities in the intermountain west. Natural Resources and Environmental Issues 1:23–44.

Keller, C. R., and K. P. Burnham. 1982. Riparian fencing, grazing, and trout habitat preference on Summit Creek, Idaho. North American Journal of Fisheries Management 2:53–59.

Kie, J.G., and B.B. Boroski. 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. Journal of Range Management 49:482–488.

Kondolf, G.M. 1993. Lag in stream channel adjustment to livestock exclosure, White Mountains, California. Restoration Ecology 1:226–230.

Larsen, R.E., W.C. Krueger, M.R. George, M.R. Barrington, J.C. Buckhouse, and D.E. Johnson. 1998. Livestock influences on riparian zones and fish habitat: Literature classification. Journal of Range Management 51:661–664.

Leege, T.A., D.J. Herman, and B. Zamora. 1981. Effects of cattle grazing on mountain meadows in Idaho. Journal of Range Management 34:324–328.

Li, H.W., G.A. Lamberti, T.N. Pearsons, C.K. Tait, J.L. Li., and J.C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day basin, Oregon. Transactions of the American Fisheries Society. 123:627–640.

Long, J.W., and A.L. Medina. 2006. Consequences of ignoring geologic variation in evaluating grazing impacts. Rangeland Ecology and Management 59:373–382.

Lusby, G.C. 1970. Hydrolgic and biotic effects of grazing vs. non-grazing near Grand Junction, Colorado. Journal of Range Management 23:256–260.

Magilligan, F.J., and P.F. McDowell. 1997. Stream channel adjustments following elimination of cattle grazing. Journal of the American Water Resources Association 33:867–878.

Marcuson, P.E. 1977. The effect of cattle grazing on brown trout in Rock Creek, Montana. Fish and Game Federal Aid Project. F-20-R-21-1a.

Matthews K. R. 1996. Habitat selctions and movement patters of California golden trout in degrasded and recovering stream sections in the Golden Trout Wilderness, California. North American Journal of Fisheries Management 16:579-590.

McEldowney, R.R., M. Flenniken, G.W. Frasier, M.J. Trlica, and W.C. Leininger. 2002. Sediment movement and filtration in a riparian meadow following cattle use. Journal of Range Management 55:367–373.

McInnis, M.L., and J. McIver. 2001. Influences of off-stream supplements on streambanks of riparian pastures. Journal of Range Management 54:648–652.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology 79:587–592.

Meehan, W.R., and W.S. Platts. 1978. Livestock grazing and the aquatic environment. Journal of Soil and Water Conservation 34:274-278.

Micheli, E. R. and J. W. Kirchner. 2002. Effects of wet meadow riparian vegetation on streambank erosion. 2. Measurements of vegetated bank strength and consequences for failure mechanics. Earth Surface Processes and Landforms 27: 687–697.

Minshall, G. W., C. T. Robinson, and D. E. Lawrence. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, USA. Canadian Journal of Fisheries and Aquatic Sciences 54: 2509–2525.

Myers, M.J. and V.H. Resh. 2000. Undercut banks: A habitat for more than just trout. Transactions of the American Fisheries Society 129: 594-597.

Myers, T. J. and S. Swanson. 1992. Variation in stream stability with stream type and livestock bank damage in northern Nevada. Journal of the American Water Resources Association 28:743–754.

Myers, T.J. and S. Swanson. 1995. Impact of deferred rotation grazing on stream characteristics in central Nevada: A case study. North American Journal of Fisheries Management 15:428-439.

Naiman, R.J., H. DeCamps, and M. Pollack. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212.

Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621–658.

National Research Council, 2002. Ecological dynamics on Yellowstone's northern range. National Academy Press, Washington, D.C.

Nakano, S., M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences. 98(1):160-165

Nelson, R.L., W.S. Platts, D.P. Larsen, and S.E. Jensen. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Transactions of the American Fisheries Society 121:405-426.

Opperman, J.J., and A.M. Merenlender. 2000. Deer herbivory as an ecological constraint to restoration of degradedriparian corridors. Restoration Ecology 8:41-47.

Overton, C. K., G. L. Chandler, and J. A. Pisano. 1994. Northern/Intermountain regions' fish habitat inventory: grazed, rested and ungrazed reference stream reaches, Silver King Creek, California. U.S. Department of Agriculture, Forest Service. General Technical Report, INT-GTR-311.

Parsons, C.T., P.A. Momont, T.DelCurto, M.McInnis, and M.L.Porath. 2003. Cattle distribution patterns and vegetation use in mountain riparian areas. Journal of Range Management. 56:334-341.

Platts, W.S. 1981. Effects of livestock grazing, USDA, Forest Service, General Technical Report PNW-124. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Portland, OR. 25 pp.

Platts, W. S. 1982. Livestock and riparian fishery interactions: what are the facts? Transactions of the North American Wildlife and Natural Resources Conference 47: 507-515.

Platts, W. S. 1991. Livestock grazing. In: Influence of forest and rangeland management on salmonid fishes and their habitats. Edited by W.R. Meehan. American Fisheries Society Special publication 19:389-423.

Platts, W. S., and F.J. Wagstaff. 1984. Fencing to control livestock grazing on riparian habitats along streams: Is it a viable alternative? North American Journal of Fisheries Management. 4:266-272.

Platts, W.S., and R.L. Nelson. 1985. Impacts of rest-rotation grazing on stream banks in forested watersheds in Idaho. North American Journal of Fisheries Management. 5:547-556.

Platts, W.S., and J.N. Rinne. 1985. Riparian and stream enhancement, management and research in the Rocky Mountains. North American Journal of Fisheries Management 5:115-125.

Platts, W.S. 1990. Fish, wildlife and livestock: Protection of riparian areas. Western Wildlands 16:16–19.

Rinne, J.N. 1988. Grazing effects on stream habitat and fishes: Research design considerations. North American Journal of Fisheries Management 8:240-247.

Rinne, J.N. 1999. Fish and grazing relationships: The facts and some pleas. Fisheries 24(8):12–21.

Ripple, W.J., E.J. Larsen, R.A. Renkin, and D.W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation. 102:227–234.

Roath, L.R., and W.C. Krueger. 1982. Cattle grazing influence on a mountain riparian zone. Journal of Range Management 35:100–103.

Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1–13.

Rosgen, D.L. 1994. A classification of natural rivers. Catena 22:169-199.

Russell, P. A. 1983. Psychological studies of exploration in animals: a repraisal. Pages 22–54 *in* L. I. A. Birke and J. Archer (editors) Exploration in animals and humans. Van Nostrand, New York.

Saunders, W. C., and K. D. Fausch. 2007. Improved grazing management increases terrestrial invertebrate inputs the feed trout in Wyoming rangeland streams. Transactions of the American Fisheries Society 136:1216-1230.

Schulz, T.T., and W.C. Leininger. 1990. Differences in riparian vegetation structure between grazed areas and exclosures. Journal of Range Management 43:295–299.

Sedgwick, J.A., and F.L. Knopf. 1991. Prescribed grazing as a secondary impact in a western riparian floodplain. Journal of Range Management 44:369–373.

Simon, A., and A. J. C. Collison. 2002. Quantifying the mechanical and ydrological effects of riparian vegetation on streambank stability. Earth Surface Processes and Landforms 27:527–546.

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern range. Journal of Range Management 47:435–443.

Summers, D. W., N. Giles, and D. N. Stubbing. 2005. The effect of riparian grazing on brown trout, *Salmo trutta*, and juvenile Atlantic salmon, *Salmo salar*, in an English chalk stream. Fisheries Management and Ecology 12:403–405.

Summers, D. W., N. Giles, and D. N. Stubbing. 2008. Rehabilitation of brown trout, *Salmo trutta*, habitat damaged by riparian grazing in an English chalkstream. Fisheries Management and Ecology 15:231-240.

Stillings, A.M., J.A. Tanaka, N.R. Rimbey, T. DelCurto, P.A. Momont, and M.L. Porath. 2003. Economic implications of off-stream water developments to improve riparian grazing. Journal of Range Management 56:418–424.

Torstenson, W.L., J.C. Mosley, T.K. Brewer, M.W. Tess, and J.E. Knight. 2006. Elk, mule deer, and cattle foraging relationships on foothill and mountain rangeland. Rangeland Ecology & Management 59:80–87.

van der Maarel, E., and A. Tityanova. 1989. Above-ground and below-ground biomass relations in steppes under different grazing conditions. Oikos 56: 364–370.

Wilson, D. S., K. Coleman, A. B. Clarke, and L. Bierderman. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. Journal of Comparative Psychology 107:250–260.

Wipfli, M. S., and J. Musselwhite. 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. Hydrobiologia 520:152–163.

Wohl, N.E., R.F. Carline. 1996. Relations between riparian grazing, sediment loads, macroinvertebrates, and fishes in three central Pennsylvania streams. Canadian Journal of Fisheries and Aquatic Sciences 53:260-266

CHAPTER 1: CHANGES IN STREAM CHANNEL MORPHOLOGY ASSOCIATED WITH LIVESTOCK AND ELK GRAZING WITHIN VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

Abstract

Variability in stream morphology can have profound influences on the spatial distribution of lotic fish species within a watershed which compels natural resource agencies to assess land-use practices influencing stream channel shape and stability. Changes in channel morphology, streambank stability and instream substrate in response to livestock and elk grazing were monitored over the first 5 years of grazing exclosures on Rio San Antonio, Valles Caldera National Preserve (VCNP), New Mexico. Characterization of riparian forage utilization at stocking rates observed in 2007 and 2008 revealed utilization rates (6-26%) below VCNP riparian forage utilization objectives (40%). Riparian vegetation communities have benefitted from grazing exclosure, as ELK sites exhibited significantly greater stubble heights than in CATTLE and OPEN sites. Baseline data collected in 2004 indicated that grazing sites exhibited similar cross-sectional measurements prior to exclusion of livestock and elk. Minimal changes in stream morphology in Rio San Antonio were noted among sites closed to livestock and elk grazing in the five years following construction of grazing exclosures. Cross sectional parameters were not different among grazing sites for any of the habitat types monitored during this research. Streambank stability ratings were typically high in all grazing sites with 73-81% of all transects being rated as covered/stable and only 9-16% rated as uncovered/unstable. Undercut streambanks exhibited greatest depth in OPEN sites

(0.33 m), the prevalence of undercut banks was greatest in ELK exclosures (87%). No differences in the percentage of fine sediments in OPEN (0.16), CATTLE (0.25), and ELK (0.21) grazing sites were noted. Minimal changes over the first five years of grazing exclosures imply that the duration of this study was too brief to observe significant changes among the stream habitat parameters monitored. In addition to the brief duration of this study, natural variability among stream reaches as well as minimal stocking rates which resulted in minimal treatment in OPEN sites may have contributed to the results observed between 2004 and 2008 in the Rio San Antonio watershed. Continued evaluation of stream morphology over the next 10-15 years may be necessary to determine the impact of livestock and elk grazing on.

Introduction

Declining abundance and ranges of native fishes across the southwestern United States has directed research to assess watershed influences accelerating the rate of decline of many threatened or endangered species. Among the influences being examined, livestock grazing has become one of the points of concern for natural resource managers throughout the southwest.

Streamside vegetation communities perform integral processes that stabilize, buffer and sustain aquatic systems. High resilience and resistance to disturbance is a characteristic of healthy riparian zones and is a function of the biodiversity found in riparian areas (Elmore and Kauffman 1994; Kauffman et al. 1997). Riparian vegetation is adapted to rapidly shifting conditions associated with seasonal flooding and other naturally occurring events (Naiman et al. 1993). In the presence of healthy riparian vegetation, high streamflow events perform a dynamic role in the formation and alteration of stream morphology, creating instream fish habitat, moderating detrimental effects of high discharge, and providing allochthonous organic input to lotic systems (Naiman and Decamps 1997; Kauffman et al. 1997; Baxter et al. 2005).

Livestock grazing has been shown to cause shifts in riparian vegetation from sedge and rush dominated communities to more xeric grass and shrub species (Belsky et al. 1999). Shifts in riparian vegetation to shallow-rooted grass species such as Kentucky bluegrass (*Poa pratensis*), may have significant implications to streambank stability in meadow streams. Physiological differences in overall root characteristics among vegetation species may result in decreased streambank shear strength (Micheli and Kirchner 2002). Removal of vegetation and compaction of soils by large herbivores decreased infiltration, resulting in increased runoff in heavily and moderately grazed pastures (Kauffman and Krueger 1984). Increased runoff can significantly alter channel morphology (Minshall et al. 1997), resulting in stream habitat conditions which may adversely impact aquatic biota.

Physical breakdown of streambanks as a result of livestock trampling has also been shown to detrimentally impact channel morphology. Comparisons of ungrazed and grazed sections of a stream in eastern Oregon showed loss of undercuts, greater amounts of sloughing streambanks and bank collapse all contributing to loss of fish and aquatic macroinvertebrate habitat (Kauffman et al. 1983a). Gunderson (1968) and Marcuson (1977), demonstrated that livestock grazing resulted in increased channel width as a combined result of streambank sloughing, and loss of streamside vegetation which lead to increased erosion during high flow events. Knapp and

Matthews (1996) noted significant differences in channel width and channel depth when comparing channel morphology inside and outside grazing exclosures in California. Similar findings were documented by Magilligan and McDowell (1997) in 14 year old grazing exclosures, as channel width decreased in ungrazed areas. Channel response to livestock exclosure varies, as several studies noted minimal changes in stream habitat conditions in exclosures which had been functioning from 4 to 24 years (Rinne 1988; Kondolf 1993; and Overton et al. 1994). Factors other than livestock grazing may have been limiting channel recovery including continued disturbance in the watershed upstream from grazing exclosures and lack of fine sediment delivery necessary for streambank aggradation (Kondolf 1993).

Due to the strong influence of stream morphology on fish populations, determination of land-use impacts on changes in channel shape, streambank stability, and instream substrate are of utmost importance. The goal of this study was to evaluate changes in stream morphology in response to removal of livestock and elk grazing in a meadow stream. Following five years of grazing exclosure, research objectives were to relate forage utilization by livestock and elk to channel cross-sectional parameters, streambank stability, undercut bank development, and instream substrate. Specific hypotheses included:

1) Decreased width–depth ratio in cattle and elk exclosures;
2) Positive change in Gini coefficient values in cattle and elk exclosures;
3) Increased undercut depth and prevalence in cattle and elk exclosures; and,
4) Lower erosion index in cattle and elk exclosures;

Methods

Cattle and Elk Grazing

Animal unit month estimates were obtained using conversion factors (cow-calf 1.0, heifer/steer 0.8, and elk 0.60; Pratt and Rasmussen 2001 Livestock stocking rates varied during this study based on management recommendations from VCNP range managers. Drought conditions observed from November 2005 through April 2006 resulted in diminished range conditions and no livestock were allowed to graze until late August 2006 following summer monsoon rains.). Elk population estimates were obtained from the New Mexico Department of Game and Fish (personal communication, S. Liley). Elk populations within VCNP during this research remained stable with population estimates between 2000-3000 animals from 2004-2008 (Table 1.1).

Riparian forage utilization by elk and livestock was monitored using paired-cage comparisons within CATTLE and OPEN sites in 2007 and 2008 (Cook and Stubbendieck 1986). Cages were constructed using cattle panels (4 gauge) with 10 x 15 cm openings, in the shape of pyramids covering an area of approximately 1 m^2 (Allison et al. 1999). Within each OPEN and CATTLE treatment, 3 paired-cages were established within the riparian zone at the beginning of the growing season in early May. Plots were haphazardly placed within 10 m of streambanks to specifically monitor riparian forage utilization. Vegetation was clipped using 0.185 m^2 rectangular plots within each protected plot prior to cattle grazing (May), and after cattle grazing had ceased at the end of the growing season (September/October).

Clipped plots from inside cages were compared to clipped plots taken from unprotected areas within similar vegetation communities (Cook and Stubbendieck 1986). Plots with negative utilization values were zeroed (Werner and Urness 1998). Utilization rates were calculated for each paired plot and mean utilization was calculated for each treatment. Utilization rates for CATTLE and OPEN sites were compared seasonally (October through April, and May through September) to evaluate the effect of elk (October through April) and the combined effect of elk and cattle (May through September). Large ungulate forage utilization within ELK exclosures was assumed to be zero under all cases.

Stubble height was measured at 0.25 m intervals along 30 m transects, which were established perpendicular to stream flow and centered on the stream allowing assessment of riparian vegetation along both streambanks. Four transects were established in each grazing site at all Rio San Antonio stream reaches in a random stratified arrangement. Buffer areas (25 m) were established along the upstream and downstream boundaries of each exclosure, preventing transects from falling into areas near exclosure fences. Stubble height measurements from each transect were averaged to determine overall stubble height within each grazing site and compared to riparian management guidelines identified by Clary and Leininger (2000).

Elk presence within all grazing sites was monitored in 2007 and 2008 using pellet group counts according to methods described by Neff (1968). Samples were collected in fall 2007, spring 2007, and fall 2008.

Stream Morphology

Within each grazing site (CATTLE, ELK, OPEN) at all Rio San Antonio stream reaches (lower, middle, upper), baseline stream morphological data were collected from three cross-sectional transects in pool, run, and riffle habitat units during June 2004. Bankfull width, wetted width, and stream depth were measured along each transect and wetted width–depth ratios were calculated for each habitat type. In 2007, 12 additional stream cross-sectional transects were established in each grazing treatment to evaluate changes in stream morphological parameters. Four transects were established perpendicular to stream flow on each of the three dominant stream habitat units (pool, run, riffle). Instream characteristics at each transect were sampled in the summer of 2007 and 2008 during base flow conditions. These characteristics including bankfull width, bankfull depth, wetted width, stream depth, residual pool depth, and maximum pool depth were measured according to methods described by Kershner et al. (2004). Determination of bankfull state was made using morphological, botanical, and topographical indicators (Leopold 1994). Pools were classified as deepwater habitat relative to adjacent habitat types, with little surface flow, small substrate, and mean water column velocity <0.1 m/s. Runs were classified as habitat exhibiting moderate depth, moderate surface agitation, diverse substrate types, and mean water velocity ranging from 0.21 to 0.60 m/s. Riffles were classified as habitat with relatively shallow depth, extensive surface agitation, and substrate composed of large gravel to cobble, and mean water velocity >0.6 m/s (Bisson et al. 1982).

Table 1.1: Cattle stocking rates and elk population estimates from 2004 to 2008 on Valles Caldera National Preserve, NM.

	Year				
	2004	2005	2006	2007	2008
Livestock	660	600	100	500	2000
AUM[1]	2376	2160	180[a]	1600	6400
Elk[2]	2000-2500	2000-2500	2000-2500	2000-2500	2000-2500
AUM[3]	10800-13500	10800-13500	10800-13500	10800-13500	10800-13500

[1] AUM calculation based on conversion factors for cow-calf, heifer/steer for 4 months

[2] Population estimates for elk obtained from NM Game and Fish.

[3] AUM calculation based on conversion factor for elk for 9 months

[a] Stocking rate based on 2.25 months of use in 2006

Residual pool depth was measured at each pool cross section to determine the ability of the stream to maintain fish populations during extreme periods of drought (Lisle 1987). Residual depth was calculated as the difference between the maximum observed depth in the pool and the maximum depth observed on the corresponding riffle crest at the tail of the pool. Pool–riffle ratio was estimated using total surface area for pools and riffles within each grazing treatment.

Width–depth ratios were calculated for both bankfull conditions and current stream flow conditions as the ratio of bankfull width to mean bankfull depth (Gregory and Walling 1973; Heede 1980) and the ratio of wetted width to mean stream depth (Myers and Swanson 1995). Gini coefficients (G) were estimated from transect data using WinXPRO Channel Cross Section Analyzer (USDA 1998). The Gini coefficient adapted from economics (Bowman 1946; Sen 1973) and plant biology (Weiner and Solbrig 1984) was also used to describe cross-sectional channel shape, and does so independent of stage height and cross-sectional area. The direction of change in the Gini coefficient reflects whether channels are becoming wide and shallow (-G) or narrow and deep (+G). Magnitude of change is on a scale between 0 and 1 with wide, shallow channels exhibiting G values near 0 and deep narrow channels exhibiting G values near 1 (Olson-Rutz and Marlow 1992). Change in Gini coefficient due to grazing treatment was calculated for each habitat unit (pool, riffle, run) and compared across sites by calculating the difference in mean area for each habitat unit under baseline conditions (2004) to the mean area for each habitat unit in each grazing site (OPEN, CATTLE, ELK) in 2008.

$$G = (G_{pre} - G_{post})$$

where G_{pre} = mean Gini coefficient for each habitat unit in all grazing sites measured in 2004 and G_{post} = Gini coefficient for each habitat unit in grazing sites measured in 2008.

Undercut bank depth was measured at any transect intersecting an undercut bank according to methods described by Kershner et al. (2004). The following criteria had to be met for banks to be considered undercut: 1) minimum depth of 5 cm; 2) minimum height of 10 cm; and 3) minimum length of 10 cm. These criteria were used to identify undercut streambanks providing instream cover to salmonids. Streambanks meeting these criteria were then measured by probing the bank for the maximum depth of the undercut. Prevalence of undercut banks was also estimated as the number of observed undercut banks divided by the total number of transects within each grazing treatment.

Streambank stability and cover were estimated according to methods described by Platts et al. (1987) and modified by Bauer and Burton (1993). Cover was visually estimated on left and right streambanks for areas 0.5 m on the upstream and downstream sides of each transect from stream margin to bankfull width. Streambanks were classified as covered if any of the following criteria were met: 1) live vegetation cover greater than 50% covering the streambank; 2) sedge or deeply rooted vegetation with roots covering greater than 50% of the streambank; 3) minimum of 50% of the streambank covered by substrate equal to or larger than 10 cm; or 4) minimum of 50% of the streambank covered by large wood greater than 10 cm in diameter (Bauer and Burton 1993). If none of the above criteria were met streambanks were classified as uncovered. Streambanks were classified as unstable if any of the following features were exhibited: 1) depositional features classified as uncovered; 2) bank angle greater than 80 degrees classified as uncovered; 3) fractured bank with slump block still attached classified as uncovered above the slump block; 4) visible fracture in the top of the streambank; or 5) fractured streambank with unattached slump block (Kershner et al. 2004). Streambanks not exhibiting any of the above criteria were classified as stable. Streambanks at each end of all transects were classified into one of four groups based on the combination of cover and stability: 1) covered/stable; 2) covered/unstable; 3) uncovered/stable; or 4) uncovered/unstable. Each group was then assigned a rating to determine erosion potential based on the combination of cover and stability (McInnis and McIver 2001).

Cover/Stability	Erosion Index
covered/stable	1
covered/unstable	2
uncovered/stable	3
uncovered/unstable	4

Erosion potential was then estimated for each grazing treatment using the following equation:

$$\text{Erosion potential} = \sum EI_{ni} / N_{total};$$

where EI_{ni}= erosion index rating for transects n=1-12 and N_{total} = total number of transects per treatment area. Percent unstable streambank was determined by measuring the total length of streambanks classified as unstable according to the criteria described above divided by the total streambank length within each grazing treatment.

Instream substrate was monitored using the pebble count method described by Bevenger and King (1995) and classified according to the modified Wentworth particle size scale of Bovee and Cochnauer (1977).

Statistical Analysis

All statistical analyses were performed using SAS version 9.1.3 (SAS Institute Inc. Cary, NC 2003). Stubble height was compared using two-way analysis of variance with grazing site and year (2007, 2008) as the main effects. Stubble height measurements were combined across stream reaches (lower, middle, upper) for each grazing site (CATTLE, ELK, OPEN) as all stream reaches were grazed for similar periods of time. Multiple comparison tests were performed using Fisher's LSD at $\alpha=0.05$. Riparian forage utilization, stubble height, and elk pellet group counts were only conducted in 2007 and 2008, precluding analysis of baseline conditions prior to the exclusion of elk and cattle.

Baseline morphological conditions (wetted width, stream depth, wetted width–depth ratio, bankfull width) observed in 2004, were analyzed using one-way ANOVA with grazing site as the main factor. Parameters for each grazing site were combined across lower, middle, and upper stream reaches. Multiple comparison tests to evaluate mean separation were run using Fisher's LSD at $\alpha=0.05$. Bankfull depth, residual pool depth, streambank stability ratings, and undercut streambank depth data were not collected in 2004, precluding analysis of baseline conditions prior to exclusion of elk and cattle.

Repeated measures analysis of variance (RMANOVA) using the GLM procedure in SAS was used to test morphological change (wetted width, stream depth, wetted width–depth ratio, bankfull width, bankfull depth, bankfull width–depth ratio, residual pool depth, max pool depth, erosion index), with grazing treatment (OPEN, CATTLE, ELK) as between subjects group, and year (2007, 2008) as the repeated variable. Analyses were run separately for each habitat type (pool, run, riffle) to evaluate differential response among habitat types to livestock and elk grazing. Data from grazing sites at each stream reach (lower, middle, upper) were combined for all parameters, as individual transects within each grazing site could not be counted as replicates due to pseudoreplication (Johnson 2002). All analyses were considered significant at $\alpha=0.05$. Significant group effects and interaction effects were tested using the least squares mean procedure at $\alpha=0.05$. Two-way ANOVA was used to test grazing site effect on undercut bank depth for data collected in 2007 and 2008. Undercut bank depth data were combined across middle and upper stream reaches, as no undercut streambanks were observed in the lower stream reach. Mean separation of significant grazing site effect was performed using Fisher's LSD at $\alpha=0.05$.

Results

Livestock and Elk Forage Utilization

Utilization estimates from paired-cage comparisons in 2007 and 2008 were well below riparian grazing standards established for VCNP (40%; VCNP Interim

Grazing Strategy). Differential utilization rates in 2007 and 2008 in OPEN sites reflect variation in stocking rates observed during that time (Figure 1.1).

Stubble height measurements in spring 2007 showed that ELK exclosures had significantly greater stubble height than both CATTLE exclosures and the grazed reference site ($F_{2,33}=18.43$; $p<0.0001$). Fall 2007 ($F_{2,33}=5.83$; $p=0.007$) and 2008 ($F_{2,26}=19.00$; $p<0.0001$) measurements also differed among grazing sites with ELK exclosures exhibiting greater vegetation height than OPEN sites (Table 1.2). Elk presence within OPEN sites and CATTLE exclosures was similar during summer 2007 and winter 2007-2008 (Table 1.3). Mean elk density (elk/ha) in CATTLE exclosures from 2007-2008 was 0.13, with similar density observed in OPEN sites (0.15) over the same period.

Baseline Stream Morphology

Baseline data collected in 2004 immediately following closure of CATTLE and ELK grazing sites reflected stream reaches exhibiting similar morphological characteristics (Table 1.4). No detectable differences were present among grazing sites across all habitat types for the parameters collected in 2004.

Stream Morphology Following 5 Years of Exclosure

Detectable differences in stream morphology were not observed among grazing sites in run and riffle habitat following 5 years of riparian grazing exclosure (Table 1.5). Pool depth in ELK grazing sites was greater than both CATTLE and OPEN sites ($F_{2,6}=7.36$; $p=0.0243$; Figure 1.2).

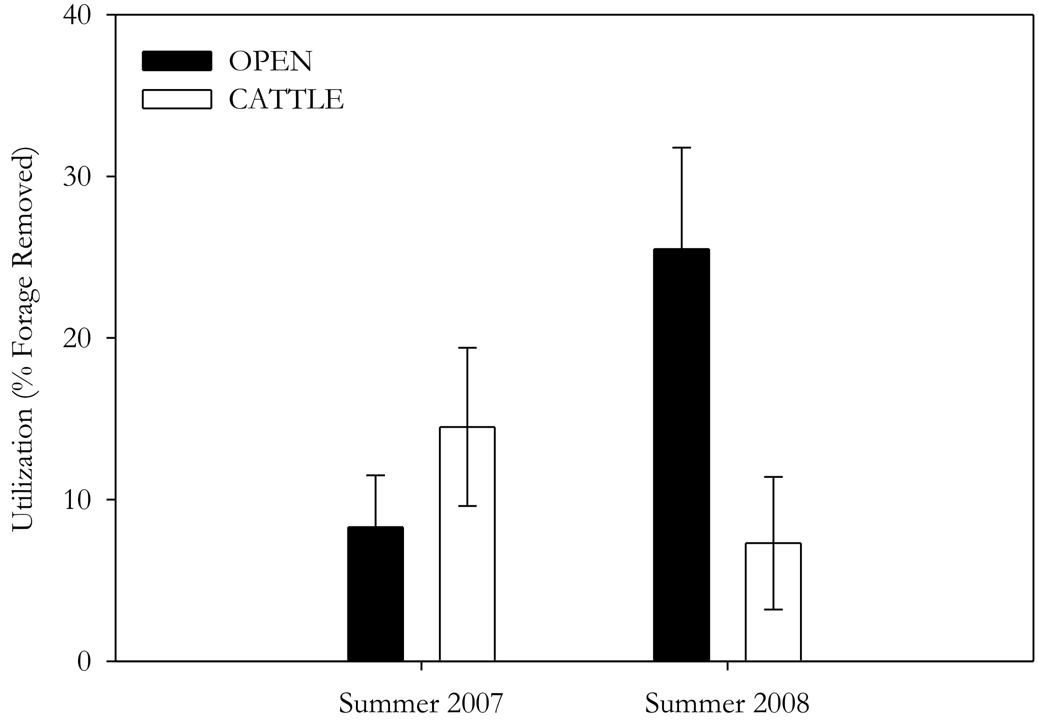


Figure 1.1: Forage utilization rate (% available forage removed by grazing) determined from paired-plot comparisons in CATTLE and OPEN exclosures.

Table 1.2: Vegetation stubble height (cm; mean ± S.E.) in CATTLE, ELK, and OPEN grazing sites. Similar superscripts among grazing sites indicate groupings based on Fisher's LSD at α=0.05.

Grazing Exclosure	2007 Spring	2007 Fall	2008 Spring	2008 Fall
OPEN	18.9 (0.45) ^{a}	31.4 (1.99) ^{a}	11.4 (0.58) ^{a}	25.1 (2.03) ^{a}
CATTLE	19.8 (0.59) ^{a}	36.3 (1.81) ^{ab}	11.8 (0.46) ^{ab}	40.4 (1.89) ^{b}
ELK	23.9 (0.78) ^{b}	40.7 (1.97) ^{b}	13.3 (0.80) ^{b}	38.6 (1.65) ^{b}

Table 1.3: Elk presence (elk/ha) within grazing exclosures during summer (May-September) and winter (October-May) and combined across lower, middle, and upper stream reaches.

Grazing Site	2007 Summer	2008 Winter	2008 Summer
OPEN	0.18	0.13	0.13
CATTLE	0.13	0.18	0.07
ELK	0	0	0

Table 1.4: Baseline morphological parameters (mean ± S.E.) collected in 2004 from pool, run, and riffle habitat types within CATTLE, ELK, and OPEN grazing sites, data were combined across lower, middle, and upper Rio San Antonio stream reaches.. Superscript letters denote groupings based on statistical differences among grazing sites using Fisher's LSD at α=0.05.

Habitat Type	Grazing Treatment	Wetted Width (m)	Stream Depth (m)	Wetted Width–Depth	Bankfull Width (m)
Pool	OPEN	4.9 (0.96)^{a}	0.28 (0.07)^{a}	17.6 (2.72)^{a}	6.3 (2.13)^{a}
	CATTLE	4.5 (1.71)^{a}	0.23 (0.07)^{a}	19.5 (5.90)^{a}	6.5 (3.84)^{a}
	ELK	5.2 (2.82)^{a}	0.49 (0.19)^{a}	10.3 (2.23)^{a}	7.1 (3.87)^{a}
Run	OPEN	2.6 (0.68)^{a}	0.19 (0.10)^{a}	17.1 (10.83)^{a}	3.9 (1.56)^{a}
	CATTLE	4.2 (2.19)^{a}	0.18 (0.09)^{a}	38.2 (44.37)^{a}	6.7 (4.32)^{a}
	ELK	3.5 (2.20)^{a}	0.19 (0.09)^{a}	24.4 (24.92)^{a}	2.8 (0.78)^{a}
Riffle	OPEN	3.9 (0.55)^{a}	0.08 (0.01)^{a}	50.5 (11.19)^{a}	5.1 (1.67)^{a}
	CATTLE	3.0 (0.61)^{a}	0.07 (0.01)^{a}	41.9 (13.41)^{a}	3.9 (0.63)^{a}
	ELK	3.3 (1.33)^{a}	0.13 (0.07)^{a}	27.5 (4.10)^{a}	4.1 (1.30)^{a}

Table 1.5: Stream morphological parameters (mean ± S.E.) collected in 2008 from pool, run, and riffle habitat types within CATTLE, ELK, and OPEN grazing sites. Data were combined across lower, middle, and upper Rio San Antonio stream reaches.. Superscript lowercase letters denote statistical differences among grazing sites within each habitat type.

Habitat Type	Grazing Site	Wetted Width (m)	Stream Depth (m)	Wetted Width–depth	Bankfull Width (m)	Bankfull Depth (m)	Bankfull Width–depth
Pool	OPEN	4.8 (0.19) ^{a}	0.28 (0.01) ^{a}	17.7 (0.59) ^{a}	6.1 (0.47) ^{a}	0.84 (0.04) ^{a}	7.3 (0.32) ^{a}
	CATTLE	5.8 (0.93) ^{a}	0.34 (0.01) ^{b}	17.7 (4.08) ^{a}	6.9 (1.21) ^{a}	0.91 (0.05) ^{a}	7.5 (0.88) ^{a}
	ELK	5.2 (1.29) ^{a}	0.39 (0.01) ^{c}	18.3 (3.91) ^{a}	6.8 (1.77) ^{a}	0.99 (0.07) ^{a}	6.7 (1.40) ^{a}
Run	OPEN	3.1 (0.67) ^{a}	0.19 (0.03) ^{a}	19.3 (4.65) ^{a}	4.9 (1.00) ^{a}	0.75 (0.03) ^{a}	6.6 (1.17) ^{a}
	CATTLE	3.0 (0.49) ^{a}	0.18 (0.01) ^{a}	17.4 (2.77) ^{a}	4.5 (0.97) ^{a}	0.74 (0.03) ^{a}	6.1 (0.98) ^{a}
	ELK	2.6 (0.55) ^{a}	0.16 (0.01) ^{a}	13.5 (3.13) ^{a}	5.6 (1.47) ^{a}	0.84 (0.04) ^{a}	6.6 (1.49) ^{a}
Riffle	OPEN	2.9 (0.62) ^{a}	0.12 (0.01) ^{a}	27.0 (6.99) ^{a}	5.4 (1.05) ^{a}	0.76 (0.02) ^{a}	7.2 (1.33) ^{a}
	CATTLE	2.8 (0.63) ^{a}	0.13 (0.01) ^{a}	22.4 (6.09) ^{a}	4.6 (0.99) ^{a}	0.71 (0.04) ^{a}	6.4 (1.01) ^{a}
	ELK	3.2 (1.16) ^{a}	0.13 (0.01) ^{a}	28.2 (9.67) ^{a}	6.7 (1.65) ^{a}	0.77 (0.01) ^{a}	9.1 (2.19) ^{a}

Variation among sites in residual pool depth was also observed ($F_{2,6}$=7.36; p=0.0243). Residual pool depth in ELK sites was greater than both CATTLE and OPEN sites (Table 1.6). No treatment differences in maximum pool depth ($F_{2,6}$=3.85; p= 0.0841) were present, suggesting that variation in residual pool depth occurred as a result of variation in the depth of the riffle tail crest rather than in maximum pool depth. Pool–riffle ratios were also similar among grazing sites ($F_{2,6}$=0.33; p=0.7316; Figure 1.3).

Channel cross-sectional shape was evaluated using the Gini coefficient comparisons among grazing sites and stream reaches between 2004 and 2008. No significant differences were found among grazing sites in 2008 ($F_{2,6}$=0.69; p=0.5089) (Table 1.7). Evaluation of Gini coefficient values for each grazing treatment indicated that CATTLE sites exhibited the highest values across all habitat types, ELK and OPEN sites were similar in pool and run habitat, and in riffle habitat, OPEN sites had higher Gini values than ELK sites. Evaluation of the change in Gini coefficient values between 2004 and 2008 among grazing sites at all Rio San Antonio stream reaches revealed little consistency in the direction or magnitude of change for any habitat type.

Undercut bank depth did not differ among grazing sites after 5 years of exclosures ($F_{2,6}$=1.45; p=0.3282; Table 1.8). The mean undercut streambank depth in OPEN sites was greater than both CATTLE and ELK grazing sites in 2008, and increased slightly between 2007 and 2008 while cattle stocking rates were at the highest level on VCNP in 5 years. In contrast, prevalence of undercut banks was lowest in OPEN sites in comparison to CATTLE and ELK grazing sites. ELK sites

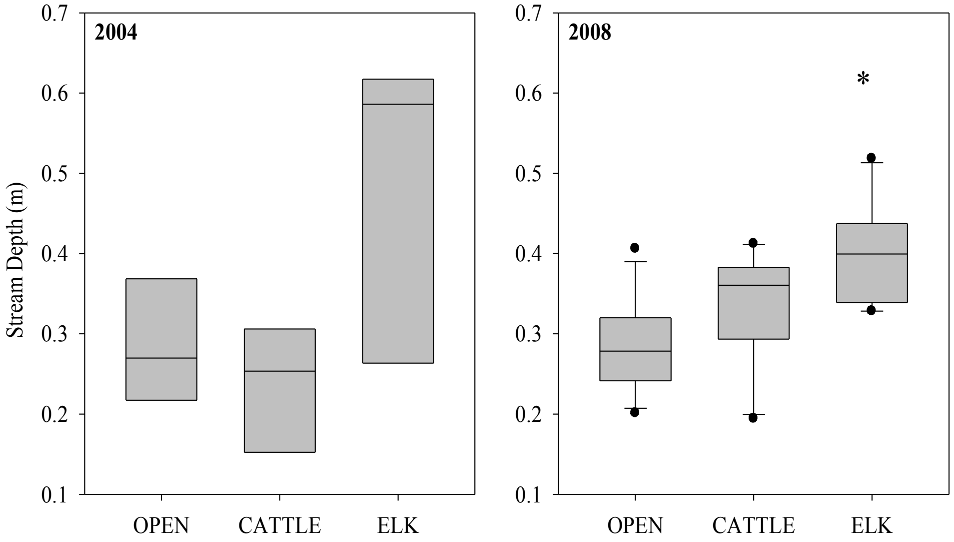


Figure 1.2: Stream depth (m) measured in pool habitat in 2004 and 2008 in OPEN, CATTLE, and ELK grazing sites on Rio San Antonio. Data were combined across lower, middle, and upper Rio San Antonio stream reaches. Boxes represent median, 25th, and 75th percentile at the lower and upper boundaries, lower and upper error bars represent 10th and 90th percentiles, and ● represent 5th and 95th percentiles. '*' denotes significant differences among grazing sites.

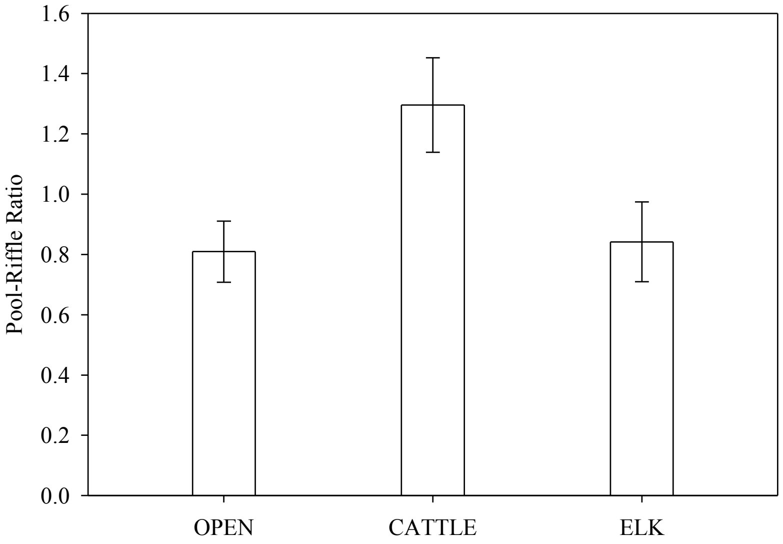


Figure 1.3: Pool–riffle ratio (mean ± S.E.) for OPEN, CATTLE, and ELK, grazing sites in 2008. Data combined for each grazing site across lower, middle, and upper Rio San Antonio stream reaches.

Table 1.6: Residual and maximum pool depth (mean ± S.E.) in 2008 within CATTLE, ELK, and OPEN grazing sites. Data were combined across lower, middle, and upper Rio San Antonio stream reaches. Superscript lowercase letters denote groupings based on statistical differences among grazing sites.

Habitat Type	Grazing Treatment	Residual Pool Depth (m)	Maximum Pool Depth (m)
Pool	OPEN	0.40 (0.02) ^{a}	0.59 (0.03) ^{a}
	CATTLE	0.46 (0.03) ^{ab}	0.67 (0.03) ^{a}
	ELK	0.51 (0.04) ^{b}	0.75 (0.09) ^{a}

Table 1.7: Changes in Gini coefficient values between 2004 and 2008. Values represent change in stream channel cross-section for pool, run, and riffle habitat in each treatment at all Rio San Antonio stream reaches.

Stream	Grazing	Habitat Unit		
Reach	Site	Pool	Run	Riffle
Lower	OPEN	-0.032	-0.052	0.065
	CATTLE	0.028	0.026	-0.152
	ELK	-0.173	-0.112	-0.006
Middle	OPEN	-0.007	-0.155	-0.030
	CATTLE	-0.018	0.042	-0.052
	ELK	-0.176	-0.187	-0.012
Upper	OPEN	-0.051	0.117	0.038
	CATTLE	-0.277	-0.037	0.058
	ELK	0.196	0.138	-0.017

exhibited an increase in prevalence by nearly 25% between 2007 and 2008 (Table 1.8). Undercut prevalence declined slightly in CATTLE sites between 2007 and 2008 while OPEN sites remained stable from 2007 to 2008.

Overall, 73-81% of all streambanks sampled in 2007 and 2008 were rated as stable/covered (Table 1.9). Between 2007 and 2008, covered/stable ratings increased 3-5% in CATTLE and ELK sites, while OPEN sites decreased by 4% in the same rating. This was likely due to increased stability in CATTLE and ELK sites which may have been a function of decreased grazing on streambank vegetation as well as lower potential for trampling or sloughing of undercut streambanks. Erosion indices showed no statistical variation in mean erosion index for grazing sites ($F_{2,6}$=0.10; p=0.9095; Table 1.9). No detectable difference in the percent fine (<4mm) sediments was observed among grazing sites ($F_{2,6}$=0.68; p=0.5410) (Table 1.10).

Discussion

Livestock and Elk Forage Utilization

Below average precipitation during the winter 2005-2006 resulted in the cessation of grazing until late summer 2006. Grazing in all other years took place during the growing season with livestock on VCNP between late May and early October. Cow-calf pairs and heifers were grazed in 2004 and 2005 and steers were grazed from 2006 through 2008. Declines in winter 2007 and summer 2008 utilization in CATTLE exclosures may have been due to decreased elk activity in exclosure areas, however, increased overwinter utilization suggests that elk were still present in these areas but may have been avoiding CATTLE exclosures (Gross and

Table 1.8: Undercut bank depth (mean ± S.E.) for CATTLE, ELK, and OPEN grazing sites in 2007 and 2008. Data were combined across middle and upper Rio San Antonio stream reaches. Superscript letters denote groupings based on statistical differences among grazing sites.

Year	Grazing Site	Undercut Depth (m)	Undercut Prevalence (%)
2007	OPEN	0.35 (0.01) ^{a}	0.31
	CATTLE	0.32 (0.01) ^{a}	0.43
	ELK	0.34 (0.03) ^{a}	0.62
2008	OPEN	0.33 (0.05) ^{a}	0.31
	CATTLE	0.31 (0.04) ^{a}	0.37
	ELK	0.23 (0.02) ^{a}	0.87

Table 1.9: Percentage of streambank classes observed in CATTLE, ELK, and OPEN grazing sites in 2007 and 2008. Data were combined across lower, middle, and upper Rio San Antonio stream reaches. Superscript letters denote groupings based on statistical differences among grazing sites.

Streambank	OPEN		CATTLE		ELK	
Parameter	2007	2008	2007	2008	2007	2008
Cover/Stable	77	73	78	81	76	81
Uncover/Stable	4	10	2	6	4	7
Cover/Unstable	7	4	5	3	11	1
Uncover/Unstable	11	13	16	10	9	10
Erosion index	1.39^{a}	1.38^{a}	1.34^{a}	1.28^{a}	1.27^{a}	1.31^{a}

Table 1.10: Results of instream substrate analysis (mean ± S.E.). Samples taken seasonally in spring and fall 2004-2008, data were combined across season, year, and stream reach. Superscript letters in each column denote significant differences among grazing sites.

Grazing Site	Percent Fine Sediments	95% CI
OPEN	0.16 (0.02) ^{a}	(0.12, 0.21)
CATTLE	0.25 (0.03) ^{a}	(0.18, 0.31)
ELK	0.21 (0.02) ^{a}	(0.15, 0.26)

Knight 2000). All grazing exclosures (CATTLE, ELK) and grazed reference sites (OPEN) exhibited stubble heights greater than 10 cm during all spring and fall sampling occasions, which is the guideline suggested by Clary and Leininger (2000) for streamside vegetation. Use declined during the summer of 2008 presumably due to increased cattle stocking rates during this time causing a shift in elk distribution away from meadow areas (Frisina 1992; Coe et al. 2001).

Results of this research suggest cattle and elk grazing observed between 2004 and 2008 did not have significant impacts streambank development or channel alteration. Research hypotheses were not supported based on the results of this study. Width–depth ratios were nearly identical in all grazing sites, with minimal changes observed between 2004 and 2008. Gini coefficient values in all habitat types indicated that alterations in channel cross–sectional shape were small, and a general trend toward increasing width–depth were observed. Undercut streambanks had the greatest depth in OPEN grazing sites in 2008, however, the prevalence of undercut banks was greatest in ELK sites. Erosion indices for OPEN, CATTLE, and ELK grazing sites ranged from 1.28 to 1.38 in 2007 and 2008, suggesting that channel morphology in Rio San Antonio has not been impacted by livestock and elk grazing over the duration of this study.

Baseline conditions in 2004 indicated that variation in average pool depth among grazing sites existed with average pool depth greater in ELK sites than both CATTLE and OPEN sites. Although average pool depth in ELK sites was detectably different among grazing sites, this represented pre-existing conditions and was not a result of livestock or elk grazing. Average pool depth decreased in ELK sites between 2004 and 2008 by approximately 8 cm while pool depth in CATTLE and OPEN sites increased over the same period (13 cm and 3 cm respectively). These findings suggest that stream channels within Rio San Antonio are aggrading throughout the watershed which may be an indicator of increased sediment loads within the drainage (Lisle 1982).

Previous exclosure studies have shown little change in stream morphology in 5 years, with little or no change after extended periods of time (Medina and Martin 1988; Kondolf 1993; Clary et al. 1996; Lancaster et al. 1998; Carline et al. 2004). Further, Kondolf (1993) cautioned that increased streamside vegetation within grazing exclosures may result in inaccurate determination of improved channel morphology and that all conclusions regarding morphological change should be based on physical measurements of streams as was conducted in this research rather than personal observations made by researchers.

Inconsistency in the direction and magnitude of change among morphological parameters evaluated in this research suggests that a portion of the observed treatment differences may have been due to natural variability in channel forming processes over time (Nagle and Clifton 2003). Low gradient (<1.5%) meadow streams such as Rio San Antonio are in a natural state of dynamic equilibrium in which erosional and depositional forces are acting constantly on streambanks (Leopold et al. 1964). Disruption of this equilibrium by livestock grazing has been shown to increase bankfull and stream width with corresponding decrease in stream depth over time (Gunderson 1968; Platts and Nelson 1985; Myers and Swanson 1995; Magilligan and McDowell 1997), theses changes were not observed during this study.

The capacity of Rio San Antonio stream morphological responses to grazing exclosures is dependent on several factors including streamside vegetation, sediment delivery, and streambank forming discharge. In order for Rio San Antonio to narrow and deepen, adequate riparian vegetation must be present creating turbulent conditions along stream margins which allows fine sediments to settle out of the water column (Tabacchi et al. 2000). Sufficient sediment supply is also necessary for channel aggradation, with streambank erosion and overland transport as the major sources of sediments in most systems (Waters 1995). Bankfull discharge which occurs on approximately 1.5 year intervals can be effective at transporting sediments allowing natural erosional and depositional events to take place, maintaining the equilibrium state of functioning lotic systems (Leopold et al. 1964).

Riparian vegetation within the Rio San Antonio watershed is relatively homogenous throughout VCNP with sedges (*Carex* spp.) and grasses (*Poa* spp.) comprising a large portion of the vegetation community. Root structure and strength of riparian species is correlated with bank stability, with sedges and rushes providing greater strength than grass species (Manning et al. 1989; Dunaway et al. 1994). Regardless of the vigor of riparian vegetation, sediment supply and bank forming streamflows are necessary for streambank aggradation. Depending on the magnitude and timing of bankfull streamflow, aggradation may take several years to occur. No streamflow data is available for Rio San Antonio within VCNP which diminishes the ability to infer the frequency and magnitude of bank forming streamflows during this research.

Current livestock stocking rates on VCNP are lower than stocking rates in the 150 years prior to federal acquisition. Livestock stocking rates varied widely throughout this research ranging from no grazing in 2006 to 2000 animals in 2008. As such, this current assessment may reflect historical alterations to stream morphology. Variation observed among grazing sites may be a result of this system returning to an equilibrium state. Variable and generally low stocking rates observed during this research support conclusions that natural variability may have had a greater influence on stream morphology between 2004 and 2008 than did riparian grazing.

In addition to natural variability in stream morphology and low stocking rates throughout this research, the low number of exclosures and transects within the exclosures may have limited the ability to detect morphological differences among grazing sites. Inherent variability in channel morphology in combination with low stocking rates and small sample sizes may have diminished the ability to detect changes in morphology resulting from riparian exclosures.

Summary and Conclusions

No detectable changes in stream channel cross-sectional shape or streambank stability were noted in the first five years following the construction of grazing exclosures on Rio San Antonio. Detectable changes in pool depth noted in 2008 may have been a function of stream habitat in Rio San Antonio approaching a dynamic equilibrium, as pool depth in all grazing sites appears to be approaching similar levels. The light grazing treatments observed in the low stocking rates, minimal riparian forage utilization, and low elk presence in the grazing sites, in combination with natural variability in stream morphology and short study duration may have contributed to these findings.

Management Implications

Continued monitoring in VCNP over the next 10 to 15 years is necessary to determine the long term response of stream morphology within livestock and elk grazing exclosures. Monitoring should be focused on riparian vegetation, and stream morphological parameters which provide the greatest amount of information regarding habitat improvement while minimizing resource expenditures. Riparian transects to determine the percentage of sedge cover along streambanks would provide data which could relate to streambank stability as well as cross-sectional shape. Wetted width–depth ratio, instream substrate, and streambank measurements including undercut prevalence, undercut depth, and bank angle have decreased levels of observer error, while providing accurate determination of land use impacts within the watershed.

Goals for stream habitat conditions should be identified by VCNP staff to include reductions in stream and channel width in conjunction with increases in stream depth. Rio San Antonio currently is classified as a C-type stream according to the Rosgen (1994) scale, with the likely historic state being an E-type stream, exhibiting lower width–depth ratios than are currently observed. Reduction in width–depth ratios may be achieved over time, however, riparian restoration of woody riparian vegetation (*Salix* spp.) may be necessary to increase the rate of recovery within this system. Evidence of beaver (*Castor canadensis*) is present in the upper

Rio San Antonio watershed suggesting that mature willow stands were historically part of the riparian community within VCNP (personal observation). Restoration of willow would provide shading along Rio San Antonio, decrease solar radiation input and reduce stream temperatures throughout the watershed. Instream habitat structures designed to reduce stream channel width generally perform poorly in C-type streams. Alterations to streamflow patterns should be considered with extreme caution, as artificial structures may have deleterious effects on stream stability resulting in unintended outcomes and often increased instability following restoration.

Cautious management of livestock grazing should continue, along with revised management of the existing grazing plan to encourage currently underutilized portions of VCNP to be grazed. Present environmental impact statements limit livestock grazing to 31,000 acres within the 90,000 acre preserve, much of which is within or directly adjacent to riparian areas bordering lotic systems in VCNP. Development of off-stream water sources along with improvement of existing stock ponds would also improve livestock distribution throughout VCNP at minimal cost to the Trust. Increasing the area available to livestock would allow improved distribution of livestock across the landscape, increasing evenness of forage utilization among upland and riparian areas while decreasing potential deleterious effects along riparian areas within VCNP.

Literature Cited

Allison, C.D., J. Boren, and T.T. Baker. 1999, Herbaceous utilization by elk in selected mountain meadows in the Gila Wilderness, Gila National Forest. New Mexico State University, Range Improvement Task Force. Cooperative Extension Service, College of Agriculture and Home Economics. Report 49 http://aces.nmsu.edu/pubs/_ritf/.

Archer, E. K., B. B. Roper, R. C. Henderson, J. L. Kershner, and S. C. Mellison. 2004. Testing common stream sampling methods for broad-scale, long-term monitoring. General Technical Report RMRS-GTR-122. Fort Collins, Colorado. U. S. Department of Agriculture, Forest Service, Rock Mountain Research Station. 15 p.

Bauer, S. B., and T. A. Burton. 1993. Monitoring protocols to evaluate water quality effects of grazing management of western rangeland streams. EPA 910/R-9-93-017. Seattle, WA: United States Environmental Protection Agency, Water Division, Surface Water Branch, Region 10. 179 p.

Baxter, C.V., K.D. Fausch, W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54: 419–431.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system for naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow, In: Armantrout, N.B. ed., Proceedings of a symposium of acquisition and utilization of aquatic habitat inventory information: Portland, OR, Western Division of the American Fisheries Society. p. 62–73.

Bowman, M. J. 1946. Readings in the theory of income distributions. Blackston, Philadelphia, PA.

Carline, R. F., M. C. Walsh, and A. M. Smith. 2004. Responses of streams to restoration of intensively grazed riparian areas: Spring Creek, West Branch Susquehanna River watershed. Report to: Chesapeake Bay Program, U.S. Environmental Protection Agency. CB–983244–01. 100 p.

Clary, W. B., N. L. Shaw, J. G. Dudleyk, V. A. Saab, J. W. Kinney, and L. C. Smithman. 1996. Response of a depleted sagebrush steppe riparian system to grazing control and woody plantings. U.S. Forest Service, Research Paper INT-RP-492.

Clary, W. C., and W. C. Leininger. 2000. Stubble height as a tool for management of riparian areas. Journal of Range Management 53:562–573.

Coe, P. K., B. K. Johnson, J. W. Kern, S. L. Findholt, J. G. Kie, and M. J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. Journal of Range Management 54:51–76.

Cook, C.W., J. Stubbendieck. 1986. Range Research: Basic problems and techniques. Society for Range Management, Denver, CO. 317 pp.

Dunaway, D., S. R. Swanson, J. Wendell, and W. Clary. 1994. The effect of herbaceous plant communities and soil texture on particle erosion of alluvial streambanks. Geomorphology 9:47–56.

Elmore, W., B. Kauffman. 1994. Riparian and watershed systems: Degradation and restoration. p 212-231 in: M. Vavra, W.A. Laycock, and R.D. Pieper (eds.), Ecological implications of livestock herbivory in the west. Society of Range Management. Denver, CO.

Frisina, M. L., 1992. Elk habitat use within a rest-rotation grazing system. Rangelands 14:93–96.

Gregory, K. J., and D. E. Walling. 1973. Drainage basin form and processes: A Geomorpholgical Approach. John Wiley & Sons. New York.

Gross, J.A., and J.E. Knight. 2000. Elk presence inside various sized cattle exclosures. Journal of Range Management 53:287–290.

Gunderson, D. R., 1968. Floodplain use related to stream morphology and fish populations. Journal of Wildlife Management 32:507–514.

Heede, B. H. 1980. Stream dynamics: an overview for land managers. United States Department of Agriculture, U.S. Forest Service, General Technical Report RM-72.

Johnson, D. H. 2002. The importance of replication in wildlife research. Journal of Wildlife Management 66: 919–932.

Kauffman, J.B., W.C. Krueger, and M. Vavra. 1983. Impacts of cattle on streambanks in north-eastern Oregon. Journal of Range Management 36:683–685.

Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications. Journal of Range Management 37:430–438.

Kauffman, J.B., R.L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. Fisheries 22(5):12-24.

Kershner, J. L., E. K. Archer, M. Coles-Ritchie, E. R. Cowley, R. C. Henderson, K. Kratz, C. M. Quimby, D. L. Turner, L. C. Ulmer, and M. R. Vinson. 2004. Guide to effective monitoring of aquatic and riparian resources. Gen. Tech. Rep. RMRS-GTR-121. Fort Collins, CO: U.S. Department of Agriculture, Rocky Mountain Research Station. 57 p.

Knapp, R. A., and K. R. Matthews. 1996. Livestock grazing, golden trout, and streams in the Golden Trout Wilderness, California: impacts and management implications. North American Journal of Fisheries Management 16:805–820.

Kondolf, G. M. 1993. Lag in stream channel adjustments to livestock exclosure, White Mountains, California. Restoration Ecology 1:226–230.

Lancaster, D. L., L. Vance, K. W. Tate, and D. Lile. 1998. The Cedar Creek Restoration project and the limits of cross-section monitoring as an indicator of change. In D.F. Potts, ed., Proceedings, AWRA Specialty Conference: Rangeland Management and Water Resources. Herndon, VA: American Water Resources Association, 136.

Leopold, L. B. 1994. A view of the river. Harvard University Press, Cambridge, MA.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco, California. 522 p.

Lisle, T. E. 1982. Effects of aggradation and degradation on riffle-pool morphology in natural gravel channels, northwestern California. Water Resources Research 18: 1643–1651.

Lisle, T. E. 1987. Using "residual depths" to monitor pool depths independently of discharge. United States Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. Res. Note PSW-394. Berkeley, CA. 4 p.

Magilligan, F. J., and P. F. McDowell. 1997. Stream channel adjustments following elimination of cattle grazing. Journal of the American Water Resources Association 33:867–878.

Manning, M. E., S. R. Swanson, T. J. Svejcar, and J. Trent. 1989. Rooting characteristics of four intermountain meadow communities. Journal of Range Management 42:309–312.

Marcuson, P.E. 1977. The effect of cattle grazing on brown trout in Rock Creek, Montana. Fish and Game Federal Aid Project. F-20-R-21-1a.

McInnis, M. L., and J. McIver. 2001. Influences of off-stream supplements on streambanks of riparian pastures. Journal of Range Management 54:648-652.

Medina, A. L., and S. C. Martin. 1988. Stream channel and vegetation changes in sections of McKnight Creek, New Mexico. Great Basin Naturalist 48:373–381.

Meehan, W. R., and W. S. Platts. 1978. Livestock grazing and the aquatic environment. Journal of Soil and Water Conservation 33:274–278.

Micheli, E. R. and J. W. Kirchner. 2002. Effects of wet meadow riparian vegetation on streambank erosion. 2. Measurements of vegetated bank strength and consequences for failure mechanics. Earth Surface Processes and Landforms 27:687–697.

Myers, T. J., and S. Swanson. 1995. Impact of deferred rotation grazing on stream characteristics in central Nevada: a case study. North American Journal of Fisheries Management 15:428–439.

Nagle, G. N., and C. F. Clifton. 2003. Channel changes over 12 years on grazed and ungrazed reaches of Wickiup Creek in eastern Oregon. Physical Geography 24:77–95.

Naiman, R.J., H. DeCamps, M. Pollack. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212.

Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621–658.

Neff, D.J. 1968. The pellet-group count technique for big game trend, census and distribution: A review. Journal of Wildlife Management 32:597–614.

Olson-Rutz, K. M., and C. B. Marlow. 1992. Analysis and interpretation of stream channel cross-sectional data. North American Journal of Fisheries Management 12:55–61.

Overton, C. K., G. L. Chandler, and J. A. Pisano. 1994. Northern/Intermountain regions’ fish habitat inventory: grazed, rested and ungrazed reference stream reaches, Silver King Creek, California. U.S. Department of Agriculture, Forest Service. General Technical Report, INT-GTR-311.

Platts, W. S., and R. L. Nelson. 1985. Impacts of rest-rotation grazing on stream banks in forested watersheds in Idaho. North American Journal of Fisheries Management 5:547–556.

Platts, W. S., C. Armour, G. D. Booth, M. Bryant, J. L. Bufford, P. Cuplin, S. Jensen, G. W. Lienkaemper, G. W. Minshall, S. P. Monsen, R. L. Nelson, J. R. Sedell, and J. S. Tuhy. 1987. Methods for evaluating riparian habitats with applications to management. United States Department of Agriculture, Forest Service. Intermountain Research Station. General Technical Report INT-221. Ogden, UT.

Pratt, M., and G. A. Rasmussen. 2001. Determining your stocking rate. Utah State University Extension Publication NR/RM/04. 7pp. http://extension.usu.edu/files/publications/publication/NR_RM_04.pdf

Rinne, J.N. 1988. Grazing effects on stream habitat and fishes: research design considerations. North American Journal of Fisheries Management 8:240–247.

Sen, A. 1973. On economic inequality. Clarendon, Oxford, UK.

Tabbachi, E., L. Lambs, H. Guilloy, A.M. Tabbacchi, E. Miller, and H. Decamps. 2000. Impacts of riparian vegetation of hydrological processes. Hydrological Processes 14: 2959–2970.

U. S. Department of Agriculture, Forest Service. 1998. WinXSPRO, A channel cross-section analyzer Version 3. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Waters, T. F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph, Bethesda, Maryland.

Werner, S. J., and P. J. Urness. 1998. Elk forage utilization within rested units of rest-rotation grazing systems. Journal of Range Management 51:14–18.

Weiner, J., and O. T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334–336.

CHAPTER 2: BROWN TROUT RESPONSE TO LIVESTOCK AND ELK GRAZING WITHIN VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

Abstract

Livestock grazing has been proposed as one of the major threats to the persistence of stream fish populations in the western United States. Responses of brown trout individual and population level characteristics to livestock and elk grazing were monitored over the first 5 years of grazing exclosures on Rio San Antonio, Valles Caldera National Preserve (VCNP), New Mexico. Three stream reaches along Rio San Antonio (lower, middle, upper) were established in 2004 with grazing exclosures allowing the comparison of livestock and elk grazing to ungrazed reference reaches. Five years after the elimination of grazing, no responses among brown trout populations within elk or cattle exclosures were observed. Evaluation of riparian forage utilization showed utilization rates ranging from 6 to 26% in OPEN and CATTLE sites, which in combination with low stocking rates suggest that current livestock or elk management have minimal impact on stream fish populations. Mean displacement distance in all grazing sites was 0 m when combined across seasons and age class. Turnover rates were similar among OPEN (0.39), CATTLE (0.36), and ELK (0.38) grazing sites in 2008. The proportion of resident fish was comparable among grazing sites. Grazed reference sites had the highest proportion of resident trout (73.2%), followed by cattle exclosures (66.8%), and elk exclosures (61.8%). Growth rates were similar among grazing sites in 2007 and 2008 (range; ΔTL=0.061-0.068, ΔW=0.19-0.21). Condition factor among all age classes (0-IV+) were not

detectably different among grazing sites. Between 2004 and 2008, adult (>120 mm TL) brown trout density were not different among OPEN (41.9 fish/100m^2), CATTLE (45.1 fish/100m^2), and ELK (62.5 fish/100m^2) grazing sites. Density for juvenile (<120 mm TL) brown trout was also similar among grazing sites (range=7.4-10.6 fish/100m^2). Similarly, standing crop was not different among grazing sites for adult or juvenile brown trout. Light stocking rates and low forage utilization among Rio San Antonio grazing sites from 2004 to 2008, in combination with minimal change in stream morphology resulted in no detectable response in brown trout populations among grazing exclosures.

Introduction

Conservation and management of salmonid populations in the western United States requires fishery biologists to have considerable understanding of the land-use practices influencing stream fish populations. Livestock grazing is among the most commonly cited land-use practices posing negative influences on stream fish populations. However, literature reviews have shown inconclusive arguments in the previous literature on the responses of stream fish populations to grazing (see Larsen et al. 1998; Rinne 1999 for reviews). Salmonid responses to management of riparian grazing is best described as an interaction between the limiting pressure imposed on riparian vegetation by grazing and the stabilizing functions provided to lotic systems by riparian vegetation. Current management is focused on controlling the impact of grazing on streams by managing the season, intensity, and duration of grazing plans (Clary and Kruse 2004). By managing riparian grazing in this manner, negative impacts of livestock may be minimized over time. Reduction of grazing or construction of grazing exclosures may be necessary under severely degraded conditions.

Research regarding population level changes in stream fish due to livestock grazing has focused on stream habitat characteristics and game fish, with few of these studies having any data concerning spatial variability among study reaches prior to exclosures (see Rinne 1999 for review). Positive responses of stream fish have widely been reported following the removal of grazing or construction of riparian exclosures. Higher adult density and biomass in ungrazed sites in comparison to grazed reaches has been shown (Gunderson 1968; Marcuson 1977; Summers et a. 2008). Higher growth rates and emigration of large individuals have been hypothesized as factors resulting in increased fish length in ungrazed reaches (Marcuson 1977; Keller and Burnham 1982; Saunders and Fausch 2007; Summers et al. 2008). Clarkson and Wilson (1995) found that salmonid biomass was related to the level of bank damage caused by ungulates, with increased damage resulting in decreased biomass.

While increased populations have been noted, other studies have reported no change in trout populations following livestock exclosure. Chapman and Knudsen (1980) compared grazed and ungrazed sites and found no difference among Age-0 and adult salmonids. Platts and Nelson (1985) noted improvements in stream habitat within grazing exclosures, however, no change in trout densities were observed. Variability in the recovery of trout populations following the elimination of grazing suggests that factors other than riparian vegetation communities or instream habitat may be influencing salmonid populations.

Though much of the previous research has focused on population level responses to livestock grazing, little information regarding individual fish response to grazing is known. The goal of this research is to evaluate both individual and population level responses to livestock and elk grazing, research objectives were to characterize movement behavior and growth rates among individual brown trout and to determine brown trout density, biomass, and condition at the population level in response to riparian grazing by livestock and elk. Specific research hypotheses included:

1) No response of brown trout populations to livestock or elk grazing;
2) Greater movement among brown trout away from sites open to livestock and elk grazing due to decreased instream cover and physical disturbance;
3) Increased growth rates among marked brown trout in elk exclosures due to increased allochthonous input;

Methods

Cattle and Elk Grazing

Animal unit month estimates were obtained using conversion factors (cow-calf 1.0, heifer/steer 0.8, and elk 0.60; Pratt and Rasmussen 2001). Elk population estimates were obtained from the New Mexico Department of Game and Fish (S. Liley). Livestock stocking rates varied during this study based on management recommendations from VCNP range managers. Drought conditions observed from

November 2005 through April 2006 resulted in diminished range conditions and no livestock were allowed to graze until late August 2006 following summer monsoon rains. Elk populations within VCNP during this research remained stable with population estimates between 2000 and 3000 animals from 2004 to 2008 (Table 1.1).

Riparian forage utilization by elk and livestock was monitored using paired-cage comparisons within CATTLE and OPEN sites in 2007 and 2008 (Cook and Stubbendieck 1986). Cages were constructed using cattle panels (4 gauge) with 10 x 15 cm openings, in the shape of pyramids covering an area of approximately 1 m^2 (Allison et al. 1999). Within each OPEN and CATTLE treatment, 3 paired-cages were established within the riparian zone at the beginning of the growing season in early May. Plots were haphazardly placed within 10 m of streambanks to specifically monitor riparian forage utilization. Vegetation was clipped using 0.185 m^2 rectangular plots within each protected plot prior to cattle grazing (May), and after cattle grazing had ceased (September/October). Clipped plots from inside cages were compared to clipped plots taken from unprotected areas within similar vegetation communities (Cook and Stubbendieck 1986). Plots with negative utilization values were zeroed (Werner and Urness 1998). Utilization rates were calculated for each paired plot and mean utilization was calculated for each treatment. Utilization rates for CATTLE and OPEN sites were compared seasonally (October through April, and May through September) to evaluate the effect of elk (October through April) and the combined effect of elk and cattle (May through September).

Table 2.1: Cattle stocking rates and elk population estimates from 2004 to 2008 on Valles Caldera National Preserve, NM.

	Year				
	2004	2005	2006	2007	2008
Livestock	660	600	100	500	2000
AUM[1]	2376	2160	180[a]	1600	6400
Elk[2]	2000-2500	2000-2500	2000-2500	2000-2500	2000-2500
AUM[3]	10800-13500	10800-13500	10800-13500	10800-13500	10800-13500

[1] AUM calculation based on conversion factors for cow-calf, heifer/steer for 4 months

[2] Population estimates for elk obtained from NM Game and Fish.

[3] AUM calculation based on conversion factor for elk for 9 months

[a] Stocking rate based on 2.25 months of use in 2006

Stubble height was measured at 0.25 m intervals along 30 m transects, which were established perpendicular to stream flow and centered on the stream allowing assessment of riparian vegetation along both streambanks. Four transects were established in each grazing site at all Rio San Antonio stream reaches in a random stratified arrangement. Buffer areas (25 m) were established along the upstream and downstream boundaries of each exclosure, preventing transects from falling into areas near exclosure fences. Stubble height measurements from each transect were averaged to determine overall stubble height within each grazing site and compared to riparian management guidelines identified by Clary and Leininger (2000).

Elk presence within all grazing sites was monitored in 2007 and 2008 using pellet group counts according to methods described by Neff (1968). Samples were collected in fall 2007, spring 2007, and fall 2008.

Mark-Recapture Sampling

Passive integrated transponder (PIT) tags were implanted in brown trout from study reaches in each grazing site at all three Rio San Antonio stream reaches to monitor movement and growth rate. Following fish collection using methods described below, brown trout were anesthetized with tricaine methanesulfonate (MS-222) to minimize stress during the implantation procedure. Individuals were then measured for TL (± 1 mm), weighed (± 1 g), PIT tags (12 mm; Biomark Inc., Boise, Idaho) were implanted in the right dorsal musculature posterior to the dorsal fin, and adipose fin clipped which provided double marking to monitor tag retention (Prentice et al. 1990; Ombredane et al. 1998; Cucherousset et al. 2006). Tagging protocol varied over the course of this study, with the initial goal being 30 marked individuals in each grazing treatment throughout the watershed. Tagging effort increased in 2008 in an effort to more accurately characterize movement behavior, with all individuals captured in middle and upper study reaches, and all individuals captured within the entire lower grazing site being marked during April, May, July, and September sampling occasions.

Recapture sampling in April, May, July, and September 2007-2008 took place over three consecutive days, during which grazing sites were sampled using single pass electrofishing starting at the downstream boundary of each grazing site and progressing upstream. Stream reaches (50 m) immediately downstream and upstream from the study reach established in 2004 were sampled on two consecutive electrofishing passes to increase capture efficiency. Main study reaches within each grazing site were isolated with block nets at the upstream and downstream boundaries and sampled using three electrofishing passes. November 2007 and 2008 sampling included approximately 17 km of single pass electrofishing outside normal sampling areas throughout Rio San Antonio to monitor long-distance movement related to spawning. During all sampling occasions at the middle Rio San Antonio stream reach, single pass electrofishing was completed on 500 m of stream between ELK and CATTLE sites.

Movement was calculated between consecutive recapture sampling sessions as the distance between the upstream boundaries of the release location and subsequent capture location for individuals moving within grazing sites. Turnover rates (1-[proportion of marked individuals]) providing a measure of immigration o f unmarked individuals into the study reach were calculated for May, July, September, and November sampling occasions in 2008 (Rodriguez 2002).

Individual growth rates were determined between consecutive recapture occasions using the instantaneous growth equations developed by Swift (1961):

$$\Delta TL = \frac{\ln L_2 - \ln L_1}{t_2 - t_1} \qquad \Delta W = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where ΔTL is the change in total length over the interval between captures, $\ln L_1$ and $\ln L_2$ are natural log initial and final total length, ΔW is the change in weight over the capture interval, $\ln W_1$ and $\ln W_2$ are natural log initial and final weight, and t_1 and t_2 are initial and final time in days.

Fish Collections

Within each grazing site (OPEN, CATTLE, ELK) at all stream reaches (lower, middle, upper), 50 m study reaches were established to monitor fish population responses to grazing exclosures. Study reaches included at least one pool, run, and riffle habitat unit. Sampling took place yearly during spring (May) and fall (September/October) between 2004 and 2008, with baseline data collected in 2004. During sampling, study reaches were isolated using 6 mm seine nets and sampled using backpack electrofishing units (Model LR-24, Smith-Root Inc., Vancouver, WA). Three consecutive upstream electrofishing passes were made on each study reach, during which fish were removed from the stream and held in tubs containing 0.8% salt solution to minimize stress during handling. Following each electrofishing pass, all captured fish were measured for total length (TL) to the nearest 1 mm and weighed to the nearest 1.0 g on an electronic balance. Fish were then held in live cars in the stream until completion of the third electrofishing pass at which time all fish were released into the study reach.

Determination of age-group was made for each sampling occasion (spring and fall), at each stream reach in Rio San Antonio (lower, middle, upper), from 2004 to 2008 to monitor changes in population structure throughout the course of this research. Length-frequency distributions were constructed using TL data collected during field sampling to identify age classes 0-IV+. Total length data were partitioned into 3 mm intervals with the initial interval being the minimum observed total length, and the final interval being the maximum total length observed among all individuals during each sampling period. Length-frequency distributions provided no clear breaks in the distribution of TL due to variable growth rate among individuals in older age-groups, thus individuals with TL greater than 290 mm were grouped as Age-IV and older, (Devries and Frie 1996).

Population estimates were calculated for each species based on Zippen (1958) maximum likelihood removal methods. Density (fish/100m^2) and standing crop (kg/ha) were estimated separately for adult (>120 mm TL) and young-of-year (<120 mm TL) trout to minimize potential overestimation of population abundance due to differential catchability among size classes. Relative density and standing crop were calculated for brown trout observed in each sampling reach using mean stream width, stream depth, and study reach length collected from cross-sectional transects within each grazing treatment. Brown trout recruitment was estimated as the number of

Age-0 individuals collected in the fall following spawning (ie., 2004 recruitment refers to 2003 spawning class). Strength of each spawning class (2003-2007) was determined by comparing density estimates for Age-0 brown trout at each grazing treatment to the overall confidence interval (95%) for Age-0 brown trout estimates at the corresponding grazing site from 2004 to 2008. Spawning classes were considered weak (W) when density estimates fell below the lower limit of the confidence interval, average (A) when density estimates were within the confidence interval, and strong (S) when density estimates were above the upper limit of the confidence interval.

Total length and weight data were used to estimate overall fish condition among brown trout in all age classes (0-IV+). Condition (K_{TL}) was calculated as:

$$K_{TL} = [\text{Weight (g)} / \text{TL (mm)}^3]*10^5$$

Statistical Analysis

Statistical analysis was performed using SAS version 9.1.3 (SAS Institute Inc. Cary, NC 2003). Effects of grazing on brown trout movement and growth rate were analyzed using Kruskal-Wallis non-parametric analysis of variance. Data were pooled across years, seasons, stream reaches, and age classes to determine grazing effects on growth rate. Mann-Whitney U-tests using Bonferroni corrected alpha levels were used for all pairwise comparisons following significant Kruskal-Wallis analysis (Zar 1984). Growth rate variation due to grazing was limited to individuals exhibiting displacement distances less than 50 m between successive relocations or total movement <500 m during the entire study. All other individuals were omitted from analysis.

Chi-square tests were used to compare the probability of individual fish being resident or mobile among grazing sites. Probability of movement was determined using logistic regression (Hosmer and Lemeshow 1989). Individual displacement ≥50 m during consecutive recapture sessions was considered movement. Individuals were coded as mobile (1) or resident (0), and univariate logistic regression analysis was performed using the logistic procedure in SAS. Categorical variable for grazing site were analyzed to evaluate movement behavior among sites. Parameters were considered significant at α=0.05. Odds ratios were used to determine the magnitude of individual parameter effects on the probability of movement (Hosmer and Lemeshow 1989).

Repeated measures analysis of variance (RMANOVA) using the GLM procedure in SAS was used to determine the effects of grazing (CATTLE, ELK, OPEN) on relative density and standing crop estimates, total length, and condition, with grazing site as the between subjects group, and year (2004-2008) as the repeated variable. Density and standing crop estimates were combined across lower, middle, and upper stream reaches due to limited replication within Rio San Antonio. Analyses were considered significant at α=0.05. Significant group effects and interaction effects observed in RMANOVA were evaluated using the least squares mean procedure at α=0.05.

Visual inspection of reach specific grazing effects at the lower, middle, and upper stream reaches were performed using median and 1st and 3rd quartiles for density, standing crop, and condition data collected from 2004 to 2008. Grazing sites within each stream reach were compared (OPEN-CATTLE, OPEN-ELK, CATTLE-ELK) and considered different when the lower median value in the comparison was less than the 1st quartile of the higher median value, and the higher median in the comparison was greater than the 3rd quartile of the lower median value.

Results

Livestock and Elk Forage Utilization

Utilization estimates from paired-cage comparisons in 2007 and 2008 were well below riparian grazing standards established for VCNP (40%; VCNP Interim Grazing Strategy). Differential utilization rates in 2007 and 2008 in OPEN sites reflect variation in stocking rates observed during that time (Figure 1.1).

Stubble height measurements in spring 2007 showed that ELK exclosures had significantly greater stubble height than both CATTLE exclosures and the grazed reference site ($F_{2,33}=18.43$; $p<0.0001$). Fall 2007 ($F_{2,33}=5.83$; $p=0.007$) and 2008 ($F_{2,26}=19.00$; $p<0.0001$) measurements also differed among grazing sites with ELK exclosures exhibiting greater vegetation height than OPEN sites (Table 1.2). Elk presence within OPEN sites and CATTLE exclosures was similar during summer 2007 and winter 2007-2008 (Table 1.3). Mean elk density (elk/ha) in CATTLE exclosures from 2007-2008 was 0.13, with slightly higher density observed in OPEN sites (0.15) over the same period.

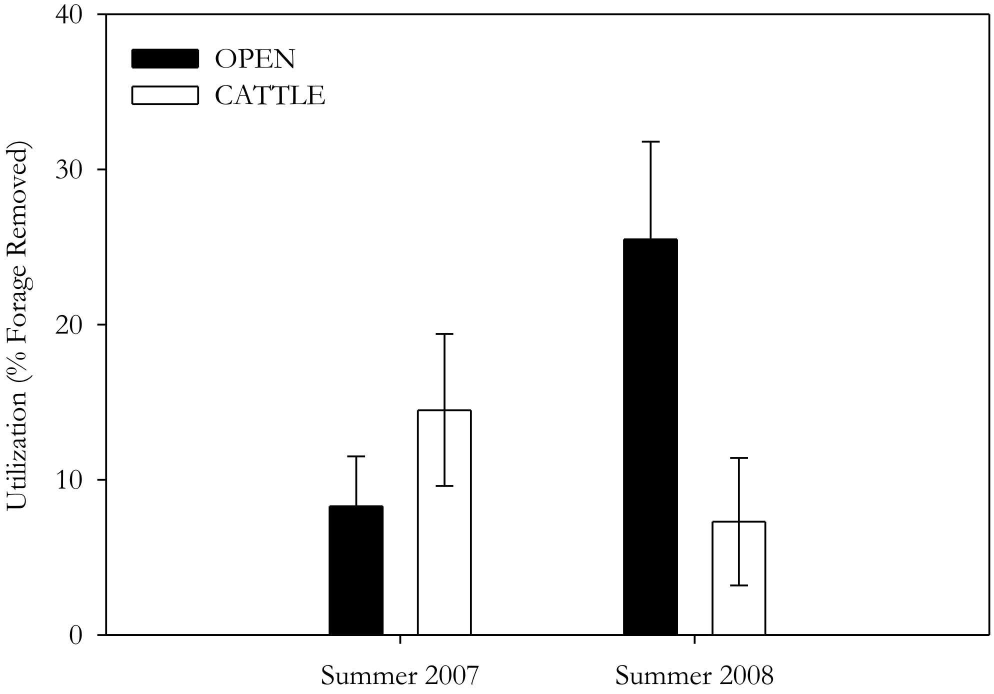


Figure 2.1: Forage utilization rate (% available forage removed by grazing) determined from paired-plot comparisons in CATTLE and OPEN exclosures.

Table 2.2: Vegetation stubble height (cm; mean ± S.E.) in CATTLE, ELK, and OPEN grazing sites. Similar superscripts among grazing sites indicate groupings based on Fisher's LSD at α=0.05.

Grazing Exclosure	2007		2008	
	Spring	Fall	Spring	Fall
OPEN	18.9 (0.45) ^{a}	31.4 (1.99) ^{a}	11.4 (0.58) ^{a}	25.1 (2.03) ^{a}
CATTLE	19.8 (0.59) ^{a}	36.3 (1.81) ^{ab}	11.8 (0.46) ^{ab}	40.4 (1.89) ^{b}
ELK	23.9 (0.78) ^{b}	40.7 (1.97) ^{b}	13.3 (0.80) ^{b}	38.6 (1.65) ^{b}

Table 2.3: Elk presence (elk/ha) within grazing exclosures during summer (May-September) and winter (October-May) and combined across lower, middle, and upper stream reaches.

Grazing Site	2007	2008	
	Summer	Winter	Summer
OPEN	0.18	0.13	0.13
CATTLE	0.13	0.18	0.07
ELK	0	0	0

Recapture Sampling and PIT Tag Retention

Between November 2006 and September 2008, 1,446 brown trout were implanted with PIT tags. Over the duration of this research a total of 491, 431, and 521 trout were marked in OPEN, CATTLE, and ELK grazing sites respectively. Recapture rates varied throughout this study from 0.21 to 0.60 with lowest recapture rates observed during high stream discharge in April 2007 and 2008 (see Appendix A.3 for details). From April 2007 through November 2008, a total 2,187 recaptures were recorded among 1,125 marked individuals, accounting for 78% of the marked population. Of the marked brown trout encountered during sampling, 65% were recaptured on multiple occasions (2-10 recaptures) and 35% were recaptured on one occasion. Tag losses were minimal (2.01%), and similar to those reported by Prentice et al. (1990). No complete adipose fin regeneration was noted, partial fin regeneration was rare and fin clips remained identifiable when partial regeneration was evident.

Individual Level Response to Riparian Grazing

Median displacement distance between successive encounter occasions in all grazing sites was 0 m. Displacement distance among marked brown trout was significantly different among grazing exclosures (χ^2=7.448, df=2, p=0.0241). Brown trout exhibited the highest mean displacement in ELK exclosures distance (82.1 m ± 39.58) followed by CATTLE (65.1 m ± 51.17), and OPEN (-6.9 m ± 31.16) sites (Table 2.4). Displacement distances among brown trout were significantly different between CATTLE and OPEN sites (χ^2=7.695, df=1, p=0.0055). The percentage of recaptures occurring within 50 m from the previous location was similar among grazing sites (Figure 2.2). Turnover rate was not significantly different among grazing sites ($F_{2,30}$=0.07; p=0.929) in 2008 (Table 2.4). Grazing also had an effect on the probability of movement with brown trout captured in CATTLE exclosures having 48% and 43% higher odds of movement than in ELK and OPEN exclosures, respectively (Table 2.5). The percent of resident fish were similar among grazing sites (Table 2.6). Grazing had no effect on ΔTL (χ^2=0.2569, df=2, p=0.8795) or ΔW (χ^2=0.2411, df=2, p=0.8865) (Table 2.4).

Population Level Response to Riparian Grazing

Brown trout density did not vary among grazing sites for adult ($F_{2,6}$=0.17; p=0.8468) or juvenile fish ($F_{2,3}$=0.47; p=0.6632) (Figure 2.3). Significant year effects were observed among adult brown trout ($F_{9,54}$=3.13; p=0.0042), due to declines in density during 2005 and 2007 spring sampling (for detail see Appendix A.1). Differences in brown trout density among grazing sites within the same stream reach revealed minimal support for response of brown trout density to the elimination or reduction of riparian grazing. Density was highest in the ELK grazing site in the lower stream reach, similar among all sites in the middle stream reach, and highest in the ELK grazing site in the upper reach (Figure 2.4).

Standing crop did not vary among grazing sites for either adult ($F_{2,6}$=0.27; p=0.7697) or juvenile ($F_{2,3}$=0.14; p=0.8715) brown trout between 2004 and 2008 (Figure 2.3). Significant year effect was observed for adult brown trout ($F_{9,54}$=2.89; p=0.0073) due to increased biomass observed during spring 2004 and fall 2008

Table 2.4: Instantaneous growth rate (ΔTL, ΔW; mean ±S.E.), displacement (m) and turnover rate for marked brown trout in OPEN, CATTLE, and ELK grazing sites, data were combined across stream reach, season, year, and age class. Superscript letters represent statistical differences among grazing sites.

Grazing Exclosure	Instantaneous Growth Rate ΔTL	ΔW	Displacement (m)	Turnover Rate
OPEN	0.06 (0.003) ^{a}	0.19 (0.013) ^{a}	-6.9 (31.15) ^{a}	0.39 (0.05) ^{a}
CATTLE	0.06 (0.003) ^{a}	0.21 (0.015) ^{a}	65.1 (51.18) ^{b}	0.36 (0.05) ^{a}
ELK	0.06 (0.003) ^{a}	0.19 (0.013) ^{a}	82.1 (39.58) ^{ab}	0.38 (0.05) ^{a}

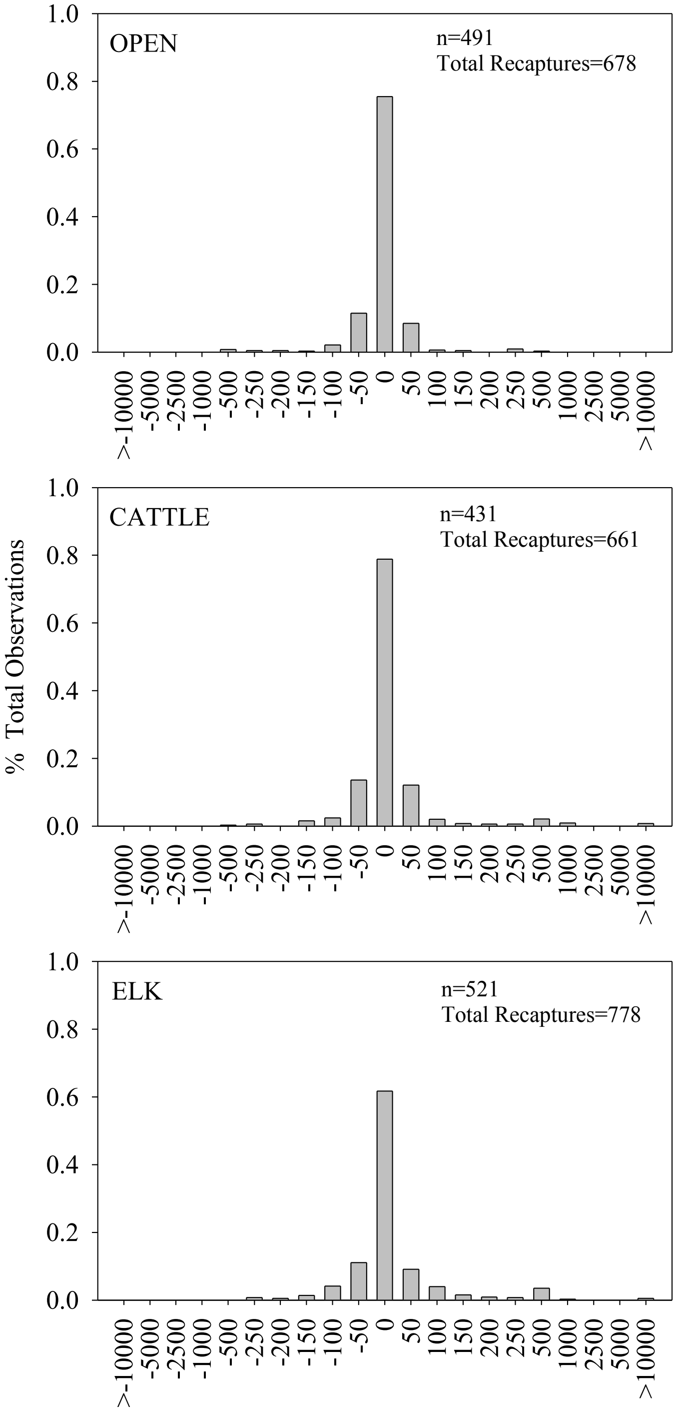


Figure 2.2: Displacement distance (m) plotted as the percentage of successive recaptures in OPEN, CATTLE, and ELK grazing sites. Data were combined across lower, middle, and upper stream reaches. Negative values signify downstream movement. Note that the scale changes to the left and right of 0 m.

Table 2.5: Results of logistic regression of the probability of brown trout movement related to grazing site. Model parameters were considered significant at $\alpha=0.05$ Significant models shown in **bold**.

	Likelihood Ratio			Parameter Estimate				Odds	95% CI	
Variable*	n	χ^2	p	β	S.E.	χ^2	p	Ratio	Lower	Upper
Treatment	**2187**	**8.66**	**0.0131**							
CATTLE/ELK	**2187**	**8.66**	**0.0131**	**0.360**	**0.152**	**5.65**	**0.0174**	**1.43**	**1.065**	**1.929**
CATTLE/OPEN	**2187**	**8.66**	**0.0131**	**0.393**	**0.148**	**6.98**	**0.008**	**1.48**	**1.107**	**1.984**
OPEN/ELK	2187	8.66	0.0131	-0.033	0.155	0.05	0.831			

Table 2.6: Results of Chi-square tests evaluating the probability of resident or mobile life history among individual brown trout in Rio San Antonio. Brown trout were classified as mobile if displacement distance was ≥50 m.

Comparison		Percent Resident	Percent Mobile	χ^2	df	p
Overall Watershed		64.5	35.5	186.49	1	<0.0001
Grazing site	OPEN	73.2	26.8	146.84	1	<0.0001
	CATTLE	66.8	33.2	87.44	1	<0.0001
	ELK	61.8	38.2	36.87	1	<0.0001

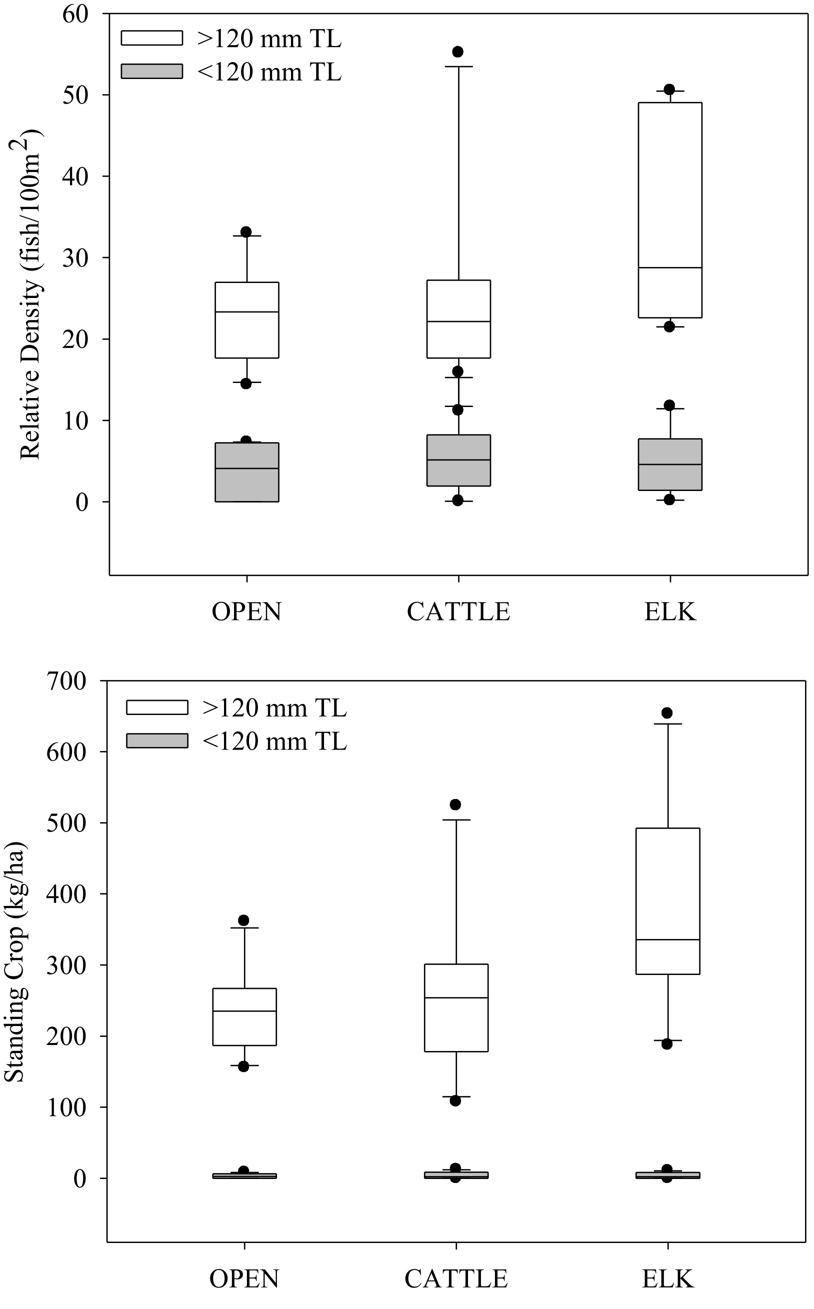


Figure 2.3: Relative density (fish/100m^2; a), standing crop (kg/ha; b) for adult (>120 mm TL) and juvenile (<120 mm TL) brown trout, and mean total length (mm; c) estimates for brown trout in CATTLE, ELK, and OPEN grazing sites. Box represents median, 25th, and 75th percentile at the lower and upper boundaries respectively, lower and upper error bars represent 10th and 90th percentiles, and ● represent 5th and 95th percentiles.

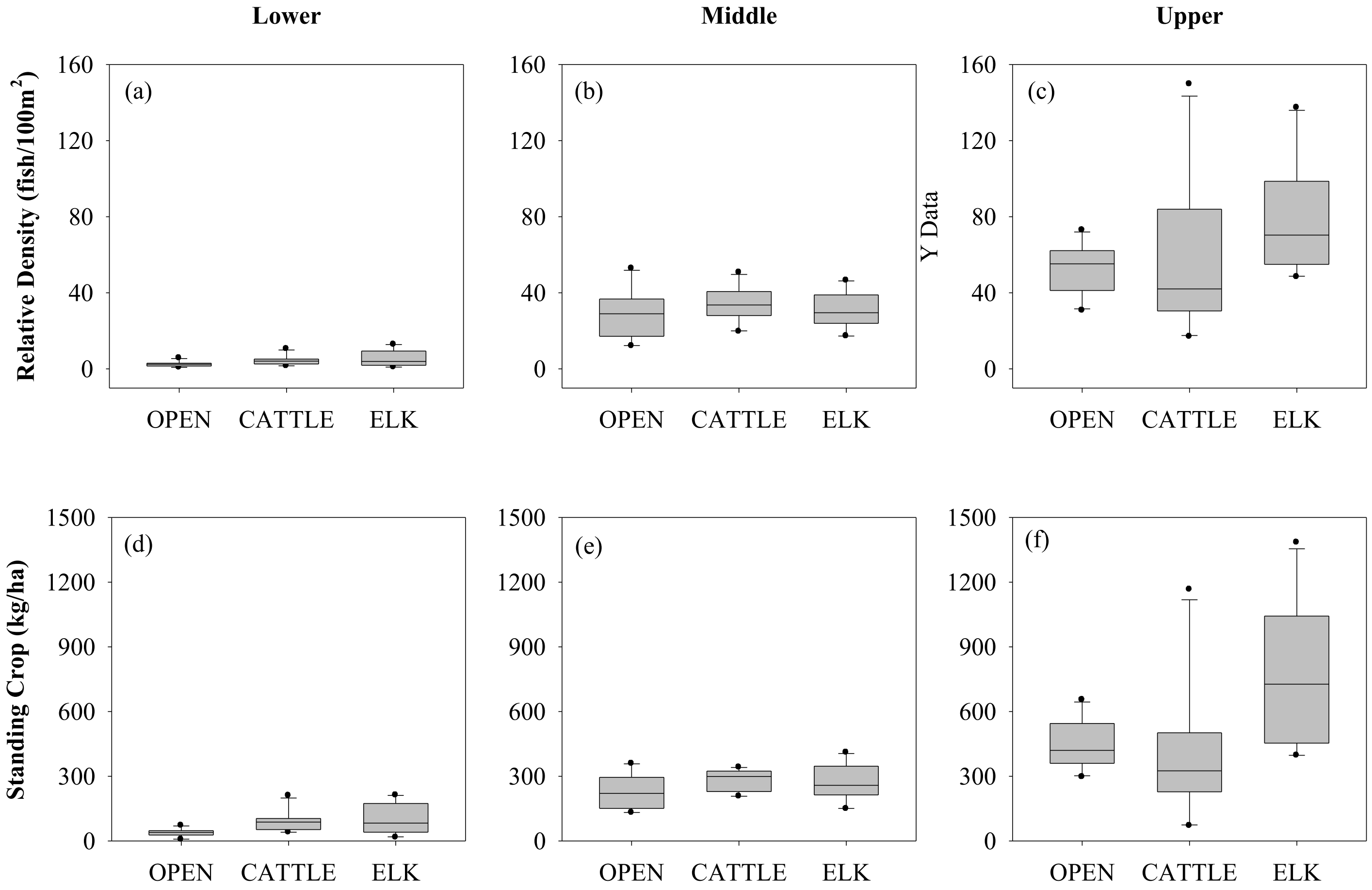


Figure 2.4: Relative density (fish/100m^2; a, b, c) and standing crop (kg/ha; d, e, f) estimates for adult brown trout in CATTLE, ELK, and OPEN grazing sites in lower (a, d), middle (b, e), and upper (c, f) Rio San Antonio stream reaches. Box represents median, 25th, and 75th percentile at the lower and upper boundaries respectively, lower and upper error bars represent 10th and 90th percentiles, and ● represent 5th and 95th percentiles.

sampling (see Appendix A.1). Visual inspection of standing crop estimates among grazing sites showed variation among all stream reaches. Within the lower and middle stream reaches, the CATTLE site exhibited highest standing crop followed by ELK and OPEN, in the upper stream reaches, both ELK and CATTLE grazing sites exhibited greater standing crops than did the OPEN site (Figure 2.3).

Brown trout recruitment was similar among grazing sites within each Rio San Antonio stream reach (lower, middle, upper) from 2004 to 2008. One year cycles of average/strong spawning classes (2004, 2006, 2008) followed by weak spawning classes (2005, 2007) were observed in the middle grazing site. Among grazing exclosures at the upper site, the OPEN treatment exhibited the lowest variability in recruitment from 2004 to 2008 (Coefficient of Variation (CV)=16.5), variability was greater in both CATTLE (CV=46.5) and ELK (CV=51.3) exclosures over the same period. Highest mean recruitment was observed in CATTLE exclosure at the lower and middle grazing sites and in the OPEN treatment at the upper grazing site (Table 2.7).

From 2004 to 2008, mean TL was not significantly different among grazing sites in either spring ($F_{2,6}$=0.00; p=0.99) or fall sampling ($F_{2,6}$=0.04; p=0.96) (Table 2.8). No significant effect of grazing site was noted for K_{TL} among all brown trout age classes (0-IV+) between 2004 and 2008 (Figure 2.5). Visual inspection of K_{TL} revealed no differences in K_{TL} among grazing sites within any of the Rio San Antonio stream reaches (see Appendix A.2).

Table 2.7: Mean (95%CI) brown trout recruitment (fish/100m^2) in CATTLE, ELK, and OPEN grazing exclosures at lower, middle, and upper Rio San Antonio grazing sites from 2004 to 2008. W=weak recruitment, A=average recruitment, S=strong recruitment.

		Mean	Year				
Site	Treatment	(95% CI)	2004	2005	2006	2007	2008
Lower		0.6 (0-1.4)	0.0 A	0.0 A	2.3 S	0.6 A	0.3 A
	OPEN	0.6 (0-1.71)	0.0 A	0.0 A	1.0 A	2.0 S	0.0 A
	CATTLE	1.2 (0-3.9)	0.0 A	0.0 A	5.0 S	0.0 A	1.0 A
	ELK	0.2 (0-0.75)	0.0 A	0.0 A	1.0 A	0.0 A	0.0 A
Middle		9.3 (5.6-13.1)	13.3 S	2.6 W	11.0 A	3.6 W	16.0 S
	OPEN	8.6 (1.9-15.2)	12.0 A	5.0 W	16.0 S	3.0 W	7.0 S
	CATTLE	11.0 (0-22.5)	15.0 S	2.0 W	9.0 A	4.0W	25.0 S
	ELK	8.4 (0.7-16.1)	13.0 A	1.0 W	8.0 A	4.0 W	16.0 S
Upper		14.3 (11.3-17.4)	13.6 A	12.3 A	8.6 W	20.3 S	16.6 A
	OPEN	17.8 (14.1-21.5)	17.0 A	19.0 S	14.0 A	22.0 S	17.0 A
	CATTLE	13.0 (5.5-20.5)	17.0 A	9.0 W	5.0 W	20.0 S	14.0 A
	ELK	12.2 (4.4-19.9)	7.0 W	9.0 W	7.0 W	19.0 S	19.0 S

Table 2.8: Total length observed among brown trout in age classes 0-IV+ during spring and fall sampling from 2004 to 2008 (Mean ± S.E.). Data combined across lower, middle, and upper stream reaches.

		Grazing Site		
Season	Age Class	Open	Cattle	Elk
Spring	0	44.1 (0.69)	41.4 (1.35)	42.4 (1.17)
	I	130.4 (1.56)	125.1 (2.4)	127.4 (1.61)
	II	190.5 (1.31)	196.0 (1.83)	200.2 (1.23)
	III	225.9 (1.18)	231.7 (1.44)	230.5 (1.14)
	IV+	266.7 (2.53)	274.2 (2.61)	271.6 (2.32)
Fall	1	100.6 (1.24)	91.6 (1.23)	95.6 (1.66)
	I	172.9 (1.15)	177.4 (1.45)	176.2 (1.24)
	II	214.7 (0.67)	217.8 (0.88)	215.9 (0.86)
	III	244.4 (0.88)	248.1 (1.01)	245.5 (0.75)
	IV+	287.6 (2.74)	292.3 (2.87)	288.9 (2.49)

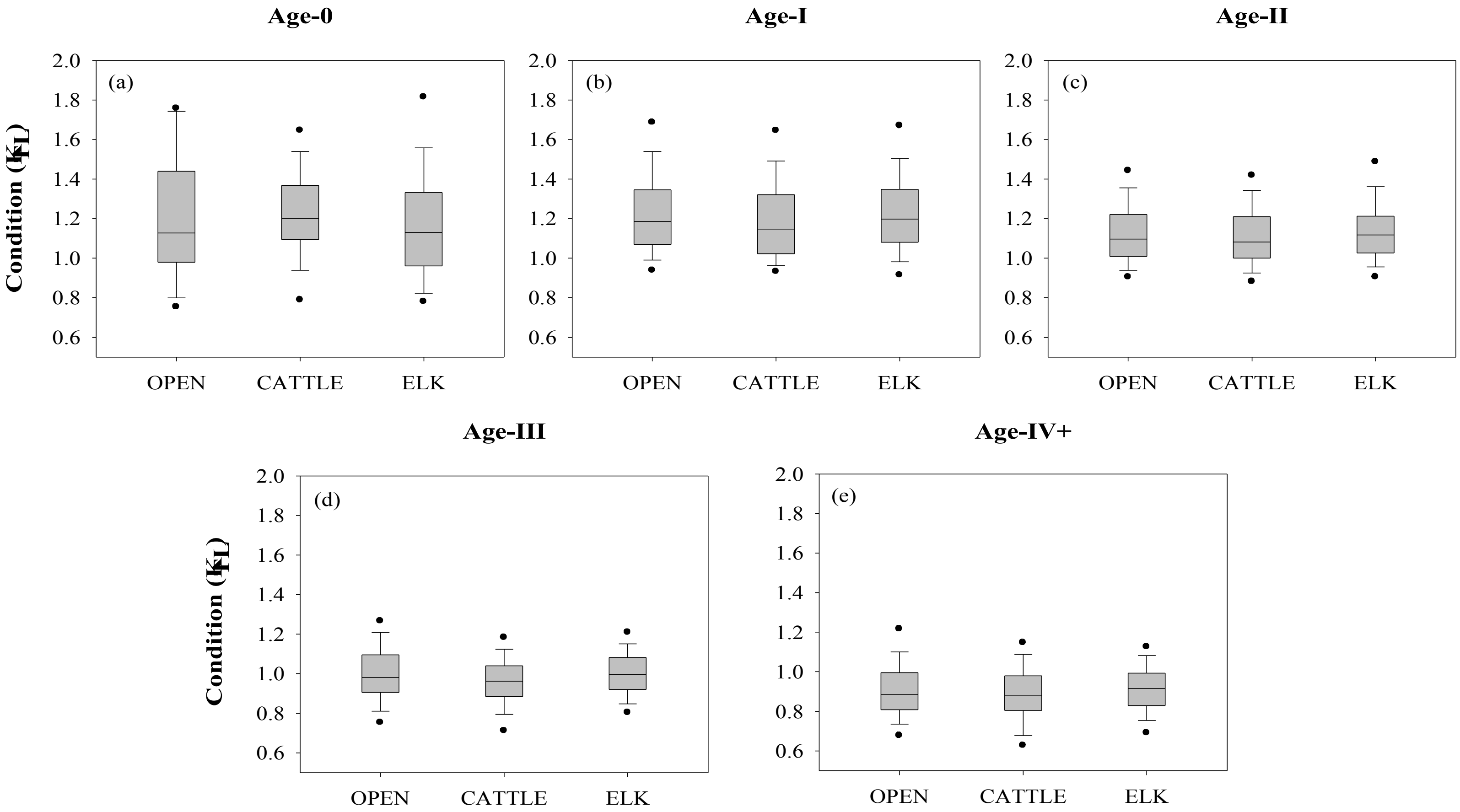


Figure 2.5: Brown trout condition (K_{TL}) scores for Age-0 (a), Age-I (b), Age-II (c), Age-III (d), and Age-IV+ (e) among CATTLE, ELK, and OPEN grazing exclosures data were combined across lower, middle, and upper stream reaches. Box represents median, 25th, and 75th percentile at the lower and upper boundaries respectively, lower and upper error bars represent 10th and 90th percentiles, and ● represent 5th and 95th percentiles.

Discussion

Response of Brown Trout to Riparian Grazing Exclosure

Livestock and elk grazing did not influence the brown trout population on the Rio San Antonio during the first five years of grazing exclosures. Hypothesized differences among grazing sites for both movement and growth rate were not supported by the results of this research. Mean displacement distance in OPEN grazing sites was lower than both CATTLE and ELK sites, which implies that movement behavior among brown trout in Rio San Antonio was driven by biotic and abiotic factors other than riparian grazing. Growth rates were also similar among grazing sites suggesting that both autochthonous and allochthonous input have not increased inside grazing exclosures at sufficient rates to increase growth. No population responses to livestock and elk grazing were noted, as low levels of livestock and elk grazing and relatively small areas of stream were occupied by grazing exclosures had little influence on density, standing crop, or recruitment in Rio San Antonio.

Of the characteristics monitored during this research (abundance, biomass, recruitment, condition, movement, and growth), only displacement distance exhibited significant effects due to riparian grazing exclosure. Displacement distances among individuals marked in livestock exclosures (CATTLE) were greater than those observed in both ELK and OPEN grazing sites. While detectably different, the biological significance of increased displacement distance is marginal. Mean displacement distance for successive relocations would have resulted in movement to adjacent stream reaches within the same grazing treatment. Resulting in trout experiencing similar grazing, stream habitat, and water quality conditions.

Population level responses to the elimination or reduction of riparian grazing rely on individual responses to improved instream conditions resulting from management actions. Individual responses to improved foraging conditions would be manifested as increased growth rate or increased fish size within grazing exclosures. Growth rates among grazing sites in this study were not significantly different, suggesting that increased terrestrial input has not increased within ELK or CATTLE sites in comparison with OPEN sites. No variation was observed for mean TL among brown trout sampled in grazing exclosures from 2004 to 2008. Saunders and Fausch (2007) reported increased allochthonous input to salmonid diet in streams under high-density short-duration (HDSD) grazing strategies in comparison with streams under rest-rotation and season long grazing plans. Larger individuals were found in HDSD streams, suggesting a positive response to increased allochthonous input, however, no difference in overall population density were noted among the different grazing strategies.

Condition factor (K_{TL}) also exhibited little variation among grazing sites from 2004 to 2008. Evaluation of condition among grazing exclosures assumes that trout were resident in specific stream reaches over a significant duration. Residence in specific reaches would then allow individual fish to respond to reach specific stream habitat, food resource, and water quality conditions which would presumably result in changes in body condition. This assumption was satisfied as evidence by minimal displacement in middle and upper Rio San Antonio grazing sites. Brown trout displacement between May and September was generally low suggesting that captured individuals would have been within respective exclosures long enough to assimilate potential resources which would then be represented by altered body condition. Displacement distance was significantly greater between successive locations within CATTLE exclosures, however, the magnitude of displacement distance would have resulted in brown trout remaining within the same grazing treatment.

Probability of movement was significantly related to the grazing site in which marked brown trout were last located. The odds of movement were greater among brown trout captured in CATTLE sites in comparison to ELK and OPEN sites respectively. The likelihood of movement (percent mobile fish) among grazing exclosures was highest in ELK exclosures, followed by CATTLE exclosures, and OPEN sites which had the highest percentage of the population as resident. Low displacement distance, in combination with high recapture rates and low turnover observed among grazing sites suggests that exclosures have yet to alter the resident or mobile component of the brown trout population in Rio San Antonio. Similar biotic and abiotic factors were found among grazing sites at each Rio San Antonio stream reach, suggesting that brown trout exhibited resident or mobile life history traits due to factors not monitored in this research.

Lack of detectable differences among grazing sites may have been a function of several factors cited by previous research focused on livestock-fishery interactions. Fundamental problems arise when attempting to observe variation among exclosures constructed in a longitudinal arrangement (Rinne 1988). The dimensions of grazing exclosures will also affect the level of recovery observed when exclosures occupy relatively small areas in relation to the remainder of the watershed (Bock et al. 1984). Lotic systems intrinsically expose organisms to similar stream habitat and water quality conditions over relatively short stream reaches (Vannote et al. 1980). Continued disturbance in the watershed upstream from grazing exclosures may also alter conditions within exclosures, even in the absence of grazing (Kondolf 1993). In addition to design difficulties described above, variable livestock stocking rates observed throughout this research further diminishes the ability to draw firm conclusions regarding potential positive or negative effects of livestock and elk grazing.

The overall lack of riparian grazing influence on brown trout abundance and biomass may be directly related to variability in abundance estimates observed from 2004 to 2008 throughout Rio San Antonio. Visual inspection of density estimates at each stream reach demonstrated that ELK grazing sites had higher density than OPEN and CATTLE sites, however, evaluation of the baseline conditions observed in 2004 show that these differences were present at the onset of the study. Stream discharge can have significant impacts on the abundance and composition of stream fish in small basins (Danehy et al. 1998; Daufresne and Renault 2006). Population fluctuation was extreme in Rio San Antonio ranging from 99-248%, which diminished the ability of this research to accurately identify potential impacts of riparian grazing. Over the duration of this research, mean annual discharge in the Jemez River watershed varied from 37-126% of the 30 year mean (USGS Stream Gauge Station #08324000). Highest mean annual discharge occurred in 2005, the same year that the lowest estimates for fish abundance were observed in Rio San Antonio. A direct correlation between fish density and discharge were not tested due to the absence of a gauge station on Rio San Antonio, and as such are presented for consideration only.

In addition to weather variability, longitudinal variation in salmonid abundance and biomass among grazing sites on Rio San Antonio may have weakened the ability to detect difference using replicated grazing exclosures to determine variation in brown trout populations. Density and biomass estimates from 2004 to 2008 were similar among all grazing sites at all three stream reaches with the exception of the OPEN grazing exclosure at the lower grazing site exhibiting slightly lower estimated biomass than either CATTLE or ELK exclosures. The difference in biomass among grazing sites at the lower Rio San Antonio reach is most likely a function of study reach attributes rather than grazing impact. Pool volume was greater in both the CATTLE (60.48 m^3) and ELK (50.6 m^3) exclosures than the OPEN grazing exclosure (21.18 m^3). Variation in stream habitat conditions among grazing exclosures should be considered prior to drawing conclusions regarding grazing impacts, as previous research has shown changes in available pool habitat can have an impact on salmonid biomass in small streams (Riley and Fausch 1995).

Minimal changes in salmonid abundance and biomass have been reported with regard to livestock grazing in the western United States. Chapman and Knudsen (1980) reported no difference in salmonid biomass between grazed and ungrazed stream sections in western Washington. The authors suggested that grazed areas supported similar salmonid biomass levels due to increased solar input resulting from decreased overhanging vegetation. In addition, livestock exclosures in combination with instream habitat improvement can result in improved stream habitat conditions without compensatory response among trout populations due to continued upstream disturbance (Platts and Nelson 1985; Kondolf 1993).

Responses of trout populations to grazing exclosures have been widely reported in previous literature, however, many of these findings are anecdotal or observational. Among the improvements cited as factors for improved aquatic conditions, recovery of riparian vegetation may be the single most important factor (Kondolf 1993; Belsky 1999). Most commonly, increased biomass and abundance of salmonids in ungrazed reaches has been reported (Marcuson 1977; Keller and Burnham 1982; Clarkson and Wilson 1995; Knapp and Matthews 1996; Summers et al. 2008). Increased fish size was also noted in the absence of grazing (Marcuson 1977; Keller and Burnham 1982). Decreased fine sediment loads observed in grazing exclosures may also have positive effects on juvenile salmonids (Wohl and Carline 1995; Summers et al. 2005; Bayley and Li 2008). Decreased home range size among golden trout (*Oncorhyncus aguabonita*) in areas with increased sedge cover which were representative of ungrazed areas (Matthews 1996). Little mention of stocking rates or historic land-use practices was made in any of the previous work, minimizing the ability to draw firm conclusions of the overall effect of grazing exclosures on salmonid populations.

Brown trout recruitment in Rio San Antonio was not impacted by riparian grazing from 2004 to 2008. Mean recruitment was highest in CATTLE exclosures at both the lower and middle sites and in the OPEN treatment at the upper site from

2004 to 2008. Positive response of Age-0 salmonid abundance to livestock exclosures has been noted in several studies, which have hypothesized increases due to overhanging vegetation (Matthews 1996), increased habitat heterogeneity (Ebersole et al. 2003), and spawning substrate availability (Beard and Carline 1991; Knapp et al. 1998). Habitat heterogeneity and percent substrate <4mm were also similar among grazed and ungrazed stream reaches at all three Rio San Antonio stream reaches (see Chapter 2).

Summary and Conclusions

There were no detectable differences in brown trout abundance, standing crop, recruitment and condition among grazing sites after the first five years of grazing exclosure. Growth rate among individually marked brown trout in 2007 and 2008 also showed no effect of grazing exclosures. Movement was greater in CATTLE exclosures in 2007 and 2008, however, the magnitude of displacement distance would result in brown trout moving to adjacent stream reaches within the same treatment, remaining exposed to similar grazing conditions and associated stream habitat conditions. Low stocking rates in combination with cautious management of riparian grazing during this study resulted in maintenance of trout populations near levels seen at the initiation of this research.

Management Implications

Responses of trout populations to grazing exclosures will most likely not be seen until significant changes in stream morphology, water quality, and aquatic macroinvertebrate assemblages inside grazing exclosures take place. Responses of individual and population level characteristics to riparian exclosures observed in this study suggest that elimination of grazing may not be enough to positively influence trout populations in Rio San Antonio. Restoration of riparian vegetation inside exclosures may positively influence trout in Rio San Antonio over a limited spatial scale, however, restoration of areas outside exclosures should be considered as a preferred management objective. Exclosures on Rio San Antonio do not occupy sufficient areas to influence stream habitat, allochthonous input, or stream temperature, which would in turn impact trout populations. VCNP staff should reevaluate the current management of fish populations in all streams within the preserve, setting specific goals which would provide focused management objectives. Potential activities which could be undertaken include restoration of riparian vegetation inside exclosures, considering alternative management plans for livestock grazing, and increasing the scope of riparian grazing exclosures.

Restoration of woody riparian vegetation inside grazing exclosures, including willow and alder, which are seen on other streams in VCNP would be the most sustainable method and may provide the greatest overall benefit. Stabilization of streambanks would result in improved stream habitat, as Rio San Antonio would, over time, narrow and deepen. Change in cross sectional shape would also change the current flow regime, increasing stream power which would lead to increased substrate size, potentially improving autochthonous production. Allochthonous input would also increase and would benefit trout through the addition of terrestrial invertebrate food sources. Restoration inside exclosures would also provide a source population which may lead to natural establishment of woody vegetation throughout the watershed.

Modification of the existing livestock grazing environmental impact statement would be necessary prior to increasing stocking rates above the current 2000 animal maximum. Present environmental impact statements limit livestock grazing to 31,000 acres within the 90,000 acre preserve, much of which is within or directly adjacent to riparian areas bordering lotic systems in VCNP. Evaluation of the data presented in this research suggests that the total number of livestock could potentially be increased, and by allowing areas of the preserve not included in the current grazing plan to be utilized grazing impacts on riparian areas could be maintained at the current levels. If any changes to the grazing program were to take place, continued monitoring of vegetation characteristics such as utilization rate and stubble height would be of utmost importance. Determination of the ability to predict grazing impacts on fish community structure and vitality of fish within that population as well as the impacts on stream morphology area using existing data would also be necessary to evaluate the response of aquatic systems to livestock and elk grazing.

Increasing the scope of riparian exclosures throughout Rio San Antonio should also be considered as an alternative, however, the construction of exclosures must be evaluated prior to further implementation. Exclosures constructed in 2003 do not occupy sufficient stream length, and as such provide little overall benefit to the watershed. New exclosures, should they be developed, must encompass greater lengths of stream and exclude both elk and cattle. Development of exclosures should only be considered in areas where stream habitat is in severely degraded condition and only after multiple surveys of both fish populations and stream habitat characteristics have taken place. Exclosures should buffer the stream by 25-30 m on both sides and encompass at least 500 m in order to not only benefit aquatic systems on a local scale but stabilize reaches directly downstream.

Literature Cited

Allison, C.D., J. Boren, and T.T. Baker. 1999, Herbaceous utilization by elk in selected mountain meadows in the Gila Wilderness, Gila National Forest. New Mexico State University, Range Improvement Task Force. Cooperative Extension Service, College of Agriculture and Home Economics. Report 49 http://aces.nmsu.edu/pubs/_ritf/.

Bayley, P. B., and H. W. Li. 2008. Stream fish response to grazing exclosures. North American Journal of Fisheries Management. 28(1): 135–147.

Beard, T. D., R. F. Carline. 1991. Influence of spawning and other stream habitat features on spatial variability of wild brown trout. Transactions of the American Fisheries Society. 120(6):711–722.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation. 54: 419–431.

Bock, C. E., J. H. Bock, W. R. Kinney. 1984 Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management. 37(3):239–242.

Chapman, D. W., and E. Knudsen. 1980. Channelization and livestock impacts on salmonid habitat and biomass in western Washington. Transactions of the American Fisheries Society. 109(4): 357–363.

Clarkson, R.W., and J.R. Wilson. 1995. Trout biomass and stream habitat relationships in the White Mountains area, east-central Arizona. Transactions of the American Fisheries Society. 124:599-612

Cook, C.W., J. Stubbendieck. 1986. Range Research: Basic problems and techniques. Society for Range Management, Denver, CO. 317 pp.

Clary, W. C., and W. C. Leininger. 2000. Stubble height as a tool for management of riparian areas. Journal of Range Management. 53:562–573.

Coe, P. K., B. K. Johnson, J. W. Kern, S. L. Findholt, J. G. Kie, and M. J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. Journal of Range Management. 54:51–76.

Cucherousset, J., D. Ombredane, J.L. Bagliniere. 2006. Linking juvenile growth and migration behaviour of brown trout (Salmo trutta) using individual PIT-tagging. Cahiers de Biologie Marine, 47:73-78

Danehy, R. J., N. H. Ringler, S. V. Stehman, J. M. Hassett. 1998. Variability of fish densities in a small catchment. Ecology of Freshwater Fish. 7:36–48.

Daufresne, M., and O. Renault. 2006. Population fluctuations, regulation and limitation in stream living brown trout. Oikos. 113:459–468.

Deverill, J. L., C. E. Adams, C. W .Bean. 1999. Prior residence, aggression and territory acquisition in hatchery–reared and wild brown trout. Journal of Fish Biology. 55(4):868–875.

Devries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512. In: B. R. Murphy and D. W. Willis (editors) Fisheries Techniques, 2nd edition. American Fisheries Society. Bethesda, Maryland.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon. Canadian Journal of Fisheries and Aquatic Sciences. 60:1266–1280.

Gross, J.A., J.E. Knight. 2000. Elk presence inside various sized cattle exclosures. Journal of Range Management. 53: 287-290

Gunderson, D. R., 1968. Floodplain use related to stream morphology and fish populations. Journal of Wildlife Management. 32:507–514.

Hosmer, D. W. and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley. New York.

Keller, C. R., and K. P. Burnham. 1982. Riparian fencing, grazing, and trout habitat preference on Summit Creek, Idaho. North American Journal of Fisheries Management. 2:53-59.

Knapp, R. A., and K. R. Matthews. 1996. Livestock grazing, golden trout, and streams in the Golden Trout Wilderness, California: impacts and management implications. North American Journal of Fisheries Management. 16: 805–820.

Knapp, R. A., V. T. Vrendenburg, K. R. Matthews. 1998. Effects of stream channel morphology on golden trout spawning habitat and recruitment. Ecological Applications. 8(4):1104–1117.

Kondolf, G.M. 1993. lag in stream channel adjustment to livestock exclosure, White Mountains, California. Restoration Ecology. 1(4):226-230

Matthews K. R. 1996. Habitat selections and movement patters of California golden trout in degraded and recovering stream sections in the Golden Trout Wilderness, California. North American Journal of Fisheries Management 16:579-590.

Marcuson, P.E. 1977. The effect of cattle grazing on brown trout in Rock Creek, Montana. Fish and Game Federal Aid Project. F-20-R-21-1a.

Ombredane, D., J.L. Bagliniere, F. Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (Salmo trutta) and their use for studying movement in a small river. Hydrobiologia, 371/372:99-106

Platts, W.S., R.L. Nelson. 1985. Impacts of rest-rotation grazing on stream banks in forested watersheds in Idaho. North American Journal of Fisheries Management. 5:547-556

Pratt, M., and G. A. Rasmussen. 2001. Determining your stocking rate. Utah State University Extension Publication NR/RM/04. 7pp. http://extension.usu.edu/files/publications/publication/NR_RM_04.pdf

Prentice, E.F., T.A. Flagg, C.S. McCutcheon. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. American Fisheries Symposium, 7:317-322

Riley, S. C. and K. D. Fausch. 1995. Trout population response to habitat enhancement in six northern Colorado streams. Canadian Journal of Fisheries and Aquatic Sciences. 52(1):34–53.

Rinne, J. N. 1988. Grazing effects on stream habitat and fishes: research design considerations. North American Journal of Fisheries Management. 8:240–247.

Rinne, J. N. 1999. Fish and grazing relationships: the facts and some pleas. Fisheries 24(8)12-21.

Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology. 83(1):1–13.

Saunders, W. C., and K. D. Fausch. 2007. Improved grazing management increases terrestrial invertebrate inputs the feed trout in Wyoming rangeland streams. Transactions of the American Fisheries Society. 136:1216-1230.

Summers, D. W., N. Giles, and D. N. Stubbing. 2005. The effect of riparian grazing on brown trout, Salmo trutta, and juvenile Atlantic salmon, Salmo salar, in an English chalk stream. Fisheries Management and Ecology. 12: 403–405.

Summers, D. W., N. Giles, and D. N. Stubbing. 2008. Rehabilitation of brown trout, *Salmo trutta*, habitat damaged by riparian grazing in an English chalkstream. Fisheries Management and Ecology. 15:231-240.

Swift, D.R. 1961. The annual growth rate cycle in brown trout (*Salmo trutta*) and its cause. Journal of Experimental Biology. 38:595-604

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences. 37 :130–138.

Werner, S. J., and P. J. Urness. 1998. Elk forage utilization within rested units of rest-rotation grazing systems. Journal of Range Management. 51:14–18.

Wohl, N.E., R.F. Carline. 1996. Relations between riparian grazing, sediment loads, macroinvertebrates, and fishes in three central Pennsylvania streams. Canadian Journal of Fisheries and Aquatic Sciences. 53(Suppl. 1):260-266

Zar, J. H. 1984. Biostatistical analysis. 2nd Edition. Prentice-Hall. Englewood Cliffs, New Jersey. 130 pp.

Zippen, C. 1958. The removal method of population estimation. *Journal of Wildlife Management.* 22:82-90.

CHAPTER 3: SPATIAL VARIABILITY IN POPULATION AND INDIVIDUAL CHARACTERISTICS IN A BROWN TROUT POPULATION, VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

Abstract

Fish surveys on Rio San Antonio, Valles Caldera National Preserve from 2004 to 2008 revealed variation among stream reaches in brown trout abundance related to variability in stream temperature, habitat quality, and aquatic macroinvertebrate biomass. Brown trout density and standing crop within the watershed are among the highest observed in the Rocky Mountains. Analysis of movement behavior revealed a largely resident population (65%) with a smaller mobile component (35%). Displacement distances were low (median =50 m; range 0-19616 m), which in combination with low turnover rates observed in middle (0.31±0.03) and upper (0.29±0.03) reaches support the finding of low movement rates. Movement, more common in the lower stream reaches, was in response to decreasing trout density and decreased food availability. Despite reduced food resources, growth rates were greatest in lower stream reaches. Seasonal growth was greatest between April and July when stream temperatures were approaching the range of optimal growth near 13°C. Adult (>120 mm TL) brown trout density and standing crop were considerably higher in the upper Rio San Antonio reach (52.6 fish/100m^2; 535.8 kg/ha) than in the lower stream reach (4.1 fish/100m^2; 77.8 kg/ha) Fish condition throughout the watershed was high for all age classes, however, Age-IV+ individuals exhibited significantly lower condition (0.88 ± 0.02) in reaches with high population density compared to Age-IV+ (0.95 ± 0.02) found in reaches with lower density. Results

indicate that the variability in population density resulting from biotic and abiotic factors in Rio San Antonio have lead to improved conditions for individual fish as evidence by higher growth rates and improved condition. Although brown trout recruitment was greatest in the upper stream reaches, it was highly variable across years. Recruitment was greatest in 2006, following low winter precipitation which led to decreased spring runoff. Rehabilitation of stream habitat in areas of Rio San Antonio may be necessary to improve the spatial distribution of brown trout within the watershed, which may lead to improved growth rates throughout the population.

Introduction

The spatial availability of food and suitable habitat define the overall distribution and abundance of salmonids in lotic systems (Chapman 1966). Longitudinal variability of abiotic factors including temperature, discharge, and substrate size are common in streams (Vannote et al. 1980). Evaluation of the responses of trout populations to the gradient of abiotic factors can provide focused implementation of management goals and objectives. Biotic interactions brought about by abiotic conditions can lead to density-dependent responses including decreased growth (Jenkins et al. 1999), reduced size (Hutchings 1993) and increased movement (Hesthagen 1988). Trout populations have been shown to fluctuate greatly in response to changing biotic and abiotic factors (Platts and Nelson 1988). Individual fish condition can moderate these fluctuations, as improved condition increases survival during periods when resources become limiting (Fausch 1984). Movement behavior among individuals within a population allows exploitation of spatiotemporally variable resources (Gowan and Fausch 2002). Movement has profound implications for management of stream fish, as special regulations limiting harvest or habitat improvement projects must occupy a large enough spatial scale to support all life history requirements.

Movement among stream fish populations has been debated widely with hypotheses ranging from restricted movement (Gerking 1959) to movement being relatively common within a watershed (Gowan et al. 1994). Critics of the restricted movement hypothesis suggest that sampling design influences the determination of resident or mobile populations. Sampling within the same stream reaches over time, low recapture rates, and reliance on marked individuals may bias against detection of movement. Behavioral differences among individuals can lead to exploratory movement in which fish seek out foraging, cover, or spawning habitat (Fraser et al. 2001). Movement rates have been shown to vary among streams and may be a function of density (Hesthagen 1988), habitat complexity (Roberts and Angermeier 2007), and food availability (Bachman 1984).

Growth rate among brown trout is regulated by stream temperature and food availability (Wootton 1990; Elliott et al. 1995). Elliott (1975a, 1975b) found optimal growth among hatchery brown trout to occur at 13°C. Field based studies have shown this value to be accurate with some populations exhibiting optimal growth at temperatures both below (Jensen et al. 2000) and above 13°C (Allen 1985; Jensen and Berg 2000). Under conditions when temperature is not limiting growth, food availability is the major determinant in fish reaching optimal growth rates (Cada et al. 1987). Trout are opportunistic feeders and respond rapidly to changes in the food supply (Bridcut and Giller 1995). Opportunistic feeding during periods of decreased aquatic macroinvertebrate production or increased availability of terrestrial invertebrates maximizes individual growth stabilizing the overall population (Fausch 1984; Cada et al. 1987).

Assessment of population and individual level variability within a watershed allows focused implementation of management goals and activities. This research combines seasonal monitoring of population level characteristics and mark-recapture methods to monitor individual characteristics allowing the evaluation of spatial variability in biotic and abiotic factors currently determining brown trout population dynamics in a high elevation meadow stream. Specific research objectives include: 1) monitor abundance, biomass, and condition, 2) characterize movement behavior, and 3) assess growth patterns in a brown trout population at three stream reaches within Rio San Antonio, Valles Caldera National Preserve, New Mexico.

Methods

Stream temperature

Water temperature was monitored on 1-hour intervals from 18 May 2007 to 15 November 2008 at each Rio San Antonio stream reach using Pro v2 data loggers (Onset Computer Corporation, Pocasett, Massachusetts). Daily average, minimum, and maximum temperatures were obtained, as well as all daily maximum observations ≥20°C and minimum <0°C.

Fish Collections

Methods used fish surveys conducted to estimate brown trout age-structure, density, standing crop, recruitment, condition, and mark-recapture sampling, were described in chapter 2.

Maximum and average fluctuations in brown trout abundance estimates were calculated using methods described by Platts and Nelson (1988); maximum fluctuation, $M_s= (X_{max}-X_{min})/ X_{min}$ and average fluctuation, $A_s=(X_{max}-X_{min})/X_{avg}$, where X_{max}= maximum estimated seasonal abundance, X_{min}= minimum estimated seasonal abundance, and X_{avg}= average estimated seasonal abundance.

Aquatic Macroinvertebrate Collections

Benthic macroinvertebrate samples were collected within each stream reach (lower, middle, upper) in May and September, 2007 and 2008, using a Surber sampler (0.10 m^2). Invertebrates were then sorted from debris, enumerated, and preserved in 95% ETOH. To determine dry biomass, samples were placed in aluminum weighing dishes, and dried at 60°C for 24 hours. Samples were then removed from the drying oven and placed in desiccators to cool to room temperature, then weighed to the nearest 0.0001 g on an electronic balance.

Statistical Analysis

Statistical analysis was performed using SAS version 9.1.3 (SAS Institute Inc. Cary, NC 2003). Growth rates were then calculated for all age classes (0-IV+) at the stream reach level. Growth rate estimates at the stream reach level were limited to individuals moving between grazing sites within the same reach on successive relocations (displacement < 500 m). Individuals moving greater than 500 m were omitted from analysis, allowing determination of growth rate as a function of characteristics specific to each stream reach, including brown trout density and stream temperature. All other individuals were omitted from analysis. Effects of stream reach, season, year, and age on brown trout movement and growth rate were analyzed using Kruskal-Wallis non-parametric analysis of variance. Mann-Whitney U-tests with Bonferroni corrected alpha levels were used for all pairwise comparisons if detectable differences were noted in the Kruskal-Wallis analysis (Zar 1984). Spearman rank correlation was also used to determine the effect of brown trout density, stream temperature, stream width and depth, and aquatic macroinvertebrate abundance and biomass on seasonal growth rates. Change in condition (ΔK_{TL}) among marked individuals was calculated as: KTL_B-K_{TLA}=ΔK_{TL}. Where K_{TLA}=condition at previous location and KTL_B=condition upon recapture.

Chi-square tests were used to compare the probability of individual fish being resident or mobile based on age and stream reach, as well as directionally biased movement. Probability of movement was determined using logistic regression (Hosmer and Lemeshow 1989). Individual displacement ≥50 m during consecutive recapture sessions was considered movement. Individuals were coded as mobile (1) or resident (0), and univariate logistic regression analysis was performed using the logistic procedure in SAS. Continuous variables included in the analysis were, brown trout density, total length, growth rate, condition, stream temperature, stream width, residual pool depth, percent of stream surface area in pools, and aquatic macroinvertebrate abundance and biomass. Categorical variables for stream reach, grazing site, and season were also analyzed. Parameters were considered significant at α=0.05. Odds ratios were used to determine the magnitude of individual parameter effects on the probability of movement (Hosmer and Lemeshow 1989).

When brown trout exhibited displacement distance ≥50 m, Spearman rank correlation was used to determine the relationship between displacement distance and total length, growth, and condition. Differences in growth and condition among resident and mobile fish (displacement ≥50 m) were tested using Kruskal-Wallis non-parametric analysis of variance and Mann-Whitney U-tests. Bonferroni corrected alpha levels were used for pairwise comparisons (Zar 1984).

Visual inspection of reach specific grazing effects were performed using median and 1st and 3rd quartiles for brown trout density, standing crop, and condition. Stream reaches within Rio San Antonio were compared (lower-middle, lower-upper, middle-upper) and considered different when the lower median value in the comparison was less than the 1st quartile of the higher median value, and the higher median in the comparison was greater than the 3rd quartile of the lower median. Spearman rank correlation was used to evaluate density dependent effects on brown trout length, weight, and condition. Analyses were considered significant at α=0.05.

Results

Stream Temperature

Mean stream temperature varied among stream reaches in Rio San Antonio, maximum daily mean, minimum, and maximum were observed in the lower stream reaches where width–depth ratio is greatest. Daily mean temperatures exceeded 20°C on 19 occasions in 2007 and 2008 in lower stream reaches, while no daily averages in either middle or upper stream reaches were observed above 20°C (Appendix A.4). Maximum daily values greater than 25°C were observed 11 times in 2007 and 15 times in 2008 within the lower Rio San Antonio, 5 times in both 2007 and 2008 within the middle stream reach, and 0 times in the upper reach. Instances of super cooling (<0°C) were also observed in the lower stream reaches on 121 occasions during the winter of 2007-2008.

Recapture Sampling and PIT Tag Retention

Between November 2006 and September 2008, 1,446 brown trout were implanted with PIT tags. Over the duration of this research a total of 401, 422, and 620 brown trout were marked in lower, middle, and upper stream reaches respectively. See Chapter 2 for additional results of recapture sampling.

Movement

Displacement distance among marked brown trout was not different among stream reaches (χ^2=3.15, df=2, p=0.207). Median displacement distance between successive encounter occasions in 2007 and 2008 was 50 m for all stream reaches, seasons, and age classes. Brown trout marked in the lower stream reach exhibited highest mean displacement distance (532.5 ± 390.75 m) followed by individuals marked in middle (39.1 ± 7.84 m) and upper (38.7 ± 12.20 m) reaches (Table 3.1). Displacement distance also similar among seasons (χ^2=1.90, df=4, p=0.754).and age class (χ^2=1.72, df=4, p=0.632) (Table 3.1) Displacement distributions were strongly leptokurtic, 80% of all recaptures occurred 50 m upstream or downstream from the stream reach where individual fish had previously been located (Figure 3.1). Total movement in the Rio San Antonio exhibited a skewed distribution, with 55% of the total movement being ≤50 m (Figure 3.2). Total movement from 2007-2008 was 813.6 ± 95.86 m (mean ± S.E.). The range of total movement was 0-48,276 m while the median value was 50.0 m.

Turnover rate was significantly higher in the lower stream reach than in both middle and upper reaches ($F_{2,30}$=19.55; p<0.0001). Sampling season also had a significant effect on turnover rate ($F_{3,29}$=4.54; p=0.0075), as higher turnover rates were observed in May compared to those observed in September and November (Table 3.1).

Within the Rio San Antonio watershed, brown trout were more likely to be resident than mobile, as reflected by a large portion of fish moving <50 m between recapture occasions (χ^2=186.49, df=1, p<0.0001). There was no directional movement bias (χ^2=2.0408, df=1, p=0.1531) among brown trout moving ≥50 m upstream or downstream. Brown trout marked in the lower Rio San Antonio grazing site were more likely to be mobile than individuals marked in either the middle or upper grazing sites. Age had no effect on the probability of trout exhibiting resident or mobile status (Table 3.2).

Probability of movement (displacement ≥50 m) was positively related to TL at previous encounter (p=0.0001) and mean stream width within the reach of previous encounter (p<0.0001) (Table 3.3). Probability of movement increased 0.5% (95% CI = 0.2-0.8%) for every l mm increase in TL, and 52% (95% CI = 38-67%) for every 1 m increase in mean stream width.

Table 3.1: Displacement (m; mean ±S.E.) and turnover rates for marked brown trout grouped by stream reach, season, and age class. Superscript letters represent statistical between stream reaches, seasons, and age classes.

	Displacement (m)	Turnover Rate
Stream Reach		
Lower	532.2 (390.74) ^{a}	0.58 (0.03) ^{a}
Middle	39.1 (7.84) ^{a}	0.31 (0.03) ^{b}
Upper	38.7 (12.2) ^{a}	0.29 (0.03) ^{b}
Season		
Nov-Apr	1280.9 (993.01) ^{a}	*
April-May	37.5 (13.95) ^{a}	0.52 (0.03) ^{a}
May-July	54.4 (11.33) ^{a}	0.38 (0.07) ^{ab}
July-Sept	41.3 (9.24) ^{a}	0.27 (0.04) ^{b}
Sept-Nov	39.6 (14.9) ^{a}	0.31 (0.02) ^{b}
Age Class		
Age-I	30.7 (10.65) ^{a}	*
Age-II	93.2 (55.16) ^{a}	*
Age-III	54.1 (14.92) ^{a}	*
Age-IV+	679.9 (560.5) ^{a}	*

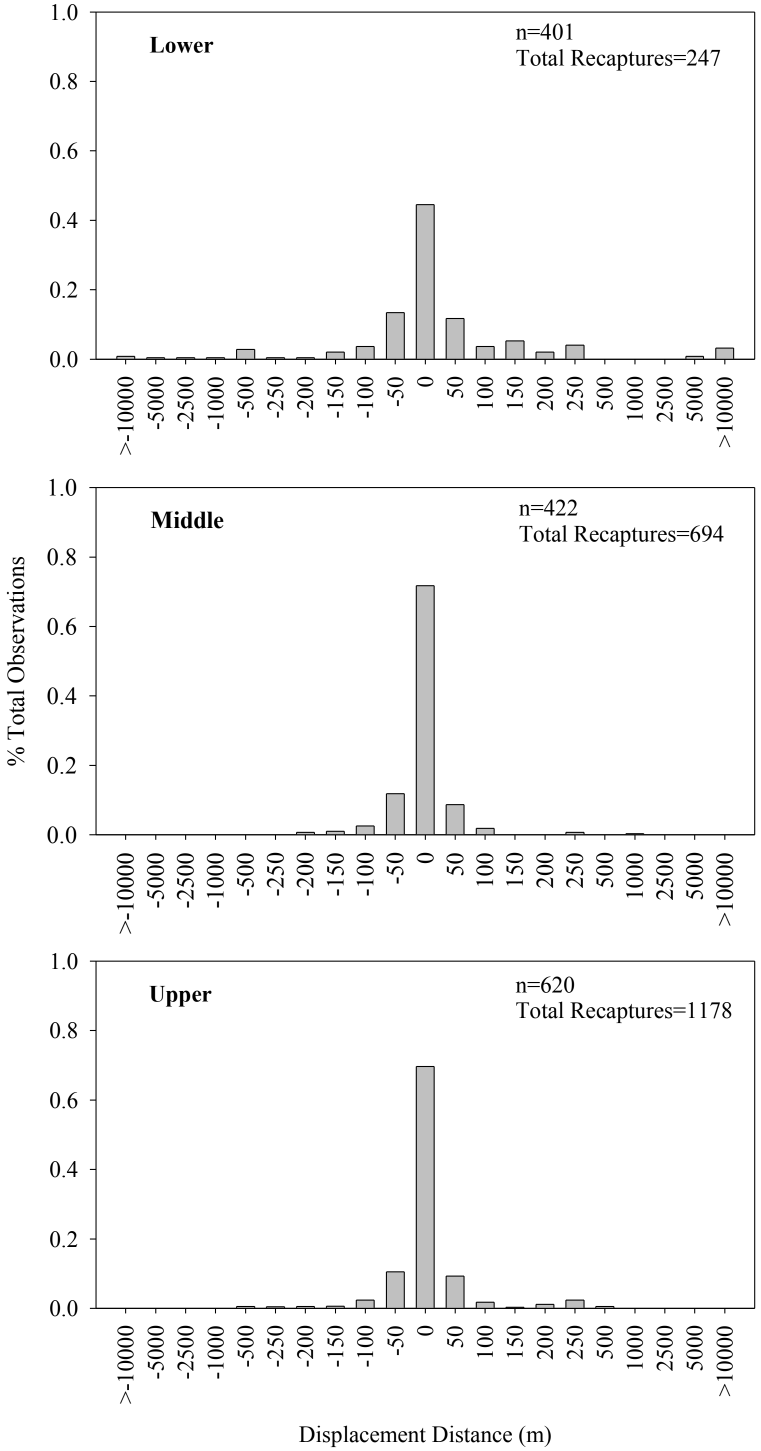


Figure 3.1: Displacement distance (m) plotted as the percentage of successive recaptures in lower, middle, and upper stream reaches. Negative values signify downstream movement. Note that the scale changes to the left and right of 0 m.

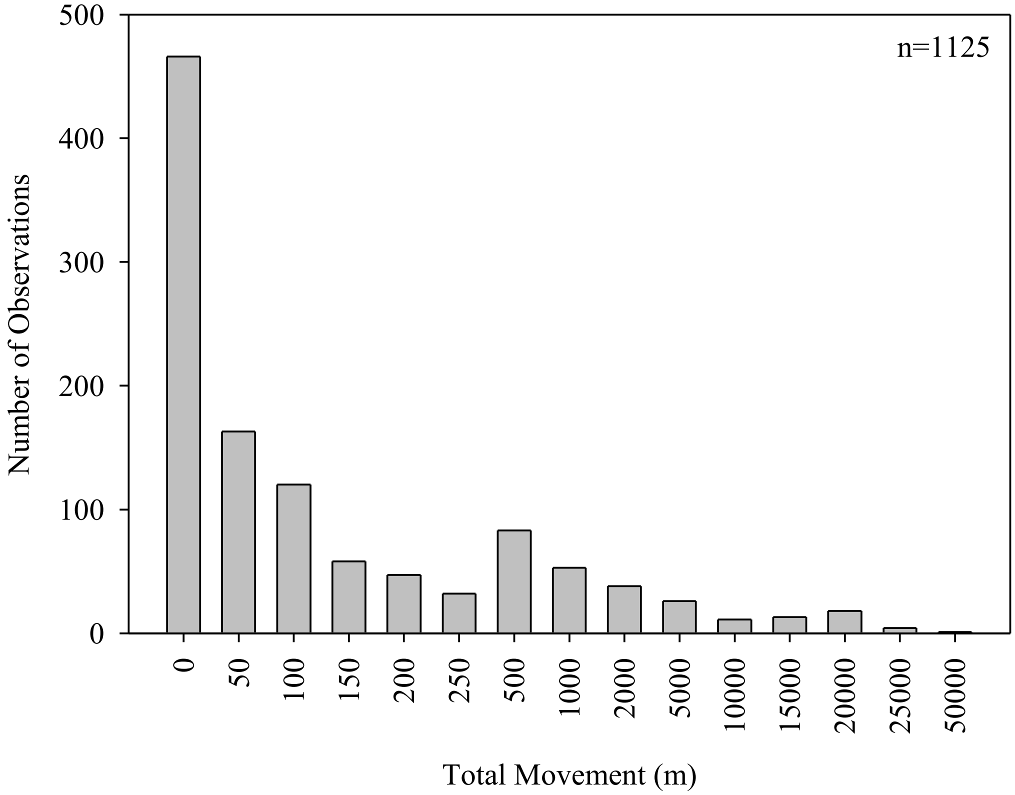


Figure 3.2: Total movement (m) among marked brown trout calculated as the sum of all movement between the initial marking occasion and the final recapture. Note that the scale changes from left to right along the x-axis.

Table 3.2: Results of Chi-square tests evaluating the probability of resident or mobile life history among individual brown trout in Rio San Antonio. Brown trout were classified as mobile if displacement distance was ≥50 m.

Comparison		Percent Resident	Percent Mobile	χ^2	df	p
Overall Watershed		64.5	35.5	186.49	1	<0.0001
Grazing site						
	Lower	**45.8**	**54.2**	**1.68**	**1**	**0.1948**
	Middle	71.3	28.7	127.23	1	<0.0001
	Upper	69.23	30.77	175.00	1	<0.0001
Age class						
	Age-I	68.5	31.5	75.66	1	<0.0001
	Age-II	59.7	40.3	25.49	1	<0.0001
	Age-III	68.0	32.0	89.39	1	<0.0001
	Age-IV+	59.0	41.0	9.58	1	0.0020

Probability of movement was negatively related to ΔW ($p=0.0002$), ΔK_{TL} ($p<0.0001$), brown trout density ($p<0.0001$), mean stream temperature ($p<0.0001$), and aquatic macroinvertebrate biomass ($p<0.0001$). Probability of movement decreased 1.5% (95% CI = 1-2%) for every 1 g increase in ΔW, 89% (95% CI = 68-97%) for every 1 unit increase in K_{TL}, 1.5% (95% CI = 1-2%) of every 1 fish/100m^2 increase in brown trout density, 6.8% (95% CI = 4-10%) for every 1°C increase in mean stream temperature, and 19.5% (95% CI = 14-25%) for every 1 g/m^2 increase in aquatic macroinvertebrate biomass (Table 3.3).

The odds of movement increased 224% during November sampling compared to May sampling. Comparison of the odds of movement in May and during all other sampling periods (April, July, September) were not significant. Probability of movement in the lower Rio San Antonio stream reach had 256% and 239% greater odds than upper and middle stream reaches respectively (Table 3.3).

Growth rate

Growth rates were significantly different among stream reaches for both ΔTL ($\chi^2=17.61$, df=2, $p=0.0001$) and ΔW ($\chi^2=16.57$, df=2, $p=0.0003$). Growth rates were higher in the lower grazing site for both ΔTL and ΔW, than in middle and upper grazing sites (Figure 3.3). Seasonal growth rates were detectably different for both ΔTL ($\chi^2=109.83$, df=4, $p<0.0001$), and ΔW ($\chi^2=209.31$, df=4, $p<0.0001$) (Table 3.4). Highest seasonal growth rates for both ΔTL and ΔW were observed between April and May and from May to July (Table 3.4). Significant differences among age classes (I-IV+) were observed both for ΔTL ($\chi^2=1061.34$, df=3, $p<0.0001$) as well as

Table 3.3: Results of logistic regression modeling of probability of brown trout movement related to individual fish characteristics, brown trout population characteristics, water quality, stream habitat, and aquatic macroinvertebrate characteristics. Significant models shown in bold.

	Likelihood Ratio			Parameter Estimate				Odds Ratio	95% CI	
Variable*	n	χ^2	p	β	S.E.	χ^2	p		Lower	Upper
Season	**2187**	**53.32**	**<0.0001**							
April	2187	53.32	<0.0002	0.123	0.417	0.09	0.7682			
May	2187	53.32	<0.0001	0.189	0.382	0.04	0.8892			
July	2187	53.32	<0.0003	0.398	0.234	2.91	0.0885			
September	2187	53.32	<0.0004	0.324	0.232	1.94	0.1631			
November	**2187**	**53.32**	**<0.0005**	**1.175**	**0.213**	**30.38**	**<0.0001**	**3.24**	**2.13**	**4.92**
Site	**2187**	**64.84**	**<0.0001**							
Lower/Upper	**2187**	**64.84**	**<0.0001**	**1.272**	**0.165**	**59.25**	**<0.0001**	**3.56**	**2.58**	**4.93**
Lower/Middle	**2187**	**64.84**	**<0.0001**	**1.221**	**0.179**	**46.28**	**<0.0001**	**3.39**	**2.385**	**4.821**
Middle/Upper	2187	64.84	<0.0001	0.051	0.144	0.12	0.7251			
TL	**2187**	**14.48**	**0.0001**	**0.005**	**0.001**	**14.48**	**0.0001**	**1.01**	**1.002**	**1.008**
Δ TL	2187	0.45	0.5033	-0.005	0.008	0.45	0.5033			
Δ W	**2187**	**9.39**	**0.0022**	**-0.015**	**0.005**	**9.39**	**0.0022**	**0.99**	**0.975**	**0.994**
K_{TL}	2187	0.35	0.5528	0.136	0.230	0.35	0.5528			
Δ K_{TL}	**2187**	**15.27**	**<0.0001**	**-2.247**	**0.575**	**15.27**	**<0.0001**	**0.11**	**0.034**	**0.326**
Density	**2187**	**25.67**	**<0.0001**	**-0.012**	**0.002**	**25.67**	**<0.0001**	**0.99**	**0.983**	**0.993**
Temperature	**2163**	**16.34**	**<0.0001**	**-0.071**	**0.018**	**16.34**	**<0.0001**	**0.93**	**0.9**	**0.964**
Wetted Width	**2187**	**73.85**	**<0.0001**	**0.419**	**0.049**	**73.85**	**<0.0001**	**1.52**	**1.38**	**1.67**
RPD	2187	3.22	0.0724	0.018	0.010	3.22	0.0724			
Percent Pool	2187	2.13	0.1438	1.240	0.848	2.13	0.1438			
AMI Abundance	2187	0.85	0.3565	-0.001	0.001	0.85	0.3565			
AMI Biomass	**2187**	**33.77**	**<0.0001**	**-0.216**	**0.037**	**33.77**	**<0.0001**	**0.81**	**0.749**	**0.867**

* TL=total length (mm), Δ TL=change in total length (mm), Δ W= change in weight (g), K_{TL}=condition factor, Δ K_{TL}=change in condition, Density=brown trout/100m^2, Temperature=mean stream temperature (°C), Wetted Width=mean stream width (m), RPD=residual pool depth in stream reach of previous capture (cm), Percent Pool=percent of total surface area composed of pools, AMI Abundance=aquatic

macroinvertebrate abundance (number/m^2), AMI biomass=aquatic macroinvertebrate biomass (grams/m^2).

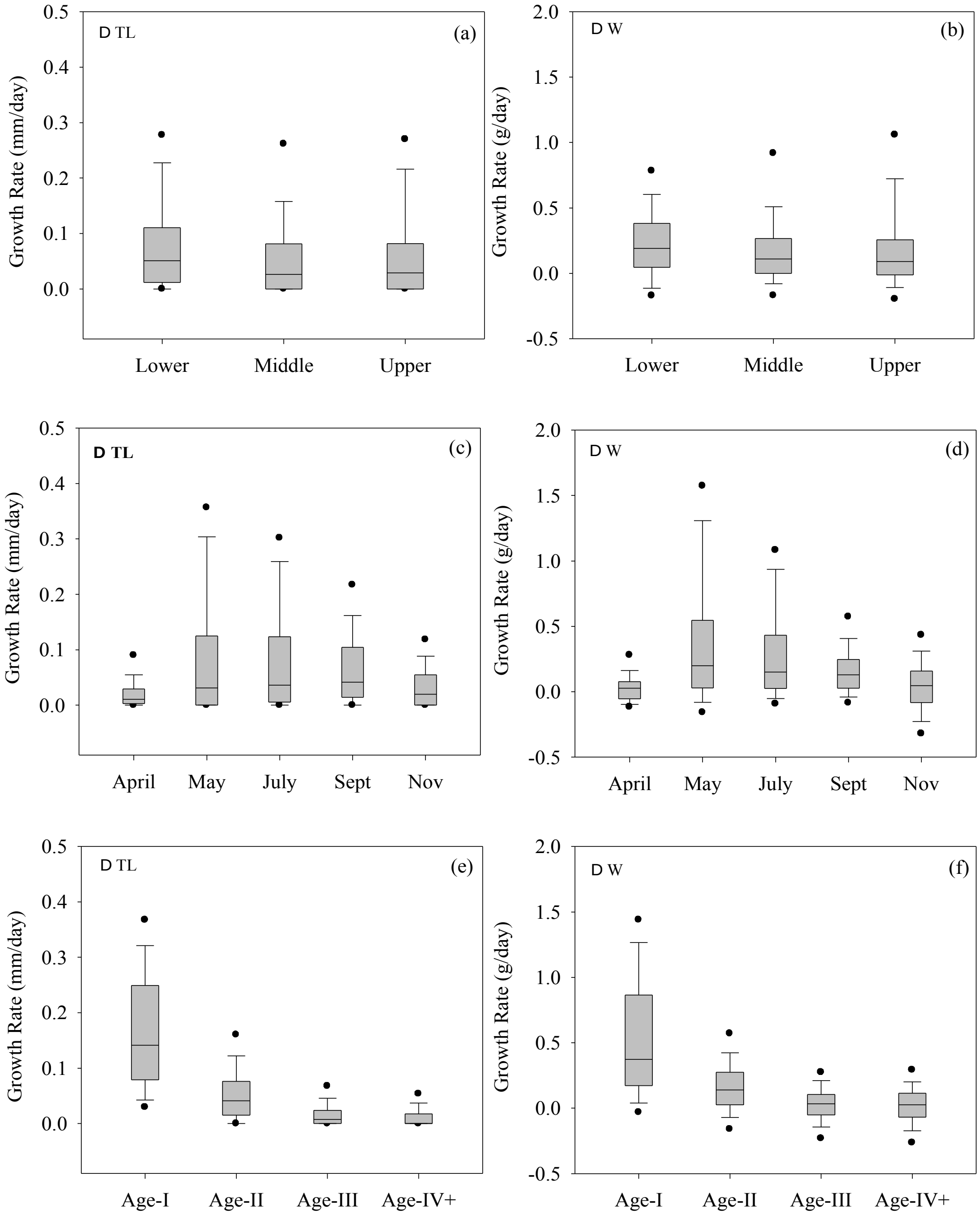


Figure 3.3: Instantaneous growth rates (ΔTL; a, c, e, g and ΔW; b, d, f, h). Stream reach comparisons (a,b) are combined seasonal and age class growth rates. Seasonal (c, d), and age class (e, f), comparisons are combined stream reach growth rates. Box represents 25th and 75th percentile at the lower and upper boundaries respectively, lower and upper error bars represent 10th and 90th percentiles, and ● represent 5th and 95th percentiles.

Table 3.4: Instantaneous growth rate (mm/day; ΔTL, grams/day; ΔW) (mean ±S.E.) for marked brown trout grouped by stream reach, season, and age class. Superscript letters represent statistical between stream reaches, seasons, and age classes.

	Instantaneous Growth Rate	
	ΔTL	ΔW
Stream Reach		
Lower	0.07 (0.005) ^{a}	0.22 (0.01) ^{a}
Middle	0.06 (0.003) ^{b}	0.18 (0.01) ^{b}
Upper	0.06 (0.002) ^{b}	0.19 (0.01) ^{b}
Season		
Nov-Apr	0.02 (0.002) ^{a}	0.02 (0.01) ^{a}
April-May	0.08 (0.006) ^{b}	0.38 (0.02) ^{b}
May-July	0.08 (0.004) ^{b}	0.29 (0.01) ^{b}
July-Sept	0.06 (0.002) ^{b}	0.16 (0.01) ^{c}
Sept-Nov	0.03 (0.002) ^{a}	0.04 (0.01) ^{a}
Age Class		
Age-I	0.16 (0.004) ^{a}	0.53 (0.02) ^{a}
Age-II	0.05 (0.002) ^{b}	0.16 (0.01) ^{b}
Age-III	0.01 (0.001) ^{c}	0.02 (0.01) ^{c}
Age-IV+	0.01 (0.001) ^{d}	0.02 (0.01) ^{c}

ΔW ($p<0.0001$) (Table 3.4). Growth rate decreased greatly between Age-I and Age-II individuals and continued to decline between Age-II and Age-III (Figure 3.3). Correlations between growth rate and brown trout population, water quality, stream habitat, and aquatic macroinvertebrate parameters were weak for both ΔTL and ΔW.

Total length gain/day was positively related to mean stream temperature (r_s=0.22, $p<0.0001$), stream depth (r_s=0.06, p=0.003), and aquatic macroinvertebrate abundance (r_s=0.09, $p<0.0001$). Weight gain/day was positively related to mean stream temperature (r_s=0.24, $p<0.0001$), stream depth (r_s=0.17, $p<0.0001$), aquatic macroinvertebrate biomass (r_s=0.14, $p<0.0001$), aquatic macroinvertebrate abundance (r_s=0.11, $p<0.0001$), and stream width (r_s=0.04, p=0.046). Both ΔTL (r_s=-0.05, p=0.007) and ΔW (r_s=-0.08, $p<0.0001$) were negatively related to brown trout density. Stream width (r_s=-0.006, p=0.757), residual pool depth (r_s=-0.007, p=.708), pool surface area (r_s=0.029, p=0.1680), and aquatic macroinvertebrate biomass (r_s=0.0006, p=0.976) were not related to ΔTL. Residual pool depth (r_s=0.004, p=0.8431) and pool surface area (r_s=0.014, p=0.497) were not related to ΔW.

Total length among brown trout was positively correlated with displacement distance (r_s=0.20, p=0.0002). Displacement distance was negatively correlated with ΔW (r_s=-0.17, p=0.002), ΔK_{TL} (r_s=-0.20, p=0.0002) and K_{TL} at the end of each sampling period (r_s=-0.24, $p<0.0001$). Displacement and ΔTL were not related (r_s=-0.05, p=0.325).

Resident brown trout had significantly lower ΔK_{TL} (-0.001 ± 0.002) than did mobile brown trout (ΔK_{TL}= -0.01 ± 0.006) from 2007-2008 (χ^2=14.98, df=1, p=0.0001; Figure 3.5). Resident trout (0.21 ± 0.009) also had significantly higher

ΔW than did mobile trout (0.11 ± 0.06; χ^2=13.9508, p=0.0002). No significant differences between resident and mobile brown trout occurred for ΔTL (χ^2=1.7907, p=0.1808), or K_{TL} observed at the end of each sampling period (χ^2=2.3073, p=0.1288). ΔK_{TL} was significantly lower from May-July among mobile individuals than among resident brown trout (χ^2=8.05, p=0.0045). Seasonal variability in ΔW was also observed among mobile and resident brown trout, mobile fish lost weight between September and November (χ^2=7.12, p=0.0076). Throughout all other sampling periods, ΔK_{TL}, ΔTL, ΔW, and final condition were typically lower among mobile trout than among resident fish, differences were not significant during those periods (Figure 3.5).

Spatial Variability in Population Level Characteristics

Variation among reaches was evident, as brown trout density (see Appendix A.1) and biomass (see Appendix A.5) were highest at the upper Rio San Antonio site and decreased progressively downstream in the watershed (Figure 3.5). Average fluctuation (A_s) in brown trout density estimates were high at all grazing sites (range=99-241%) between 2004 and 2008, due to variable biotic and abiotic conditions observed over the duration of this research. Brown trout density was negatively correlated with mean stream width (r_s=-0.75, p<0.0001, n=90) and stream depth (r_s = -0.21, p=0.0424, n=90).

Recruitment in the lower Rio San Antonio grazing was rare, as no Age-0 brown trout were observed during fall sampling in 2004 and 2005. One year cycles of average/strong spawning classes (2004, 2006, 2008) followed by weak spawning

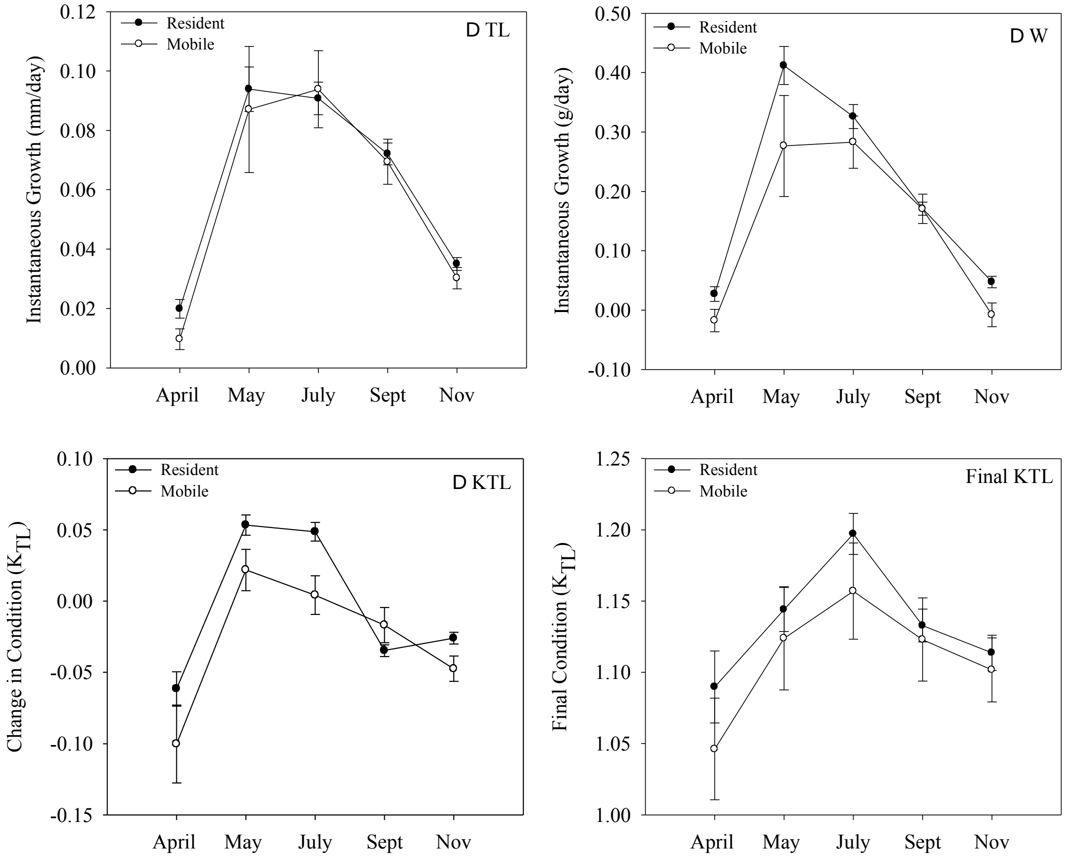


Figure 3.4: Differences (mean ± S.E) in ΔTL (a), ΔW (b), ΔKTL (c), and final KTL (d) between resident and mobile brown trout for intervals November-April (April), April-May (May), May-July (July), July-September (Sept), and September-November (Nov).

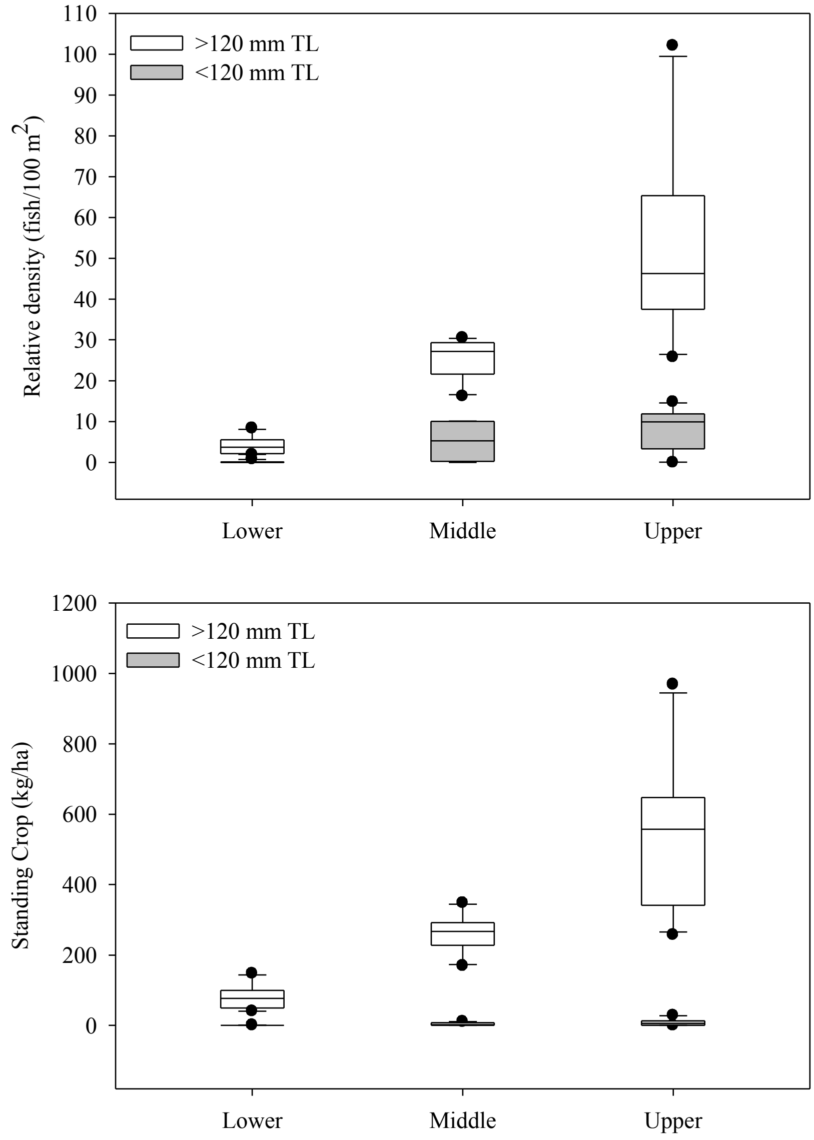


Figure 3.5: Density (fish/100m^2) and standing crop (kg/ha) estimated for adult and juvenile brown trout in lower, middle, and upper stream reaches in Rio San Antonio between 2004 and 2008. Data were combined across fall and spring sampling occasions.

classes (2005, 2007) were observed in the middle grazing site. In the upper stream reaches recruitment also followed cyclical patterns, the lag between high and low recruitment was variable among years (Table 3.5).

Adult brown trout (Age-II-IV+) collected in the lower Rio San Antonio reach exhibited greater TL in spring and fall than middle, and upper stream reaches (Figure 3.6). Age-0 brown trout exhibited greater total length in upper and middle stream reaches during spring sampling, however, Age-0 trout in the lower reach exhibited greater total length by fall sampling. There were no differences among reaches for Age-I brown trout (Figure 3.6). Mean total length ($r_s = -0.7105$, $p<0.0001$, $n=90$) and mean weight ($r_s = -0.6847$, $p<0.0001$, $n=90$) among individual fish were negatively correlated with brown trout density observed in Rio San Antonio between 2004 and 2008.

Variation among stream reaches did occur in Age-I brown trout, with individuals in the upper Rio San Antonio grazing site exhibiting higher condition scores than did trout sampled in the middle and lower reaches in both spring and fall (Figure 3.6). Age-IV+ exhibited highest K_{TL} in lower stream reaches during both spring and fall sampling, while Age-II and Age-III brown trout did not differ among stream reaches (Figure 3.6). Mean condition was highest among Age-0 and Age-I brown trout, steadily declining in Age-II and older fish. Mean K_{TL} among Age-0 through Age-III brown trout in Rio San Antonio was equal to or above condition scores considered optimal ($K_{TL}=1.0$), however, Age-IV+ brown trout K_{TL} scores

Table 3.5: Brown trout recruitment (fish/100m^2) in CATTLE, ELK, and OPEN grazing exclosures at lower, middle, and upper Rio San Antonio grazing sites from 2004-2008. W=weak recruitment, A=average recruitment, S=strong recruitment when compared to long tern confidence interval.

		Year				
Site	Mean (95% CI)	2004	2005	2006	2007	2008
Lower	0.6 (0-1.4)	0.0 A	0.0 A	2.3 S	0.6 A	0.3 A
Middle	9.3 (5.6-13.1)	13.3 S	2.6 W	11.0 A	3.6 W	16.0 S
Upper	14.3 (11.3-17.4)	13.6 A	12.3 A	8.6 W	20.3 S	16.6 A

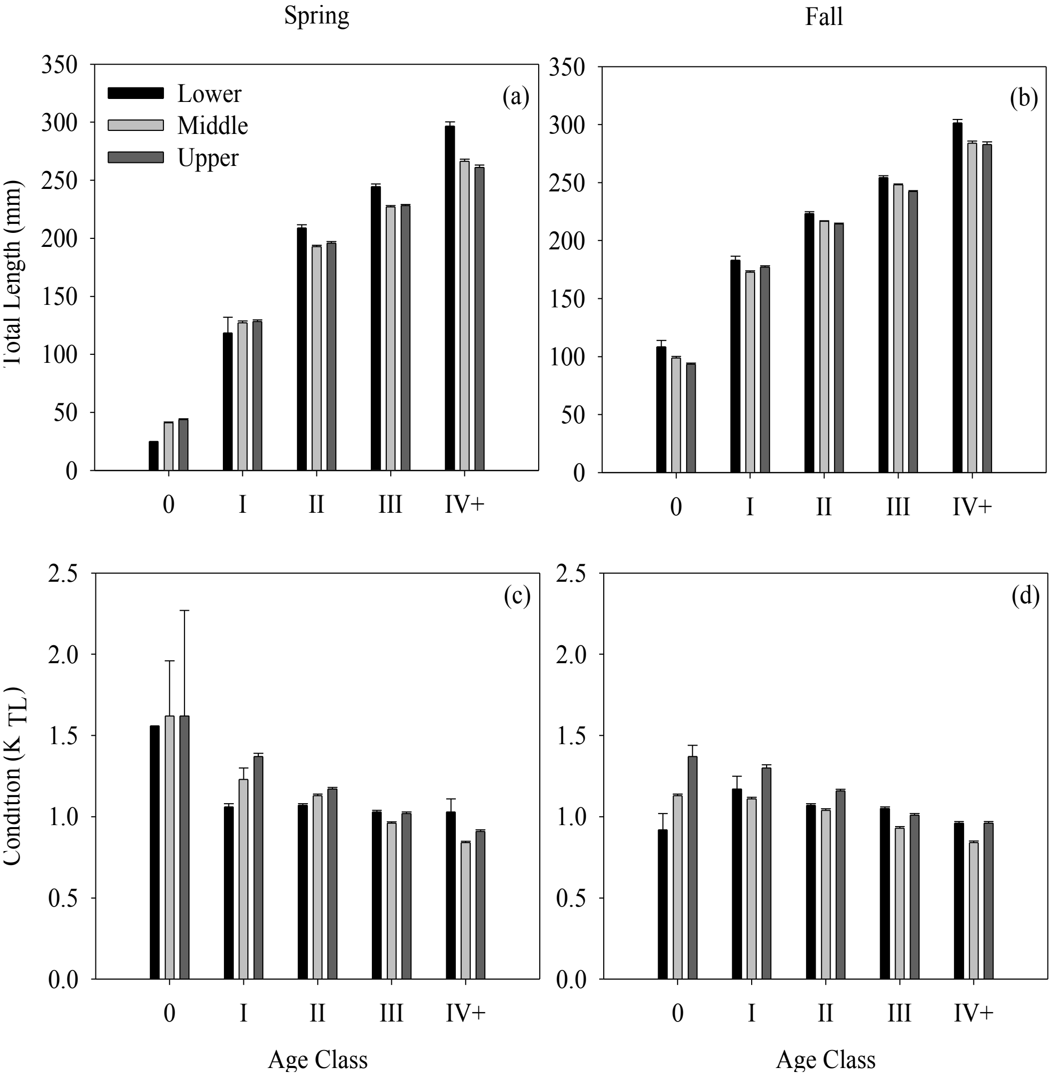


Figure 3.6: Mean (mm ±S.E) total length (a, b) and condition (c, d) among Age-0 to Age-IV+ brown trout captured in lower, middle, and upper Rio San Antonio during spring (a, c) and fall (b, d) sampling between 2004 and 2008.

throughout the watershed were below optimal (K_{TL}=0.9178; 95% C.I. = 0.892-0.943) (Appendix A.6). K_{TL} and brown trout density in Rio San Antonio were. positively correlated among Age-I trout (r_s= 0.334, p=0.0054, n=68) and negatively correlated for Age-IV+ trout (r_s = -0.216, p=0.044, n=87). Age-0 (r_s= 0.17, p=0.208, n=54), Age-II (r_s= 0.20, p=0.064, n=84), and Age-III (r_s= -0.18, p=0.0939, n=84) condition scores were not correlated with brown trout density.

Discussion

Biomass and abundance estimates for brown trout populations in Rio San Antonio are among the highest observed in the western United States (Platts and McHenry 1988). Biomass estimates from 2004 to 2008, and averaged across all sampled stream reaches along Rio San Antonio occur rarely (<10%) among trout in the Rocky Mountains. High density and abundance over a relatively small spatial scale was due to variability in biotic and abiotic factors among stream reaches. Spatial differences in population level characteristics allowed the evaluation of population level characteristics on individual fish in the form of movement behavior and growth rate.

Throughout this research distinct longitudinal differences among lower, middle and upper stream reaches were observed. Analysis of movement behavior in Rio San Antonio revealed a largely resident population with a smaller portion of mobile individuals. Movement rates varied among stream reaches with brown trout marked in the lower reach exhibiting greater mobility than fish in either the middle or upper reaches. Growth rates varied as a function of stream reach, age, and season, reflecting individual responses to biotic and abiotic factors occurring over a longitudinal gradient in Rio San Antonio. Condition factor (K_{TL}) also varied as a factor of watershed position and age class. Brown trout density, standing crop, and recruitment declined in a downstream direction. Variation among stream reaches within VCNP appear to be due to several biotic and abiotic factors which can influence the stability and productivity of trout.

Movement Behavior

Assessment of movement patterns among lotic salmonid populations has focused greatly on the hypothesis of restricted movement of Gerking (1959) and the hypothesis of Gowan et al. (1994), in which movement is common among stream fish. Gowan et al. (1994) determined that research supporting restricted movement have been biased by sampling design. High recapture rates in combination with extensive stream surveys and evaluation of multiple movement metrics make conclusions drawn regarding movement patterns among brown trout in Rio San Antonio robust to sources of bias suggested by Gowan et al. (1994).

The proportion of resident and mobile fish sampled in Rio San Antonio (64.5% resident, 35.5% mobile) is similar to results reported for salmonids (Funk 1957; Heggeness et al. 1991). Partitioning of populations into a small mobile component within an overall resident population may be due to several factors. Mobile individuals may be displaced juvenile or sub-adults (Funk 1957). Brown trout total length was positively related to displacement distance, suggesting that juvenile fish were not moving at great rates. This finding is supported by Gowan and

Fausch (2002) that large adult fish possess superior competitive advantage and thus are more likely to be mobile. Gowan and Fausch (1996 b) observed increased movement as a result of poor condition which was similar to findings in this research where mobile fish exhibited increased decline in condition in comparison to resident trout. Mobility within a population may also be determined by salmonid abundance, with movement increasing above a certain threshold of density (Hesthagen 1988). Individual variation in boldness may also lead to increased rates of mobility (Fraser et al. 2001; Sneddon 2003). Increased habitat complexity (Roberts and Angermeir 2007) and abundant food supply (Bachman 1984) have been shown to increase the likelihood of increased resident portions of a population. Observed proportions of resident brown trout was slightly higher than the overall watershed mean in middle and upper Rio San Antonio reaches (71.3% and 69.2% respectively) while the mobile portion of the population was highest (54.2%) in the lower site. Variation among sites in the composition of resident and mobile portions of the population suggests a response to differential biotic and abiotic factors observed among sites.

Brown trout captured in the lower stream reach exhibited a greater probability of movement than individuals in the middle and upper stream reaches. In addition, negative relationship between movement, density, and macroinvertebrate abundance, and a positive relationship between movement and stream width were predicted. Within Rio San Antonio, lowest observed brown trout abundance and macroinvertebrate abundance occurs in the lower site which is also where stream width is greatest. The combination of these factors in addition to high mean stream temperatures results in a highly spatiotemporally variable environment and may result in increased movement as brown trout search for thermal refuge, cover, and increased food resources.

Leptokurtic frequency distributions of displacement distance are common among mobile animals are common (Fraser et al. 2001). Among trout, leptokurtosis has been noted commonly in previous studies (Harcup et al. 1984; Heggenes et al. 1991; Gowan and Fausch 1996 b). Fraser et al. (2001) evaluated of leptokurtosis among non-game fish in an attempt to explain the driving forces behind leptokurtosis. After controlling for variation among age, size, and social status, leptokurtic distributions remained evident, suggesting that other factors largely determine displacement distributions. Among the commonly proposed explanations for continued leptokurtic distributions variation in boldness among individuals within a population appears to be a strong determinant of the probability for movement (Fraser et al. 2001). Boldness is defined as the propensity to move through and explore unfamiliar areas (Russell 1983; Wilson et al. 1993). In natural systems bold individuals may have increased encounter with variable resource conditions and by maximizing positive encounters with beneficial resources, fitness may be increased (Hilderbrand and Kershner 2000; Fraser et al. 2001; Gowan and Fasuch 2002). The frequency of long distance displacement among individuals has significant implications for the stability of fish populations over broad spatial scales. Repatriation of defaunated stream reaches following episodic disturbance (drought, fire, flood) requires exploratory movement behavior to be present among individuals within the population.

Median displacement among all grazing sites, stream reaches, sampling seasons, and age classes observed in 2007 and 2008 was 0 m. Mean displacement distance was highly variable and skewed by long distance displacement in both upstream and downstream directions. Overall 80% of the recaptures were within stream reaches where brown trout had been marked and released or previously encountered exhibiting strong site fidelity. High site fidelity among trout populations is common in brown trout (Allen 1951; Mense 1975; Hesthagen 1988; Heggeness et al. 1991). Determination of home range size among brown trout in Rio San Antonio based on these data suggests that home range is less than 50 m, however, diel movements which can be high (Clapp et al. 1990; Diana et al. 2004) would lead underestimation of home range size under the current sampling protocol. Previous work has estimated home ranges among stream dwelling to be variable among watersheds and seasonally, estimates of 15 m (Bachman 1984), 27-98 m (Burrell et al. 2000), 75 m (Hesthagen 1988), 131 m (Young et al 1997), <340 m (Young 1994) have been reported which agree with the findings in this research.

Moderate turnover rates in combination with short displacement distances have been observed among many populations (Gowan and Fausch 1996 b; Rodriguez 2002). Turnover rates observed in Rio San Antonio in 2008 varied among stream reaches, as high turnover was observed in the lower site (58%; April-November) in comparison, middle (31%) and upper (29%) exhibited significantly lower turnover rate. These findings suggest that brown trout in the lower site are responding to generally poorer conditions (increased maximum stream temperature, width–depth ratio), or that decreased population density has reduced negative associations of competition allowing trout to actively seek out more profitable foraging positions. Seasonal turnover rates may have been a function of increased tagging effort, as local movement among individuals in the middle and upper stream reaches between April and May lead to increased proportion of unmarked fish in each study area. This is supported by lower turnover rates in July, September, and November, following increased tagging effort in April and May.

Increased movement at lower population density differs from previous work which has reported a positive relationship between movement and density (Mense 1975; Hesthagen 1988), other work has shown movement to be independent of population density (Bohlin et al. 2002). This finding is supported by results reported in which resident fish exhibited a competitive advantage over mobile individuals (Deverill et al. 1999; Bohlin et al. 2002). Gowan and Fausch (2002) determined that large fish moving in summer held a competitive advantage over smaller, subordinate individuals allowing mobile trout to actively search out and exploit patchily distributed resources. Movement of trout to exploit spatially and temporally variable food resources may only be profitable in instances where food becomes limiting (Hojesjo et al. 2007). The decision to move should then be based on potential gain in fitness by moving to another area where resources may not be limiting (Olsson et al 2006). Conflicting viewpoints on the likelihood of movement based on individual fish size are common, with increased size being positively related to movement (Young 1994; Gowan and Fausch 1996 b; Gowan and Fausch 2002), negatively related to movement (Schrank and Rahel 2006), or not related to movement (Skalski and Gilliam 2000; Bohlin et al. 2002; Albanese et al. 2004). Among brown trout in

Rio San Antonio, total length was positively correlated with displacement distance and was a significant predictor for the probability of movement, however, displacement distances were not significantly different among age classes.

Differences in condition and growth among resident and mobile brown trout observed in Rio San Antonio is supported by prior research which has determined that mobile fish are generally in poorer condition than resident fish (Gowan and Fausch 1996 b; Hilderbrand and Kershner 2004). In addition, ΔK_{TL} and ΔW were negatively related to the probability of movement among brown trout in Rio San Antonio. Hilderbrand and Kershner (2004) found that mobile individuals that transitioned to resident fish improved in condition the period immediately following movement. Seasonal differences in ΔW among resident and mobile trout in Rio San Antonio were greatest over the sampling interval from September through November, which may be a function of spawning movement. Though trout sampled in the middle and upper stream reaches were gravid in November, the increase in fish size among individuals at the lower stream reach suggests increased reproductive capability. Had a large number of the mobile portion of the population been captured post-spawning, the difference in resident and mobile weight gains may have reflected both the energetic costs of movement and decreased body condition as a result of spawning.

Growth and Condition

Highest growth rates observed in this research occurred over the April-May and May-July sampling intervals, with mean stream temperatures during these intervals 9-11°C and 14-16°C respectively, supporting findings of previous research (Allen 1985; Jensen et al. 2000). Elliott (1975) identified 13°C as the optimal temperature for growth in brown trout fed to satiation. Subsequent field research has determined the models developed and subsequently modified in Elliott et al. (1995), to be relatively accurate with some fluctuation in optimal growth rates occurring at slightly lower (Jensen et al. 2000) and higher temperatures (Allen 1985; Jensen and Berg 1995). Variability in optimal growth temperatures has been hypothesized to be due to adaptations of populations to local thermal regimes (Allen 1985; Jensen et al. 2000).

Shift in resource allocation from somatic tissue to gonad development among fall spawning salmonids occurs during mid-late summer. Decreased growth rates observed during September sampling occasions may be explained by increased gonad development during this period (Nicola and Almodovar 2002). Changes in photoperiod (Nicola and Almodovar 2004), decreasing stream temperature (Jensen and Berg 1995), exposure to high temperatures (Johnstone and Rahel 2003; Meeuwig et al. 2004), and decreased food availability (Carlson et al. 2007) have also been hypothesized to influence decreased growth rates observed in early autumn. Seasonal abundance of aquatic macroinvertebrates was similar in spring and fall throughout Rio San Antonio suggesting that declining growth rate may be due to decreased stream temperature as well as gonad development. Photoperiod may result in lead to decreased somatic growth, as resources are allocated to reproduction based on hormone production. 17β–estradiol released from the ovary stimulates vitellogenesis, and in Rio Grande chub (*Gila pandora*) has been shown to reach highest concentrations during the longest photoperiod (Caldwell et al. 2004). The majority of maximum observed stream temperatures in Rio San Antonio occurred during the July-September sampling interval during both 2007 and 2008. Decreased feeding as a stress response to high daily maximum temperatures may have resulted in depression of growth rates over this time (Elliott 1981). Decreased food availability is less supported, as aquatic macroinvertebrate abundance and biomass were similar during spring and fall sampling at all Rio San Antonio stream reaches (Appendix A.8).

Condition factor among brown trout in Rio San Antonio among all age classes were in a range considered optimal (Age-0, I, II) or normal (Age-III, IV+). No significant differences existed among upper and lower stream reaches between 2004 and 2008, suggesting that aquatic macroinvertebrate biomass observed among sampling sites in 2007 and 2008 was sufficient to support observed population density without impacting individual fish condition. Brown trout sampled from the middle Rio San Antonio stream reach exhibited the lowest K_{TL} overall among all sites, with significantly lower condition observed in fall 2004 and 2007 for all age classes. Weakly negative correlation between density and condition among Age-IV+ brown trout was observed, condition decreased rapidly between Age-III and Age-IV+ individuals in both middle (-11%) and upper (-10%) stream reaches, however, Age-IV+ trout sampled in lower Rio San Antonio stream reaches decreased in condition less than both middle and upper sites (-5%). The percentage of fish in poor condition was low overall, with only 3% of the brown trout sampled between 2004 and 2008 had K_{TL} values lower than 0.70. Decreased condition may result in decreased fecundity (Pender and Kwak 2002). In addition, during periods when resources are limited, survival may be adversely affected by decreased condition.

Expression of variable life history characteristics among individuals within a population can be viewed as a trade-off between vital rates which increases individual fitness (Stearns 1976). Among brown trout sampled in Rio San Antonio, this trade-off appears to be present as brown trout sampled in middle and upper reaches tend to allocate resources to gonadal development rather than somatic growth at earlier life stages. Hutchings (1993) demonstrated that differential growth rates among brook trout in two streams with similar thermal regimes and habitat conditions exhibited variable life history characteristics. Increased juvenile growth rates and decreased adult growth rates are major determinants for onset of maturation. Juvenile fish growing at greater rates than other individuals gain fitness through age specific fecundity, while decreased adult growth rates increases potential mortality which results in decreased age at maturity and increased early reproductive effort (Hutchings 1993). Similar results have been observed among brown trout (Jonsson and Sandlund 1979; Nicola and Almodovar 2002) and arctic grayling (*Thymallus arcticus*; Haugen 2000). Growth rates among Age-III and Age-IV+ brown trout in Rio San Antonio exhibited characteristics of variable life histories among stream reaches. Age-III individuals captured in lower stream reaches allocated more resources to somatic growth than did individuals captured in the middle and upper stream reaches. This difference was evident across all sampling seasons, with the magnitude of difference being greatest in May and July samples. Observed increases in growth and overall mean total length of brown trout in the lower Rio San Antonio may positively influence fitness through increased number and size of eggs, and increased survival, allowing multiple reproductive attempts (Wootton 1990).

Variability in growth rate across spatial and temporal scales may also be influenced by density dependent effects. Intraspecific competition for food and space resources may result in displacement of subordinate fish to foraging areas where growth rates are not optimal (Hutchings 1993). Brown trout captured in middle and upper stream reaches, where trout density is significantly higher, exhibited decreased growth rate in comparison to trout captured in lower stream reaches. Aquatic macroinvertebrate abundance was similar among reaches, and biomass was considerably higher in the middle and upper Rio San Antonio. Combined across all age classes, growth rates observed in middle and upper stream reaches during May and July were greater than growth observed in the lower stream reaches over the same period. This trend was reversed during September and November sampling occasions, as individuals sampled in the lower stream reaches exhibited higher ΔW than both middle and upper stream reaches. The relationship between food availability and growth rates has been shown to be significant among brown trout (Cada et al. 1987; Bohlin et al. 2002) and cutthroat trout (Boss and Richardson 2002), and warrants further investigation within VCNP.

Density dependent effects on individual growth of salmonids have generally focused on the relationship between Age-0 growth rates and overall population density (Jenkins et al. 1999; Bohlin et al. 2002). Population density was determined to negatively impact growth rate among juveniles in both instances. This research was limited to Age-I and older brown trout, as Age-0 fish were not large enough to be marked until September sampling occasions. Density dependent growth among Age-I and older has been shown in previous research. Analyses controlling season, age, body size, and temperature exhibited significant variation among sites due to brown trout density (Vollestad et al. 2002). While weakly negative correlation between growth rate and brown trout density were observed in this research, results are likely a function of sample size rather than biologically significant relationships.

Population Level Characteristics

High variability in trout abundance has been reported in previous literature regarding lotic salmonid populations (Platts and Nelson 1988; Gowan and Fausch 1996a). Biotic and abiotic factors interact to shape the diversity and abundance of fish assemblages within a watershed, including inter- and intraspecies competition, food resources, habitat availability, and thermal regime.

Within Rio San Antonio, simplification of historical native fish communities has resulted from introduction of non-native species and land-use practices at VCNP. Currently, brown trout are the only fish species throughout much of Rio San Antonio. Longnose dace (*Rhinichthys cataractae*) are observed rarely and restricted to areas supporting low brown trout density. Decreased interspecific competition for food and habitat resources has allowed brown trout populations to increase to current levels which, in the upper reaches of Rio San Antonio, appear to be approaching or exceeding carrying capacity. In the absence of interspecific competition, increased levels of intraspecific competition has manifested itself through density dependent responses among brown trout. Negative correlations between brown trout density and average body size were noted and are indications of density dependence (Bohlin et al. 1994). The largest individual captured during this study was 452 mm, suggesting that productivity is sufficient in Rio San Antonio to produce large fish, and that overall density may be limiting maximum size. Reduction in fish size as a response to increased density may have profound biological and socioeconomic effect on VCNP. Current angling programs within VCNP may also be adversely impacted by decreased fish size, as demand for fishing access may decline. In addition to decreased total length, fish condition was negatively related to density among Age-IV and older brown trout within Rio San Antonio. Lowest K_{TL} values were observed in the upper stream reaches where condition was 15% lower than K_{TL} values observed in the lower stream reaches where brown trout populations were significantly lower. Decreased growth rates were also observed in the middle and upper stream reaches of Rio San Antonio in comparison to downstream reaches, which further explains observed differences in average fish length among stream reaches. Decreased growth rates due to increased population density may be a function of shifts in habitat use as subordinate fish may be forced into habitat were foraging is suboptimal (Chapman 1966).

Variation in salmonid abundance and biomass has also been related to local difference in food supply. Increases in abundance (63%) and biomass (78%) were noted by Mason and Chapman (1965) in a laboratory experiment where abundance of macroinvertebrate drift was controlled. Further, limitation of food resources may result in increased agonistic behavior among conspecifics, which could in turn result in displacement of subordinate individuals to suboptimal foraging positions

(Chapman 1966; Alanara et al. 2001). Dominance is positively related to condition among stream fish (Fausch 1984), maintenance of adequate body condition by individual fish stabilizes the overall population as a result of increased odds of survival during periods when resources are limited. Within Rio San Antonio, aquatic macroinvertebrate abundance and biomass fluctuated as a function of season and longitudinal position in the watershed. Upper and middle stream reaches were characterized by high abundance and biomass of species from the Orders Plecoptera, Ephemeroptera, and Trichoptera, generally considered indicators of high water quality. Lower stream reaches were characterized by high abundance of species from the Orders Diptera and Trichoptera, however, biomass was lowest among all stream reaches sampled in 2007 and 2008.

Variability in fish populations as a result of habitat availability (Chapman 1966) and quality (Bjornn and Reiser 1991) is evident from previous research, however, species and life stages respond in different manners to stream habitat characteristics. Brown trout exhibit flexible habitat selection under variable environmental conditions as well as among different life stages (Elliott 1994; Heggenes et al. 1999). Stream habitat characteristics within Rio San Antonio suggest that longitudinal variation among lower, middle, and upper stream reaches in VCNP falls within the generally acceptable range of habitat use for lotic brown trout (Heggeness 2002). Heterogeneity in habitat on both the watershed and stream reach scale is necessary to support all life stages, as juvenile salmonids require different habitat than do adult fish. Plasticity in habitat use among stream fish is common in spatiotemporally variable environments (Slobodkin and Rapoport 1974). Ebersole et al. (2003) determined a negative relationship between width–depth ratio and salmonid abundance in northeast Oregon streams. Of the stream habitat parameters assessed during this research width–depth ratio and streambed substrate were most variable among sites, with the lower Rio San Antonio exhibiting higher width–depth ratio and embeddedness than both the middle and upper stream reaches.

Implications of increased width–depth ratio include increased exposure to solar radiation which has an additive effect progressing downstream in the watershed. Upper incipient lethal temperature (UILT) for brown trout acclimated to 15°C is between 25.6-27.7°C (Elliott 1981). Observed stream temperatures within Rio San Antonio exceeded stream temperature standards (20°C; New Mexico Environment Department) during July and August 2007 and 2008. Maximum daily temperatures were observed approaching UILT for brown trout on 11 occasions in 2007 and 15 occasions in 2008 at the lower Rio San Antonio site, and on 5 occasions in 2007 and 2008 at the middle site. Maximum temperatures observed at the upper Rio San Antonio site never exceeded 23°C during this research. Maximum temperatures largely occurred over a short duration each day (1-4 hours) followed by significant declines to the daily minimum temperature which was typically 5-10°C lower than observed maximum temperatures. Wide diel fluctuations in stream temperature may allow salmonids to survive periods of increased temperature, however, high temperatures have been shown to significantly reduce growth in salmonids (Johnstone and Rahel 2003; Meeuwig et al. 2004). Suppression of growth rates are a result of decreased feeding activity and increased stress occurring during acute periods of exposure to increased temperature (Elliott 1981). Supercooling (<0°C) occurred in

2007 and 2008 at the lower Rio San Antonio reach, while stream temperatures <0°C were not observed at middle or upper reaches. During periods of supercooling anchor and frazil ice form (Jakober et al. 1998) which can lead to periods of habitat isolation. Frazil ice can adversely affect trout, causing gill hemorrhaging, suffocation, and in extreme cases mortality (Brown et al. 1994). Determination of the spatial variability of fish characteristics provides valuable information regarding the biotic and abiotic factors influencing population dynamics on a watershed scale. Assessment of limiting factors can influence focused management objectives which can be implemented to improve both individual and population level fish characteristics.

Summary and Conclusions

Variation in brown trout density, biomass, recruitment, condition, growth, and movement among stream reaches within Rio San Antonio were evident between 2004 and 2008. Movement behavior among brown trout in Rio San Antonio suggests a high resident component and a small mobile portion of the population. These conclusions are supported by the combination of short displacement distance, low turnover rates, and overall high recapture rates. Variability in the proportion of resident and mobile individuals was observed among stream reaches, as an increase in the percent mobile brown trout was observed in the lower Rio San Antonio inside VCNP. Increased mobility may be a response to higher variability in the spatial and temporal availability of resources as well as potential exploration for optimal foraging areas or thermal refuge.

Decreased brown trout density and biomass observed in the lower stream reaches are presumably a function of increased variability in stream temperatures as the lower site experienced the highest and lowest annual temperatures within Rio San Antonio. Low population density may translate to increased condition and growth rate at the lower stream reach, as individuals do not have the effects of increased competition observed at higher population densities in middle and upper stream reaches. Abundance and biomass estimates within the upper reach suggest that the population is at or near carrying capacity with some evidence of density–dependent growth and condition being reflected among individual brown trout in this area.

Management Implications

Development of long term goals by VCNP trustees on the desired future conditions of the fish populations in not only Rio San Antonio, but all streams within the preserve is necessary prior to undertaking any long term stream improvement projects. Potential activities that could be undertaken in VCNP to improve the overall condition of the fish community in Rio San Antonio include annual mechanical suppression of brown trout populations and reintroduction of the above species; implementation of liberal catch regulations in the middle and upper stream reaches to decrease fish populations; restoration of degrade riparian communities, installation of instream structures to increase the availability of fish habitat; and chemical and mechanical renovation of the brown trout population, and restoration of native species including Rio Grande cutthroat, Rio Grande sucker, and Rio Grande chub.

Implementation of liberal take limits in middle and upper Rio San Antonio fishing beats may result in direct and indirect increases in angling related mortality, reducing brown trout populations in certain stream reaches. Reduction of the overall population may benefit remaining individuals through increased growth thereby increasing size and age at maturity. Compensatory response of increased juvenile survival resulting for increased adult mortality may diminish the potential of success for this alternative, however, current regulations are not having positive effects on brown trout and as such all possible alternatives must be considered.

Restoration of riparian vegetation along Rio San Antonio including reintroduction of willow and other native woody vegetation as well as sedges and other deeply rooted riparian species may impart several benefits on salmonid populations. Initially, increased overhanging vegetation will provide insulating properties, buffering temperature minima and maxima, which would then result in a more stable environment for salmonids. Increased riparian vegetation may also increase the productivity of Rio San Antonio through allochthonous input of terrestrial invertebrates and other organic matter. Over an increased temporal scale, riparian vegetation communities would also result in improved stream habitat conditions, manifest in decreased width–depth ratio, decreased fine sediments, and decreased stream temperature. The stabilizing properties of riparian vegetation are preferable to instream habitat structures aimed at improving fish habitat conditions. Instream habitat structures designed to reduce stream channel width generally perform poorly in C-type streams, altering streamflow patterns which has been shown to have deleterious effects on stream stability resulting in unintended outcomes and often increased instability following restoration.

Restoration of fish communities within the Jemez River watershed provides a unique opportunity to increase the range of Rio Grande cutthroat, which has been petitioned to be listed under the endangered species act. Restoration of Rio San Antonio alone would add significant stream distance to the current range of Rio Grande cutthroat trout in New Mexico (approximately 35-40 stream km). Rio Grande cutthroat trout restoration would also increase the biodiversity of Rio San Antonio, as the species has evolved in sympatry with non-game species, whereas brown trout are known to be highly piscivorous reducing non-game populations to the point of local extinction. The presence of a native salmonid may also impart an economic boon to VCNP as anglers may be more likely to seek out opportunity to fish VCNP waters home to native fish rather than brown trout. Restoration of Rio San Antonio would require significant resources to be committed to the project, as well as increased public relations and outreach to neighboring communities to garner support for restoration. Piscicide application should be considered for the restoration as mechanical removal within a stream of this size may be logistically impossible. Alternatively, suppression of the brown trout population through annual electrofishing may sufficiently reduce populations within Rio San Antonio allowing reintroduction of Rio Grande cutthroat trout. The presence of rainbow trout in Rio San Antonio among stream reaches not sampled in this research would make this alternative undesirable as introgression with cutthroat would likely occur.

Literature Cited

Alanara, A., M. D. Burns, and N. B. Metcalfe. 2001. Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. Journal of Animal Ecology 70:980–986.

Albanese, B., P. L. Angermeier, S. Dorai–Raj. 2004. Ecological correlates of fish movement in a network of Virginia streams 61:857–869.

Allen, K. R. 1951. The Horokiwi Stream: a study of a trout population. New Zealand Marine Department of Fisheries Bulletin 10, Wellington, New Zealand.

Allen, K. R. 1985. Comparison of growth rate of brown trout (*Salmo trutta*) in a New Zealand stream with experimental fish in Britain. Journal of Animal Ecology 54:487–495.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1–32.

Bjornn, T. C., D. W. Reiser. 1991. Habitat requirements of salmonids in streams. In: Influence of forest and rangeland management on salmonid fishes and their habitats. Edited by W.R. Meehan. American Fisheries Society Special publication 19:83–138.

Bohlin, T., C. Dellefors, and U. Faremo. 1994. Probability of first sexual maturation of parr males in a wild sea-run brown trout *Salmo trutta* depends on condition factor one year in advance. Canadian Journal of Fisheries and Aquatic Sciences 51:1929–1936.

Bohlin, T., L. F. Sundstron, J. I. Johnsson, J. Hojesjo, and J. Pettersson. 2002. Density–dependent growth in brown trout: effects of introducing wild and hatchery fish. Journal of Animal Ecology 71:683–692.

Boss, S. M. and J. S. Richardson. 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout(*Oncorhyncus clarki*) in coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 59:1044–1053.

Bridcut, E. E., and P. S. Giller. 1995. Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals. Canadian Journal of Fisheries and Aquatic Sciences 52:2543–2552.

Brown, R. S., S. S. Stanislawski, and W. C. Mackay. 1994. Effects of frazil ice on fish. *In* Proceedings of the Workshop on the Environmental Aspects of River Ice, Saskatoon, SK. 18–20 August 1993. Edited by T. D. Prowse. NHRI Symp. Ser. No. 12. National Hydrology Research Institute, Saskatoon, SK. pp. 261–278.

Burrell, K. H., J. J. Isely, D. B. Bunnell Jr., D. H. Van Lear, and C. A. Dolloff. 2000. Seasonal movement of brown trout in a southern Appalachian River. Transactions of the American Fisheries Society 129:1373–1379.

Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. Transactions of the American Fisheries Society 116:692–702.

Caldwell, C. A., S. A. Fuller, W. R. Gould, P. R. Turner, and D. M. Hallford. 2004. Seasonal changes in the 17β–estradiol of the Rio Grande chub (*Gila Pandora*) in south-central New Mexico. Southwestern Naturalist 49:311–315.

Carlson, S. M., A. P. Hendry, and B. H. Letcher. 2007. Growth rate differences between resident native brook trout and non-native brown trout. Journal of Fish Biology. 71:1430–1447.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345–357.

Clapp, D. F., R. D. Clark, and J. S. Diana. 1990. Range, activity, and habitat of large, free–ranging brown trout in a Michigan stream. Transactions of the American Fisheries Society 119:1022–1034.

Cucherousset, J., D. Ombredane, and J.L. Bagliniere. 2006. Linking juvenile growth and migration behaviour of brown trout (*Salmo trutta*) using individual PIT-tagging. Cahiers de Biologie Marine 47:73-78

Deverill, J. L., C. E. Adams, C. W .Bean. 1999. Prior residence, aggression and territory acquisition in hatchery–reared and wild brown trout. Journal of Fish Biology 55:868–875.

Devries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512. In: B. R. Murphy and D. W. Willis (editors) Fisheries Techniques, 2nd edition. American Fisheries Society. Bethesda, Maryland.

Diana, J. S., J. P. Hudson, and R. D. Clark. 2004. Movement patterns of large brown trout in the mainstream Au Sable River, Michigan. Transactions of the American Fisheries Society 133:34–44.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon. Canadian Journal of Fisheries and Aquatic Sciences 60:1266–1280.

Elliott, J. M. 1975a. The growth rate of brown trout (*Salmo trutta*) fed on maximum rations. Journal of Animal Ecology 44:805–821.

Elliott, J. M. 1975b. The growth rate of brown trout (*Salmo trutta*) fed on reduced rations. Journal of Animal Ecology 44:823–842.

Elliott, J. M. 1981. Some aspects of thermal stress on freshwater fishes. In: Pickering A. D. (editor). Stress and Fish. London, England. Academic Press pp 209-245.

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford.

Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Functional Ecology 9:290–298.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. The American Naturalist 158: 124–135.

Funk, J. L. 1957. Movement of stream fishes in Missouri. Transactions of the American Fisheries Society 85:39–57.

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

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

Gowan, C. M. and K. D. Fausch. 1996a. Long-term demographic responses of trout populations to habitat manipulations in six Colorado streams. Ecological Applications 6:931–946.

Gowan, C. M., and K. D. Fausch. 1996b. Mobile brook trout in two high–elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370–1381.

Gowan, C. M. and K. D. Fausch. 2002. Why do foraging stream salmonids move in summer? Environmental Biology of Fishes 64:139–153.

Harcup, M. F., R. Williams, and D. M. Ellis. 1984. Movements of brown trout, *Salmo trutta* L., in the River Gwyddon, South Wales. Journal of Fish Biology 24: 415–426.

Haugen, T.O. 2000. Growth and survival effects on maturation pattern in populations of grayling with recent common ancestors. Oikos 90:107–118.

Heggenes, J. 2002. Flexible summer habitat selection by wild, allopatric brown trout in lotic environments. Transactions of the American Fisheries Society 131:287–298.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhyncus clarki*) in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48:757–762.

Heggenes, J., J. L. Bagliniere, and R. A. Cunjak. 1999. Spatial niche variability for young Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in heterogeneous streams. Ecology of Freshwater Fish 8:1–21.

Hesthagen, T. 1988. Movements of brown trout, *Salmo trutta*, and juvenile Atlantic salmon, *Salmo salar*, in a coastal stream in northern Norway. Journal of Fish Biology 32:639–653.

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

Hilderbrand, R. H, and J. L. Kershner. 2004. Are there differences in growth and condition between mobile and resident cutthroat trout? Transactions of the American Fisheries Society 133:1042–1046.

Hojesjo, J., F. Okland, L. F. Sundstrom, J. Pettersson, and J. I. Johnsson. 2007. Movement and home range in relation to dominance; a telemetry study on brown trout, *Salmo trutta*. Journal of Fish Biology 70:257–268.

Hosmer, D. W. and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley. New York.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth. Ecology 74:673–684.

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

Jenkins, T. M., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 8:941–956.

Jensen, A. J., T. Forseth, and B. O. Johnsen. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69:1010–1020.

Jensen, J. W., and T. Berg. 1995. The annual growth rate cycle of brown trout. The Progressive Fish-Culturist 57:231–237.

Jonsson, B., and O. T. Sandlund. 1979, Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta* m. *fario*) in Sore Osa river system, Norway. Environmental Biology of Fishes 4:43–54.

Johnstone, H, C, and F. J. Rahel. 2003. Assessing temperature tolerance of Bonneville cutthroat trout based on constant and cycling thermal regimes. Transactions of the American Fisheries Society 132:92–99.

Mason, J. C., and D. W. Chapman. 1966. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. Journal of the Fisheries Research Board of Canada 22:173–190.

Meeuwig, M. H. J. B. Dunham, J. P. Hayes, and G. L. Vinyard. 2004. Effects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variable sizes. Ecology of Freshwater Fish 13:208–216.

Mense, J. B. 1975. Relation of density to brown trout movement in a Michigan stream. Transactions of the American Fisheries Society 104:688–695.

Nicola, G. C., and A. Almodovar. 2002. Reproductive traits of stream–dwelling brown trout, *Salmo trutta*, in contrasting neighbouring rivers of central Spain. Freshwater Biology 47:1353–1365.

Nicola, G. C., and A. Almodovar. 2004. Growth pattern of stream–dwelling brown trout under contrasting thermal conditions. Transactions of the American Fisheries Society 133:66–78.

Olsson, I. C., L. A.. Greenberg, E. Bergman, and K. Wysujack. 2006. Environmentally induced migration: the importance of food. Ecology Letters 9:645–651.

Ombredane, D., J.L. Bagliniere, and F. Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (*Salmo trutta*) and their use for studying movement in a small river. Hydrobiologia 371/372:99-106

Pender, D. R., and T. J. Kwak. 2002. Factors influencing brown trout reproductive success in Ozark tailwaters. Transactions of the American Fisheries Society 131:698–717.

Platts, W.S., R.L. Nelson. 1985. Impacts of rest-rotation grazing on stream banks in forested watersheds in Idaho. North American Journal of Fisheries Management 5:547-556

Platts, W. S., and M. L. McHenry. 1988. Density and biomass of trout and char in western streams. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT–241.

Platts, W. S., and R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land–use evaluation. North American Journal of Fisheries Management 8:333–345.

Prentice, E.F., T.A. Flagg, C.S. McCutcheon. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. American Fisheries Symposium, 7:317-322

Roberts, J. H., and P. L. Angermeier. 2007. Spatiotemporal variability of stream habitat and movement of three species of fish. Oecologia 151:417–430

Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1–13.

Russell, P. A. 1983. Psychological studies of exploration in animals: a repraisal. Pages 22–54 *in* L. I. A. Birke and J. Archer (editors) Exploration in animals and humans. Van Nostrand, New York.

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

Skalski, G. T., J. F. Gilliam. 2000. Modelling diffusive spread in a heterogeneous population: a movement study with stream fish. Ecology 81:1685–1700.

Slobodkin, L. B., and A. Rapoport. 1974. An optimal strategy of evolution. The Quarterly Review of Biology 49:181–200.

Sneddon, L. U. 2003. The bold and the shy: individual differences in rainbow trout. Journal of Fish Biology 62:971–975.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. The Quarterly Review of Biology 51:3–47.

Swift, D.R. 1961. The annual growth rate cycle in brown trout (*Salmo trutta*) and its cause. Journal of Experimental Biology 38:595-604

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–138.

Vollestad, L. A., E. M. Olsen, and T. Forseth. 2002. Growth-rate variation in brown trout in small neighbouring streams: evidence for density-dependence? Journal of Fish Biology 61:1513–1527.

Wilson, D. S., K. Coleman, A. B. Clarke, and L. Bierderman. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. Journal of Comparative Psychology 107:250–260.

Wooton, R. J. 1990. The ecology of teleost fishes. Chapman and Hall. London. 404 pp.

Young, M. K. 1994. Brown trout mobility in south–central Wyoming streams. Canadian Journal of Zoology 72:2078–2083.

Young, M. K., R. A. Wilkison, J. M .Phelps, and J. S. Griffith. 1997. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. Great Basin Naturalist 57:238–244.

Zar, J. H. 1984. Biostatistical analysis. 2nd Edition. Prentice-Hall. Englewood Cliffs, New Jersey. 130 pp.

Zippen, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82-90.

Appendix

A.1: Density (fish/100m^2) and standing crop (kg/ha) (mean ± S.E.) for adult (>120 mm) and juvenile (<120 mm) brown trout sampled in CATTLE, ELK, and OPEN grazing sites, Rio San Antonio, Valles Caldera National Preserve, New Mexico, 2004-2008.

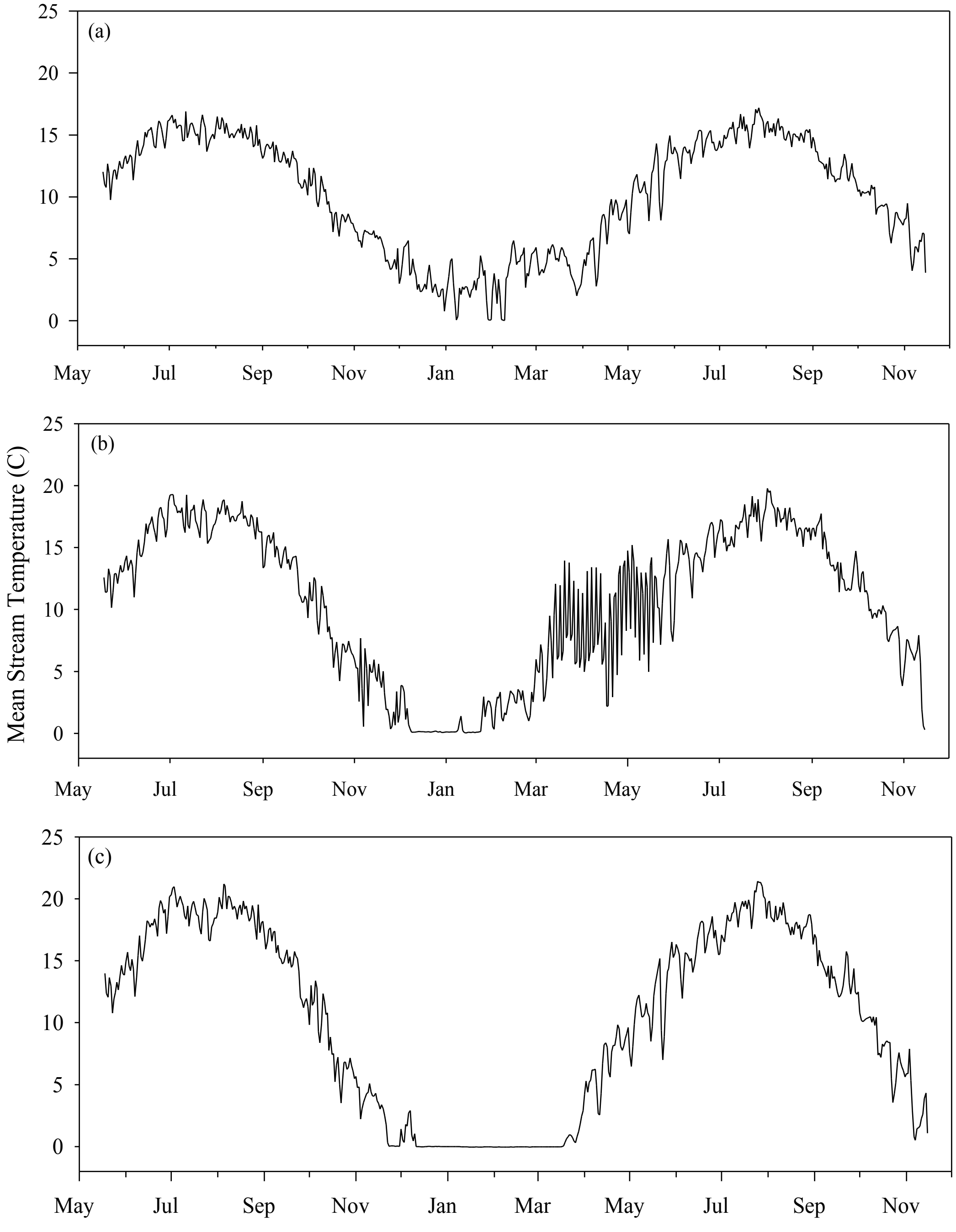
		Density		Standing Crop	
		Adult (fish/100m^2)	Juvenile (fish/100m^2)	Adult (kg/ha)	Juvenile (kg/ha)
Spring 2004	Cattle	55.2 (38.9)	5.0 (4.3)	524.2 (328.9)	0.57 (0.51)
	Elk	48.9 (33.4)	7.4 (5.8)	485.8 (302.3)	0.83 (0.67)
	Open	33.0 (16.4)	7.3 (3.7)	361.4 (168.1)	0.91 (0.47)
Fall 2004	Cattle	22.7 (8.9)	7.8 (3.9)	294.2 (100.0)	7.3 (3.7)
	Elk	27.6 (17.8)	3.8 (1.9)	363.4 (233.2)	3.5 (1.9)
	Open	21.6 (13.1)	4.7 (3.1)	270.3 (155.4)	5.6 (4.2)
Spring 2005	Cattle	18.1 (8.7)	0.08 (0.08)	178.6 (64.1)	0.01 (0.01)
	Elk	21.4 (13.2)	0.66 (0.66)	187.5 (111.3)	0.02 (0.02)
	Open	17.9 (10.8)	0	185.1 (89.3)	0
Fall 2005	Cattle	21.6 (8.3)	4.5 (4.2)	257.4 (80.4)	3.9 (3.4)
	Elk	26.5 (17.3)	3.4 (3.1)	307.6 (189.9)	3.3 (3.1)
	Open	25.9 (12.9)	3.5 (2.6)	265.8 (122.8)	2.8 (2.2)
Spring 2006	Cattle	16.5 (7.2)	5.4 (4.8)	175.8 (68.1)	0.46 (0.41)
	Elk	29.9 (14.6)	5.6 (3.1)	299.5 (112.0)	0.88 (0.60)
	Open	25.1 (13.6)	7.0 (3.5)	229.1 (113.9)	2.5 (1.4)
Fall 2006	Cattle	18.1 (7.3)	7.4 (3.3)	224.4 (76.1)	8.5 (3.7)
	Elk	22.6 (11.3)	5.3 (2.9)	298.7 (132.2)	8.6 (6.08)
	Open	20.5 (10.0)	7.2 (3.4)	240.7 (116.9)	8.1 (3.8)
Spring 2007	Cattle	11.2 (6.5)	2.5 (2.5)	107.8 (53.1)	0.22 (0.22)
	Elk	22.5 (10.4)	1.6 (1.6)	250.7 (95.1)	0.09 (0.09)
	Open	14.4 (8.32)	0	155.9 (75.0)	0
Fall 2007	Cattle	23.6 (9.1)	15.9 (14.5)	276.8 (92.4)	12.4 (11.0)
	Elk	50.5 (27.9)	11.7 (8.6)	653.1 (372.3)	10.7 (8.5)
	Open	17.0 (8.6)	7.3 (6.5)	187.3 (99.3)	8.4 (7.6)
Spring 2008	Cattle	37.9 (23.6)	0.18 (0.18)	322.1 (191.9)	0.01 (0.01)
	Elk	44.1 (23.7)	0.17 (0.17)	404.0 (183.9)	0.02 (0.02)
	Open	29.1 (14.5)	0	227.8 (104.6)	0
Fall 2008	Cattle	23.1 (6.3)	9.6 (5.1)	250.6 (20.7)	9.0 (4.7)
	Elk	48.5 (27.5)	8.8 (5.3)	512.7 (259.9)	8.5 (5.8)
	Open	26.3 (15.4)	3.5 (1.8)	257.9 (150.3)	4.5 (2.6)

A.2: Condition factor (K_{TL};mean ±S.E.) among Age-0 to Age-IV+ brown trout captured in CATTLE, ELK, and OPEN grazing sites during spring and fall sampling between 2004 and 2008.

		2004		2005		2006		2007		2008	
Site	Age	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Cattle	0	1.22 (0.17)	1.38 (0.04)	1.28 (0)	1.31 (0.04)	1.74 (0.39)	1.18 (0.04)	2.09 (0.09)	1.26 (0.01)	1.11 (0)	1.10 (0.02)
	I	1.16 (0.03)	1.20 (0.04)	1.58 (0.12)	1.12 (0.02)	1.27 (0.20)	1.20 (0.04)	1.25 (0.06)	1.08 (0.04)	1.29 (0.04)	1.18 (0.03)
	II	1.12 (0.02)	1.12 (0.02)	1.08 (0.03)	1.06 (0.03)	1.12 (0.02)	1.11 (0.02)	1.16 (0.05)	1.15 (0.03)	1.11 (0.02)	1.03 (0.01)
	III	0.96 (0.01)	0.98 (0.02)	0.93 (0.02)	0.87 (0.02)	1.01 (0.01)	0.94 (0.03)	1.02 (0.04)	0.99 (0.03)	1.29 (0.04)	0.93 (0.01)
	IV+	0.83 (0.01)	0.95 (0.03)	0.82 (0.03)	0.87 (0.03)	0.86 (0.03)	0.93 (0.04)	0.99 (0.07)	0.92 (0.05)	1.11 (0.02)	0.91 (0.01)
Elk	0	1.10 (0.10)	1.39 (0.07)	2.5 (0)	1.37 (0.10)	1.58 (0.29)	1.14 (0.06)	1.33 (0)	1.23 (0.05)	1.09 (0)	1.18 (0.02)
	I	1.23 (0.03)	1.22 (0.04)	1.13 (0.03)	1.13 (0.03)	1.26 (0.03)	1.31 (0.04)	1.23 (0.07)	1.28 (0.04)	1.24 (0.02)	1.21 (0.03)
	II	1.06 (0.01)	1.08 (0.01)	1.06 (0.01)	1.08 (0.02)	1.16 (0.03)	1.11 (0.04)	1.41 (0.04)	1.17 (0.03)	1.12 (0.01)	1.14 (0.01)
	III	0.97 (0.01)	1.02 (0.01)	0.93 (0.02)	0.97 (0.02)	1.01 (0.02)	1.04 (0.02)	1.14 (0.02)	1.05 (0.02)	0.96 (0.02)	0.96 (0.01)
	IV+	0.85 (0.01)	0.90 (0.02)	0.85 (0.01)	0.91 (0.02)	0.88 (0.01)	0.95 (0.04)	0.99 (0.02)	1.02 (0.02)	0.85 (0.02)	0.89 (0.03)
Open	0	1.48 (0.07)	1.39 (0.06)	-	1.16 (0.07)	1.93 (0.21)	1.01 (0.02)	-	1.16 (0.02)	-	1.18 (0.03)
	I	1.32 (0.05)	1.14 (0.03)	1.10 (0.03)	1.09 (0.02)	1.35 (0.05)	1.19 (0.04)	1.31 (0.05)	1.16 (0.04)	1.27 (0.02)	1.23 (0.02)
	II	1.15 (0.02)	1.09 (0.02)	1.12 (0.03)	1.04 (0.01)	1.17 (0.02)	1.10 (0.01)	1.27 (0.04)	1.13 (0.03)	1.10 (0.01)	1.11 (0.02)
	III	1.03 (0.02)	1.03 (0.02)	0.95 (0.01)	0.95 (0.02)	1.02 (0.01)	1.02 (0.02)	1.15 (0.03)	0.99 (0.03)	0.92 (0.03)	0.94 (0.02)
	IV+	0.91 (0.02)	0.91 (0.02)	0.83 (0.02)	0.84 (0.02)	0.86 (0.02)	0.91 (0.04)	1.02 (0.03)	1.06 (0.05)	1.18 (0.03)	0.98 (0.05)

A.3: Mark-recapture statistics used to monitor growth rate and movement in brown trout between November 2006 and November 2008 in Rio San Antonio.

Sample Number	Start date	End date	Total marked during sampling	Cumulative number marked	Total recaptured during sampling
1	24-Oct-06	4-Nov-06	102		*
2	14-Apr-07	15-Apr-07	127	102	21
3	22-May-07	24-May-07	12	229	92
4	24-Jul-07	25-Jul-07	47	241	100
5	22-Sep-07	26-Sep-07	7	288	140
6	2-Nov-07	11-Nov-07	14	295	176
7	18-Apr-08	20-Apr-08	372	309	87
8	19-May-08	21-May-08	355	681	356
9	28-Jul-08	30-Jul-08	214	1036	528
10	26-Sep-08	28-Sep-08	196	1250	596
11	7-Nov-08	15-Nov-08	*	1446	732



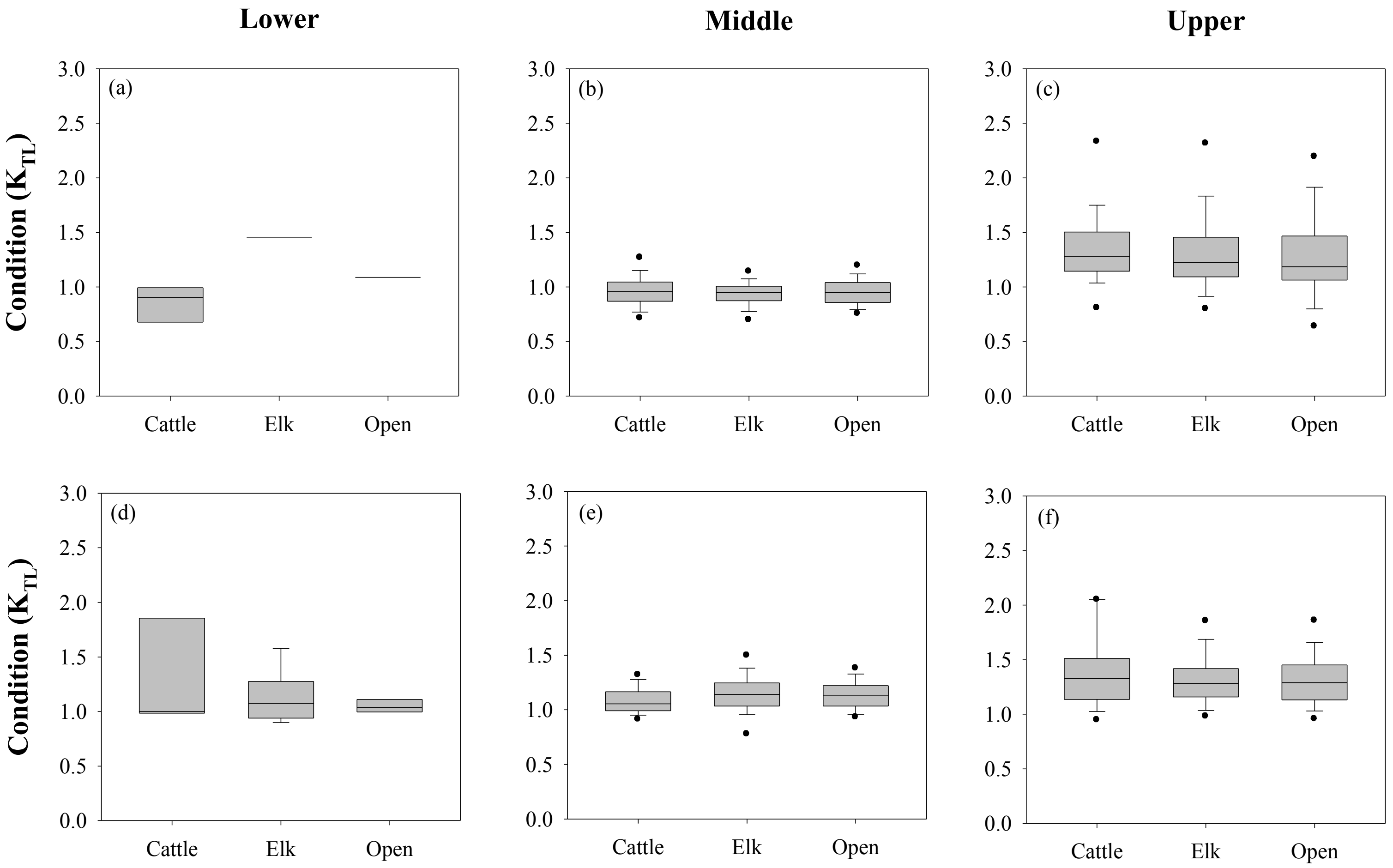
A.4: Daily mean stream temperature (°C) observed at upper (a), middle (b), and lower (c) stream reaches within Rio San Antonio between 18 May 2007 and 15 November 2008.

A.5: Density (fish/100m^2) and standing crop (kg/ha) (mean ± S.E.) for adult (>120 mm) and juvenile (<120 mm) brown trout sampled in lower, middle, and upper stream reaches, Rio San Antonio, Valles Caldera National Preserve, New Mexico, 2004-2008.

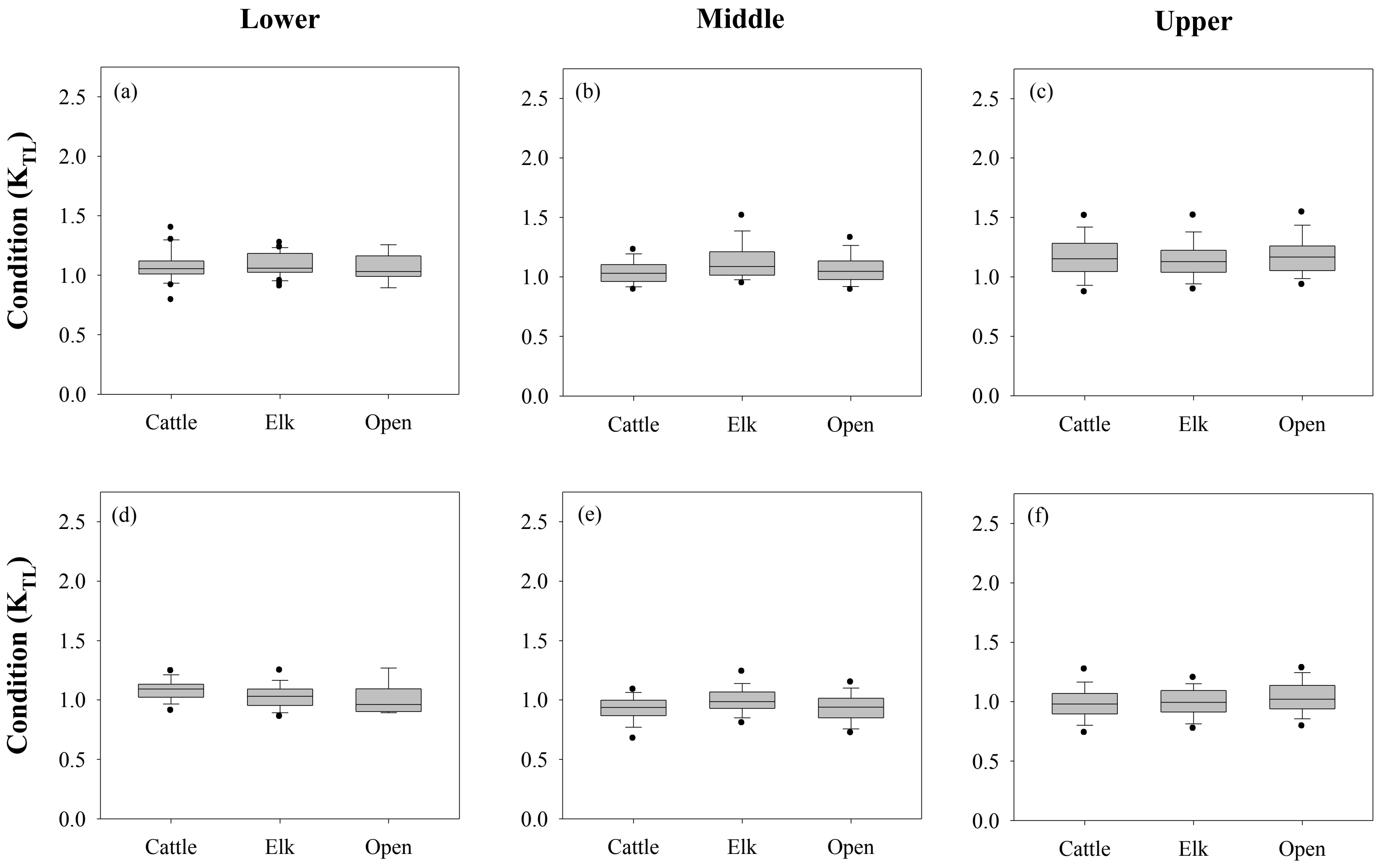
		Density		Standing Crop	
		Adult (fish/100m^2)	Juvenile (fish/100m^2)	Adult (kg/ha)	Juvenile (kg/ha)
Spring 2004	Lower	4.5 (1.2)	0	88.8 (17.4)	0
	Middle	30.5 (3.0)	4.9 (2.7)	313.8 (33.7)	0.52 (0.30)
	Upper	102.1 (21.4)	14.8 (2.1)	968.8 (159.0)	1.8 (0.18)
Fall 2004	Lower	2.6 (1.2)	0	52.3 (25.6)	0
	Middle	22.1 (3.6)	6.9 (2.0)	273.1 (34.1)	7.1 (2.5)
	Upper	47.2 (8.1)	9.4 (2.3)	605.5 (111.3)	9.4 (2.9)
Spring 2005	Lower	2.0 (0.5)	0.08 (0.08)	40.5 (12.2)	0.01 (0.01)
	Middle	16.2 (1.8)	0	169.5 (18.5)	0
	Upper	39.2 (3.9)	0.66 (0.66)	341.1 (36.1)	0.02 (0.02)
Fall 2005	Lower	3.3 (0.9)	0	73.0 (15.6)	0
	Middle	25.5 (4.6)	1.0 (0.48)	248.6 (39.2)	0.92 (0.27)
	Upper	45.4 (8.8)	10.4 (1.3)	509.1 (91.7)	9.1 (1.1)
Spring 2006	Lower	4.1 (0.9)	0	80.0 (16.9)	0
	Middle	27.6 (2.2)	5.6 (2.4)	284.2 (42.4)	1.8 (1.5)
	Upper	39.7 (12.8)	12.3 (1.3)	340.2 (114.8)	2.0 (0.43)
Fall 2006	Lower	1.9 (0.8)	0.8 (0.45)	41.1 (19.4)	0.77 (0.05)
	Middle	26.7 (1.6)	10.0 (2.3)	348.1 (14.5)	10.6 (2.7)
	Upper	32.5 (4.5)	9.2 (0.78)	374.6 (59.6)	13.8 (3.3)
Spring 2007	Lower	2.2 (0.5)	0	52.7 (12.4)	0
	Middle	20.1 (4.4)	0	204.2 (40.1)	0
	Upper	25.8 (9.1)	4.2 (2.2)	257.4 (98.6)	0.32 (0.19)
Fall 2007	Lower	5.3 (1.8)	0.11 (0.11)	103.9 (36.2)	0.11 (0.11)
	Middle	29.2 (6.6)	10.1 (4.1)	284.9 (76.6)	2.9 (0.99)
	Upper	56.6 (23.4)	11.7 (3.6)	728.3 (328.2)	28.5 (3.2)
Spring 2008	Lower	6.1 (3.2)	0	97.8 (57.1)	0
	Middle	29.5 (0.8)	0.36 (0.18)	235.5 (4.5)	0.02 (0.01)
	Upper	75.6 (11.4)	0	620.6 (112.5)	0
Fall 2008	Lower	8.4 (3.4)	0.11 (0.11)	147.5 (58.0)	0.09 (0.09)
	Middle	28.5 (3.1)	10.1 (4.1)	261.0 (31.9)	8.9 (3.7)
	Upper	61.9 (22.1)	11.7 (3.6)	612.9 (222.7)	13.1 (3.3)

A.6: Condition factor (K_{TL};mean ±S.E.) among Age-0 to Age-IV+ brown trout captured in lower, middle, and upper Rio San Antonio stream reaches during spring and fall sampling between 2004 and 2008.

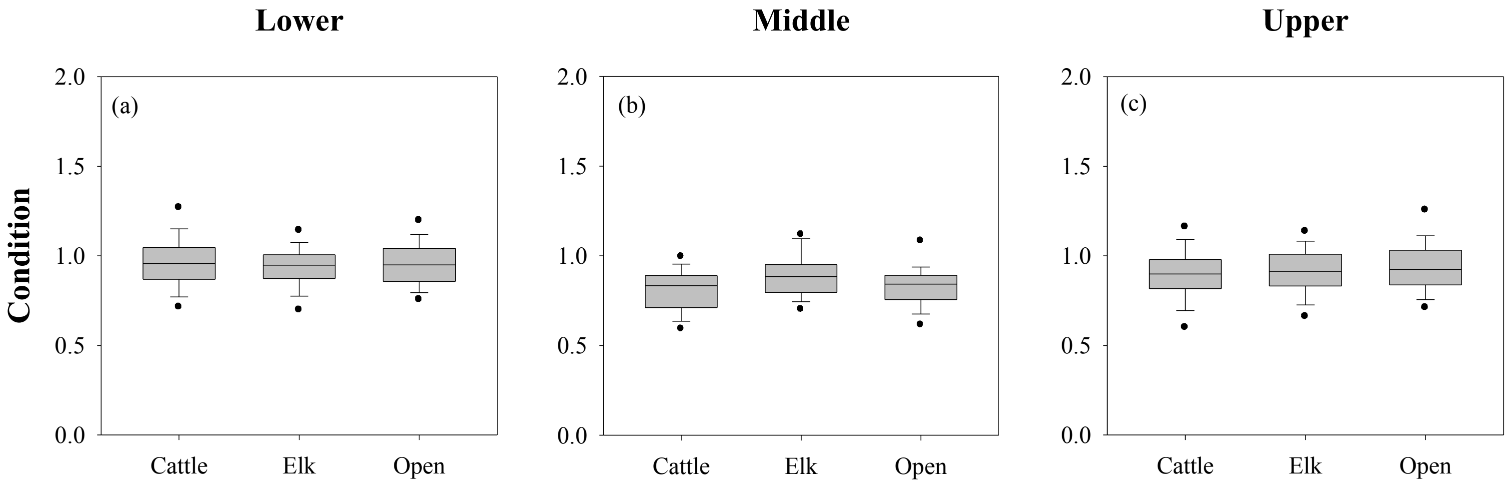
		2004		2005		2006		2007		2008	
Site	Age	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Lower	0	-	-	1.28 (0)	-	-	0.79 (0.06)	-	1.16 (0)	-	1.34 (0.35)
	I	-	-	-	-	-	1.24 (0)	-	1.10 (0.05)	1.06 (0.02)	1.09 (0.08)
	II	1.12 (0.05)	1.19 (0.08)	1.06 (0.01)	1.05 (0.06)	1.10 (0.02)	1.08 (0.08)	1.39 (0)	1.01 (0.01)	1.06 (0.02)	1.07 (0.02)
	III	1.00 (0.02)	1.10 (0.03)	0.92 (0)	1.12 (0.05)	1.06 (0.03)	0.99 (0.02)	1.18 (0.02)	1.13 (0.03)	1.03 (0.03)	0.98 (0.01)
	IV+	0.89 (0.02)	0.99 (0.03)	0.91 (0.04)	0.93 (0.02)	0.95 (0.02)	0.98 (0.04)	1.06 (0.07)	1.00 (0.02)	0.88 (0.03)	0.93 (0.02)
Middle	0	1.5 (0.08)	1.24 (0.05)	-	1.10 (0.05)	1.28 (0.26)	1.11 (0.02)	-	1.15 (0.04)	1.10 (0.01)	1.08 (0.01)
	I	1.18 (0.03)	1.10 (0.02)	1.07 (0.04)	1.06 (0.01)	1.15 (0.02)	1.21 (0.03)	1.14 (0.03)	1.08 (0.02)	1.12 (0.02)	1.13 (0.01)
	II	1.13 (0.02)	1.05 (0.01)	1.08 (0.03)	1.00 (0.01)	1.16 (0.02)	1.07 (0.01)	1.14 (0.03)	1.02 (0.02)	1.06 (0.01)	1.05 (0.02)
	III	0.97 (0.01)	0.96 (0.01)	0.94 (0.01)	0.87 (0.01)	1.01 (0.01)	0.97 (0.02)	1.04 (0.03)	0.93 (0.02)	0.91 (0.01)	0.91 (0.01)
	IV+	0.83 (0.01)	0.85 (0.02)	0.77 (0.01)	0.78 (0.02)	0.84 (0.01)	0.91 (0.03)	0.92 (0.02)	0.82 (0.08)	0.82 (0.02)	0.84 (0.02)
Upper	0	1.24 (0.07)	1.51 (0.04)	2.5 (0)	1.29 (0.04)	2.01 (0.19)	1.12 (0.04)	1.78 (0.10)	1.24 (0.02)	-	1.22 (0.02)
	I	1.25 (0.03)	1.27 (0.03)	1.27 (0.03)	1.17 (0.02)	1.36 (0.04)	1.27 (0.04)	1.41 (0.05)	1.34 (0.05)	1.34 (0.02)	1.30 (0.02)
	II	1.10 (0.01)	1.15 (0.01)	1.15 (0.01)	1.10 (0.01)	1.16 (0.02)	1.16 (0.02)	1.41 (0.04)	1.26 (0.02)	1.16 (0.01)	1.15 (0.01)
	III	1.02 (0.02)	1.04 (0.02)	1.04 (0.01)	0.97 (0.01)	1.01 (0.01)	1.04 (0.02)	1.19 (0.02)	1.09 (0.02)	0.96 (0.01)	0.96 (0.01)
	IV+	0.89 (0.02)	0.95 (0.01)	0.95 (0.01)	0.91 (0.02)	0.85 (0.02)	0.90 (0.07)	1.05 (0.02)	1.04 (0.04)	0.88 (0.03)	0.96 (0.06)



A.7: Condition (K_{TL}) of Age-0 (a,b,c) and Age-I (d,e,f) brown trout captured in CATTLE, ELK, and OPEN grazing sites at lower (a,d), middle (b,e), and upper (c,f) Rio San Antonio stream reaches during spring and fall sampling occasions between 2004 and 2008.



A.7 (continued): Condition (K_{TL}) of Age-II (a,b,c) and Age-III (d,e,f) brown trout captured in CATTLE, ELK, and OPEN grazing sites at lower (a,d), middle (b,e), and upper (c,f) Rio San Antonio stream reaches during spring and fall sampling occasions between 2004 and 2008.



A.7 (continued): Condition (K_{TL}) of Age-IV+ (a,b,c) brown trout captured in CATTLE, ELK, and OPEN grazing sites at lower (a), middle (b), and upper (c) Rio San Antonio stream reaches during spring and fall sampling occasions between 2004 and 2008.

A.8: Aquatic macroinvertebrate abundance (number/m^2) and biomass (g/m^2) collected during May and September sampling occasions in 2007 and 2008. Overall stream reach abundance and biomass were estimated as the mean value observed among CATTLE, ELK, and OPEN grazing sites within each stream reach.

		May-07		Sep-07		May-08		Sep-08	
		Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Lower		1101	0.42	4383	1.73	877	0.89	1596	0.83
	Cattle	1022	0.53	6412	3.96	751	0.89	782	0.25
	Elk	708	0.28	3367	0.63	1047	0.9	1858	1.03
	Open	1574	0.46	3370	0.6	834	0.89	2149	1.2
Middle		1417	1.14	2772	2.29	2318	5.81	2300	2.52
	Cattle	1534	1.19	2670	2.16	2176	5.03	1811	2.45
	Elk	1208	0.68	3261	2.53	1988	5.73	3261	3.29
	Open	1509	1.56	2385	2.18	2791	6.68	1829	1.8
Upper		3500	4.47	4453	2.62	2856	5.14	2402	1.48
	Cattle	2772	3.56	5743	2.98	3803	3.35	2784	1.65
	Elk	3888	6.34	3914	2.24	1432	7.97	2669	1.75
	Open	3839	3.52	3702	2.65	3334	4.11	1754	1.05

A.9: Instantaneous growth rate (ΔTL; mean±S.E.) for Age-0 to Age-IV+ marked brown trout in CATTLE, ELK, and OPEN grazing sites for April, May, July, September, and November sampling occasions.

Site	Age	April	May	July	September	November
Cattle	0	-	-	-	-	0.22 (0)
	I	0.07 (0.009)	0.29 (0.021)	0.25 (0.011)	0.15 (0.016)	0.08 (0.008)
	II	0.02 (0.005)	0.05 (0.008)	0.04 (0.006)	0.07 (0.008)	0.03 (0.004)
	III	0.01 (0.002)	0.01 (0.003)	0.01 (0.002)	0.02 (0.004)	0.01 (0.001)
	IV+	0.01 (0.002)	0.01 (0.003)	0.01 (0.001)	0.01 (0.003)	0.01 (0.001)
Elk	0	-	-	-	-	0 (0)
	I	-	0.31 (0.021)	0.28 (0.014)	0.17 (0.011)	0.07 (0.007)
	II	0 02 (0.003)	0.07 (0.011)	0.07 (0.007)	0.08 (0.007)	0.04 (0.005)
	III	0.01 (0.001)	0.02 (0.005)	0.02 (0.002)	0.02 (0.003)	0.01 (0.002)
	IV+	0.01 (0.001)	0.01 (0.004)	0.01 (0.003)	0.02 (0.004)	0.01 (0.003)
Open	0	-	-	-	-	0.26 (0.015)
	I	0.10 (0.007)	0.26 (0.022)	0.21 (0.01)	0.12 (0.006)	0.06 (0.007)
	II	0.02 (0.004)	0.05 (0.008)	0.05 (0.008)	0.05 (0.007)	0.01 (0.003)
	III	0.01 (0.001)	0.02 (0.005)	0.01 (0.002)	0.02 (0.003)	0.01 (0.002)
	IV+	0.01 (0.002)	0.01 (0.005)	0.01 (0.012)	0.02 (0.005)	0.01 (0.003)

A.10: Instantaneous growth rate (ΔW; mean±S.E.) for Age-0 to Age-IV+ marked brown trout in CATTLE, ELK, and OPEN grazing sites for April, May, July, September, and November sampling occasions.

Site	Age	April	May	July	September	November
Cattle	0	-	-	-	-	1.19 (0.02)
	I	0.25 (0.038)	1.32 (0.072)	0.89 (0.036)	0.39 (0.051)	0.19 (0.024)
	II	0.11 (0.015)	0.27 (0.041)	0.21 (0.027)	0.15 (0.027)	0.04 (0.027)
	III	-0.03 (0.017)	0.01 (0.041)	0.03 (0.012)	0.05 (0.018)	0.02 (0.022)
	IV+	-0.02 (0.021)	-0.04 (0.051)	0.03 (0.017)	0.17 (0.07)	-0.11 (0.03)
Elk	0	-	-	-	-	0.18 (0)
	I	-	1.24 (0.116)	1.00 (0.049)	0.33 (0.036)	0.14 (0.02)
	II	0.06 (0.014)	0.36 (0.071)	0.26 (0.021)	0.19 (0.026)	0.07 (0.024)
	III	-0.06 (0.023)	0.14 (0.029)	0.03 (0.012)	0.06 (0.015)	-0.04 (0.02)
	IV+	-0.94 (0.032)	0.07 (0.032)	0.02 (0.019)	0.06 (0.019)	-0.11 (0.03)
Open	0	-	-	-	-	0.53 (0.013)
	I	0.27 (0.045)	1.14 (0.100)	0.74 (0.047)	0.27 (0.021)	0.16 (0.033)
	II	0.03 (0.02)	0.23 (0.035)	0.16 (0.031)	0.09 (0.024)	0.02 (0.031)
	III	-0.01 (0.015)	0.05 (0.029)	0.07 (0.036)	0.05 (0.016)	-0.06 (0.023)
	IV+	-0.07 (0.012)	0.11 (0.04)	0.04 (0.037)	0.05 (0.031)	-0.04 (0.065)

A.11: Instantaneous growth rate (ΔTL; mean±S.E.) for Age-0 to Age-IV+ marked brown trout in lower, middle, and upper Rio San Antonio stream reaches for April, May, July, September, and November sampling occasions.

Site	Age	April	May	July	September	November
Lower	0	-	-	-	-	0.22 (0)
	I	-	0.22 (0.033)	0.24 (0.065)	0.28 (0.014)	0.12 (0.012)
	II	0.03 (0.01)	0.09 (0.015)	0.12 (0.023)	0.17 (0.015)	0.07 (0.010)
	III	-	0.07 (0.010)	0.02 (0.004)	0.08 (0.013)	0.02 (0.005)
	IV+	0.01 (0)	0.03 (0.005)	0.01 (0.002)	0.02 (0.003)	0.01 (0.003)
Middle	0	-	-	-	-	0 (0)
	I	-	0.35 (0.034)	0.23 (0.018)	0.15 (0.008)	0.07 (0.007)
	II	0.02 (0.004)	0.06 (0.007)	0.06 (0.005)	0.06 (0.006)	0.03 (0.004)
	III	0.01 (0.001)	0.01 (0.003)	0.01 (0.002)	0.03 (0.003)	0.01 (0.002)
	IV+	0.01 (0.001)	0.01 (0.005)	0.01 (0.003)	0.02 (0.005)	0.01 (0.004)
Upper	0	-	-	-	-	0.26 (0.015)
	I	0.08 (0.007)	0.27 (0.011)	0.24 (0.007)	0.12 (0.005)	0.07 (0.005)
	II	0.03 (0.003)	0.06 (0.007)	0.06 (0.005)	0.05 (0.004)	0.02 (0.002)
	III	0.01 (0.001)	0.02 (0.003)	0.02 (0.001)	0.02 (0.001)	0.01 (0.001)
	IV+	0.01 (0.001)	0.01 (0.001)	0.01 (0.007)	0.01 (0.003)	0.01 (0.001)

A.12: Instantaneous growth rate (ΔTL; mean±S.E.) for Age-0 to Age-IV+ marked brown trout in lower, middle, and upper Rio San Antonio stream reaches for April, May, July, September, and November sampling occasions.

Site	Age	April	May	July	September	November
Lower	0	-	-	-	-	1.19 (0)
	I	-	0.44 (0.579)	1.26 (0.27)	0.72 (0.036)	0.31 (0.044)
	II	0.06 (0.002)	0.18 (0.082)	0.32 (0.105)	0.42 (0.052)	0.19 (0.035)
	III	-	0.26 (0.053)	0.01 (0.033)	0.30 (0.050)	0.09 (0.043)
	IV+	0.02 (0)	0.09 (0.040)	-0.01 (0.045)	0.15 (0.016)	-0.09 (0.042)
Middle	0	-	-	-	-	0.18 (0)
	I	-	1.31 (0.105)	0.89 (0.057)	0.30 (0.026)	0.17 (0.031)
	II	0.06 (0.019)	0.29 (0.042)	0.21 (0.020)	0.15 (0.016)	0.04 (0.026)
	III	-0.01 (0.015)	0.06 (0.028)	0.03 (0.011)	0.08 (0.015)	-0.01 (0.023)
	IV+	-0.04 (0.028)	0.04 (0.038)	0.05 (0.023)	0.12 (0.071)	-0.05 (0.032)
Upper	0	-	-	-	-	0.53 (0.013)
	I	0.26 (0.027)	1.22 (0.061)	0.85 (0.029)	0.26 (0.021)	0.12 (0.21)
	II	0.06 (0.012)	0.29 (0.038)	0.21 (0.021)	0.09 (0.015)	0.01 (0.019)
	III	-0.05 (0.014)	0.05 (0.029)	0.05 (0.021)	0.03 (0.008)	-0.08 (0.017)
	IV+	-0.05 (0.015)	0.05 (0.037)	0.05 (0.035)	0.03 (0.023)	-0.14 (0.03)