

DISSERTATION

COLORADO STATE UNIVERSITY

EFFECTS OF RIPARIAN GRAZING ON TERRESTRIAL INVERTEBRATE
SUBSIDIES THAT FEED TROUT IN CENTRAL ROCKY MOUNTAIN STREAMS

Submitted by

William Carl Saunders

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Paul J. McMahon

Paul D. French

Paul D. French

Paul D. French

Paul D. French

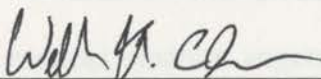
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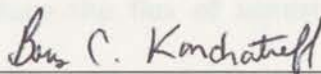
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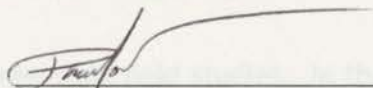
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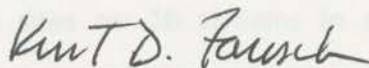
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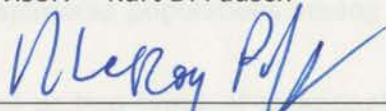
Boris C. Kondratieff



Paul J. Meiman



Advisor: Kurt D. Fausch



Director: N. LeRoy Poff

ABSTRACT OF DISSERTATION

EFFECTS OF RIPARIAN GRAZING ON TERRESTRIAL INVERTEBRATE SUBSIDIES THAT FEED TROUT IN CENTRAL ROCKY MOUNTAIN STREAMS

Habitat degradation is the leading cause of biodiversity loss worldwide, affecting plant and animal populations directly through habitat loss, but also indirectly by decoupling important linkages among habitats. Linkages between streams and the terrestrial environments they drain are likely to be especially important because streams have small habitat area but long boundaries with the adjacent riparian zone. Riparian livestock grazing reduces riparian vegetation, altering the stream-riparian interface, and so may reduce the flux of terrestrial invertebrates to streams. To evaluate the potential for riparian grazing to affect trout populations by reducing this flux, I conducted two large-scale field studies. In the first, a study of three commonly used grazing systems at sites on 16 streams in northern Colorado, I compared invertebrate resources and salmonid populations among stream reaches managed for season-long (i.e., continuous) or two types of rotational livestock grazing, as well as

streams grazed by wildlife only. Rotational grazing generally supported greater inputs of terrestrial invertebrates to streams (2-5 times more), and trout at rotational grazing sites consumed 2 - 4 times the biomass of these prey as trout at sites grazed season-long. However, factors influencing the flux of invertebrates to streams were complex and resulted in variable responses by trout populations. In the second field study, a large-scale grazing experiment conducted in four streams in western Wyoming, I evaluated whether two levels of grazing intensity (i.e., the amount of vegetation removed) and manual removal of streamside woody vegetation influenced terrestrial prey resources for trout when compared to controls with wildlife grazing only. Two grazing treatments, designed to reduce vegetation to 10-15-cm stubble height (moderate intensity grazing) or 5-7.5-cm stubble height (high intensity grazing) within a few days, had no detectable effect on terrestrial invertebrates entering streams, whereas high intensity grazing combined with manual removal of two-thirds of streamside woody vegetation reduced inputs of terrestrial invertebrates to streams by 45%. In contrast, all treatments reduced the biomass of these prey in trout diets by 50 - 75%, relative to control sites. However, neither grazing nor removal of woody vegetation affected the biomass of fish that remained in treatment reaches. Finally, I conducted field research and computer simulations to validate removal estimates of

trout abundance, based on night-time electrofishing, to address recent concerns over the accuracy of these types of estimators. I found that night-time electrofishing was highly effective for estimating abundance of trout in small streams like those where I studied the effects of cattle grazing in Colorado and Wyoming. Furthermore, I show that modern analytical methods provide powerful tools to account for heterogeneity in capture probability among individual fish.

William Carl Saunders
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Fall 2010

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grazing is one of the dominant land uses that may cause habitat degradation, occurring on more than half of all agricultural land (27% of the land surface, Ramanathan et al. 2008), including >150 million acres in the U.S. (NAD 1983; NAD 2002), primarily in the West. Although riparian zones make up <1% of agricultural cattle congregate in these sensitive areas to find forage, shade, and water (Dunham et al. 1991), and can have both direct and indirect impacts to fishery and in particular, on fish populations. Direct impacts include grazing that affect fish populations by trampling stream banks and overgrazing streamside vegetation, leading to bank erosion, shifting of streambeds, gravel, and reduced habitat complexity (Platts 1991; Kaufman and Naegele 1994; Selby et al. 1996). In turn, this can reduce aquatic invertebrate production, growth and reproduction of trout, and ultimately, trout abundance and production.

Streams have small habitat area but long boundaries with the adjacent riparian ecosystem, and so are strongly influenced by fluxes from the terrestrial habitats they drain (Wallace et al. 1997; Nakano and Minamoto 2001; see reviews by Sedell et al. 2005; Jensen et al. 2010). Therefore, an additional indirect pathway by which cattle grazing may influence trout is to decrease inputs of terrestrial inputs to trout habitat via runoff. In addition to riparian areas polluted within the stream, terrestrial habitats also

INTRODUCTION

Habitat degradation is the leading cause of biodiversity loss worldwide (Vitousek et al. 1997; Dirzo and Raven 2003; Fahrig 2003), affecting plant and animal populations directly through habitat loss, but also indirectly by decoupling important linkages among habitats and communities (Foley et al. 2005; Hooper et al. 2005). Globally, livestock grazing is one of the dominant land uses that may cause habitat degradation, occurring on more than half of all agricultural land (22% of the land surface, Ramankutty et al. 2008), including >850 million acres in the U.S. (GAO 1988; NRCS 2002), primarily in the West. Although riparian zones make up <1% of rangelands, cattle congregate in these sensitive areas to find forage, shade, and water (Armour et al. 1991), and can have both direct and indirect impacts to biodiversity, and in particular, to fish populations. Poorly managed riparian grazing can affect fish populations by trampling stream banks and overgrazing streamside vegetation, leading to bank erosion, siltation of streambed gravel, and reduced habitat complexity (Platts 1981; Kauffman and Krueger 1984; Belsky et al. 1999). In turn, this can reduce aquatic invertebrate production, growth and reproduction of trout, and ultimately, trout abundance and production.

Streams have small habitat area but long boundaries with the adjacent riparian ecosystem, and so are strongly influenced by fluxes from the terrestrial habitats they drain (Wallace et al. 1997; Nakano and Murakami 2001; see reviews by Baxter et al. 2005; Fausch et al. 2010). Therefore, an additional indirect pathway by which cattle grazing may influence trout is to decrease inputs of terrestrial insects on which trout rely. In addition to invertebrates produced within the stream, terrestrial invertebrates

that fall, crawl, or blow into streams from riparian vegetation account for 50 – 85% of trout diets during summer months (e.g., Dineen et al. 2007; Utz and Hartman 2007) and provide about 50% of their annual energy budget (Kawaguchi and Nakano 2001; Nakano and Murakami 2001; Sweka and Hartman 2008).

Although past research highlights the importance of riparian vegetation in supplying terrestrial invertebrates that help sustain stream salmonids, we have yet to fully evaluate how actual land uses alter these prey subsidies so that managers can apply the results. In this dissertation research, I conducted two studies to evaluate the effects of cattle grazing on inputs of terrestrial invertebrates to rangeland streams in the central Rocky Mountains, and their use by trout. I also conducted a third study to evaluate methods used to estimate trout abundance in these small streams, which is important to detecting potential effects of cattle grazing.

In the first study (Chapter 2), I test whether more intensive grazing management practices result in greater terrestrial invertebrate subsidies to streams, and more robust trout populations. I conducted a large-scale comparative field study of three grazing systems and compared these to sites ungrazed by livestock (i.e., used by wildlife only). During summer 2007, I measured riparian vegetation, terrestrial invertebrate biomass entering streams and in trout diets, and trout populations, at 16 sites in northern Colorado that were selected to represent the spectrum of commonly used grazing systems in the central Rocky Mountains. Sites were selected that were managed for traditional season-long grazing (i.e., continuous grazing requiring less intensive management), simple rotational grazing where cattle remain in pastures for 35 – 45 d,

and intensive rotational grazing where cattle remain in pastures for < 21 d and are moved frequently. I also compared these effects to sites grazed only by wildlife (i.e., no livestock use).

The second study (Chapter 3) is a large-scale field experiment to test the short-term effects caused by riparian grazing and loss of woody riparian vegetation on terrestrial prey inputs to trout streams. During summer 2008, four treatments, which employed actual cattle grazing (i.e., not mowing), were randomly assigned to four riparian pastures on each of four streams in central Wyoming in a randomized complete block design (i.e., streams were treated as blocks). Two treatments tested the effects of grazing intensity, a moderate-intensity grazing treatment where herbaceous riparian vegetation was reduced to 10-15 cm, and a high-intensity treatment where cattle reduced riparian vegetation to 5-7.5 cm. A third treatment simulated riparian conditions that may result from prolonged season-long grazing by combining the same high-intensity grazing with removal of two-thirds of the streamside woody vegetation within 10 m of the channel. The fourth treatment was a control where cattle were excluded from the riparian area throughout the duration of the experiment, allowing only wildlife grazing. I measured riparian vegetation, input of terrestrial invertebrates and adult aquatic insects to streams, use of invertebrate prey resources by trout, and trout abundance, both before and after the experiment (i.e., using a BACI design; Stewart-Oaten et al. 1986; Manly 2001).

The third study (Chapter 1) was an evaluation of removal estimates of trout abundance based on night electrofishing, which was used extensively throughout this

research to detect effects of cattle grazing on trout populations. During the summers of 2006 and 2009, nighttime electrofishing was conducted on 200-m stream reaches ($n=10$), fenced at the upstream and downstream ends, to evaluate whether this method is efficient for capturing trout in small streams similar to those on which grazing evaluations were conducted. To evaluate removal estimates, a portion of the trout population in each study reach was marked and released to create a population of known size. Abundance estimation was conducted using modern analytical methods, available in Program MARK, capable of accounting for individual heterogeneity in capture probability by incorporating both individual and site-level covariates.

Overall, I show using the comparative study (Chapter 2) that rotational grazing management (either simple or intensive), resulted in more riparian vegetation, greater inputs of terrestrial invertebrates, greater biomass of terrestrial invertebrate prey in trout diets, and more trout biomass than season-long grazing. However, throughout northern Colorado, these differences were frequently inconsistent owing to high variability, especially for trout diets and biomass. Furthermore, I show that riparian vegetation, and terrestrial invertebrates entering streams and in trout diets, at sites managed for rotational grazing were similar to sites managed for wildlife grazing only.

In contrast, results of the grazing experiment (Chapter 3) showed that short durations of moderate or intensive cattle grazing, which rapidly reduced riparian vegetation by 50 – 80%, had no detectable effect on the biomass of terrestrial invertebrates entering streams, but did reduce the biomass of this prey in trout diets in late summer. However, intensive grazing plus removal of streamside woody vegetation

caused reductions in both terrestrial invertebrate inputs to streams and the biomass of terrestrial invertebrates in trout diets. Nevertheless, neither trout biomass nor density was reduced during the experiment.

Finally, I show that nighttime electrofishing was highly effective for sampling salmonid populations in small streams (Chapter 1), resulting in an average of 98% of marked fish being captured in three-pass removal estimates. Furthermore, I demonstrate through simulations that individual covariates (e.g., fish length) can improve estimates of trout abundance when adequate sample sizes are available, such as when data are pooled from estimates on multiple streams.

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Abstract -- Estimation of stream fish abundance using removal electrofishing is imprecise, and allows sampling of fish populations during a single session. However, recent evaluations demonstrated that removal estimates can substantially underestimate fish abundance, and have caused concern over the use of this method. I evaluated removal estimates of trout abundance using night electrofishing in 10 study reaches of Rocky Mountain streams, and compared the data using new analytical

CHAPTER 1:

Accurate Estimation of Salmonid Abundance in Small Streams using Three-Pass Removal Electrofishing and Program MARK: an Evaluation using Marked Fish

For removal estimates to be accurate, the number of marked fish in study reaches, and removal estimates of total fish abundance were similar to mark-recapture estimates. In general, capture probabilities were high (average = 37% over three passes), and removal estimates had narrow 95% confidence intervals that included the known number of marked fish for all but 1 of 17 estimates for three trout species. Capture probability increased with fish length, and was greater on the first than subsequent electrofishing passes. Additionally, capture probability varied among sites, but this variation was not accounted for by any measured habitat parameters. Finally, fish that had been previously marked were slightly more likely to be captured during electrofishing, even though recovery periods for most fish exceeded 24 h. Simulations confirmed the finding that accounting for heterogeneity in capture probability due to fish size reduced bias in removal estimates. My results demonstrate that three-pass removal electrofishing can provide accurate estimates of fish abundance

Abstract.-- Estimation of stream fish abundance using removal electrofishing is common, and allows sampling of fish populations during a single site visit. However, recent evaluations demonstrated that removal estimates can substantially underestimate fish abundance, and have caused concern over the use of this method. I evaluated removal estimates of trout abundance using night electrofishing in 10 study reaches of Rocky Mountain streams, and analyzed the data using new analytical methods available in Program MARK to account for potential sources of bias. Removal estimates were validated using populations of previously captured and marked resident fish. Overall, removal estimates were accurate estimates of the number of marked fish in study reaches, and removal estimates of total fish abundance were similar to mark-recapture estimates. In general, capture probabilities were high (average = 97% over three passes), and removal estimates had narrow 95% confidence intervals that included the known number of marked fish for all but 1 of 17 estimates for three trout species. Capture probability increased with fish length, and was greater on the first than subsequent electrofishing passes. Additionally, capture probability varied among sites, but this variation was not accounted for by any measured habitat parameters. Finally, fish that had been previously marked were slightly more likely to be captured during electrofishing, even though recovery periods for most fish exceeded 24 h. Simulations confirmed the finding that accounting for heterogeneity in capture probability due to fish size reduced bias in removal estimates. My results demonstrate that three-pass removal electrofishing can provide accurate estimates of fish abundance

when field methods are designed to maximize capture probability and when modern analytical tools are used to account for heterogeneity in capture probability.

Introduction

Biologists responsible for studying and managing fish and wildlife species often rely on estimates of animal abundance for testing treatment effects of management (e.g., Gowan and Fausch 1996; Saunders and Fausch 2007; Bayley and Li 2008), and determining whether conservation goals are met (Shepard et al. 1997; Labonne and Gaudin 2006; Al-Chokhachy et al. 2009). Closed-population estimators, such as mark-recapture (Ricker 1975) and removal estimators (Zippin 1956, 1958), are commonly used to draw inferences about animal abundance in discrete areas (e.g., enclosed or defined sections of stream) and when estimates can be conducted over short time periods. However, these abundance estimates can be biased if key assumptions are not met. For example, movement of animals can violate the assumption of a closed population (Nordwall 1999; Skalski and Gilliam 2000). Likewise, use of selective gear (Reynolds 1996; Dolan and Miranda 2003) or behavioral responses by animals can cause unequal capture probability (Mesa and Schreck 1989).

Otis et al. (1978) and White et al. (1982) provided a framework for more sophisticated analyses of closed populations to address these assumptions of heterogeneous capture probability, and wildlife biologists have continued to develop new analytical techniques to account for such heterogeneity (Huggins 1989, 1991; Pledger 2000). Furthermore, several investigators have recently developed methods to improve performance of closed-population estimators by incorporating covariates

measured on either sites or individual animals (Pollock 2000; White 2005, 2008). In contrast, most fisheries professionals continue to use computationally simple, but less efficient model designs and analysis methods (see Pine et al. 2003).

In wadeable streams, one of the most common methods for estimating fish abundance is multiple-pass removal electrofishing, because it can be conducted in a single site visit. However, removal estimates have been shown to underestimate fish abundance (Riley and Fausch 1992; Riley et al. 1993), which may be caused by several related problems. First, electrofishing is known to be size-selective (Dolan and Miranda 2003), so larger fish are captured on the first pass, leaving a greater proportion of smaller fish with lower capture probabilities available for capture on subsequent passes. Second, fish exposed to electricity but not captured on early passes may exhibit a behavioral response to avoid later capture. Both problems can cause lower capture probability on later passes, which if not accounted for lead to underestimation of fish abundance.

Fisheries biologists have proposed three solutions to reduce bias caused by size-selectivity and behavioral responses that produce heterogeneity in capture probability: 1) select appropriate methods to achieve high capture probability so that most fish of all sizes are captured on the first pass (Riley and Fausch 1992, 1995), 2) analyze data separately by age or size classes to account for the effect of fish size on capture probability, and 3) fit separate capture probabilities by pass to account for reduced capture probability on subsequent passes. The last requires comparing the fit of a model with different capture probabilities by pass (model M_{bh} in Program CAPTURE;

White et al. 1982) to one with a constant capture probability (model M_b). However, three problems are common. First, capture probabilities needed to produce estimates with small bias may be difficult to achieve without intensive sampling, and bias increases with reduced capture probability (Riley and Fausch 1992; Riley et al. 1993; Peterson et al. 2004). Second, computing separate estimates by size or age classes creates small samples, and can cause imprecise or inaccurate estimates. Third, removal estimators that incorporate two or more capture probabilities (i.e., Model M_{bh}) are rarely supported based on chi-square goodness-of-fit tests in Program CAPTURE, owing to low power (e.g., Riley et al. 1993; Rosenberger and Dunham 2005).

One potential means to achieve high capture probability for salmonids is to sample at night. Nighttime electrofishing has proven effective for sampling lentic habitats (Dumont and Dennis 1997; Pierce et al. 2001; Schoenebeck et al. 2005) and large rivers (Sanders 1992), and is currently being integrated into monitoring programs for these types of habitat (e.g., Emery et al. 2003). Furthermore, studies of the diel behavior of salmonids suggest that many species seek cover during daylight, but are more active at night (Young 1999; Jakober et al. 2000; Diana et al. 2004; Schmetterling and Adams 2004). These activity patterns may lead to increased capture efficiency at night relative to daytime sampling, as has been reported for snorkeling (Dumont and Dennis 1997; Thurow et al. 2006). Therefore, in this study I used nighttime electrofishing to maximize capture probability for salmonids. However, this method has never been evaluated in small headwater streams for estimation of salmonid abundance.

Two recent evaluations of stream fish abundance estimates based on removal electrofishing indicate that even when attempting to minimize bias by analyzing size classes separately, and fitting separate capture probabilities by pass, fish abundance can be substantially underestimated (Peterson et al. 2004; Rosenberger and Dunham 2005). Furthermore, the negative bias was far greater than expected (e.g., 33% in Rosenberger and Dunham 2005). These researchers found that electrofishing removal estimates overestimated capture probability and, therefore, underestimated abundance. Furthermore, the degree to which abundance was underestimated was greatest for low capture probabilities. They suggested that the primary reason is that removal estimators assume constant capture probability across passes, whereas they found that capture probability decreased on subsequent passes. As a result, other authors have concluded that removal estimators are often unsuitable, and have questioned research findings based on these methods (Sweka et al. 2006; Temple and Pearsons 2006; Neville et al. 2009).

The goals of this study were to 1) evaluate whether nighttime removal electrofishing produces high capture probabilities and accurate estimates of fish abundance in mountain streams, when steps are taken to address known sources of bias (i.e., size-selectivity, behavioral response), and 2) use modern analytical tools (i.e., Program MARK; White and Burnham 1999) to account for heterogeneity in capture probability and improve parameter estimation by including covariates and sharing information across multiple streams. I evaluated removal estimates by creating known populations of marked fish using individuals inhabiting study reaches, and compared

estimates of fish abundance from mark-recapture and removal estimators. I demonstrate that electrofishing removal methods can produce accurate abundance estimates, and show the power of new analytical methods to account for heterogeneity in capture probability and to address problems that arise from estimating capture probabilities for small populations. Finally, I use simulations to show that incorporating fish length as an individual covariate reduces bias in removal estimates compared to models that assume constant capture probability.

Methods

Study area. – This study was conducted on tributaries of the North Platte, Elk, and Colorado rivers in the Medicine Bow-Routt National Forests in northern Colorado and southern Wyoming (Table 1). The 10 study sites were in remote sections of wadeable headwater streams to reduce the potential for vandalism of study apparatus, and fishing mortality that could affect trout populations. This evaluation was linked to a large-scale study investigating effects of riparian cattle grazing on stream food webs and salmonid populations, so streams were selected to be similar to others in that study. All streams had naturally-reproducing populations of brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, or rainbow trout *Oncorhynchus mykiss*, and were second- to fourth-order mountain streams of moderate gradient with riparian vegetation dominated by shrubs (predominantly *Salix* spp.) with an herbaceous understory (Table 2). Sampling was conducted during July to September of 2006 and 2009. Except for two

sites, one sampled each year, electrofishing estimates were conducted at or near base flow. The other estimates were conducted at moderate flow, well below bankfull.

Field methods. – To increase the number of adult fish captured in each sample, reaches were about 200 to 300 m long (Table 1). Two to three days before electrofishing each reach, crews constructed fences at the upstream and downstream ends, at locations with low velocities that lacked undercut banks (e.g., downstream ends of pools). Fences were designed to create a closed population, and were constructed using 6.3-mm plastic mesh to withstand physical destruction by debris accumulation and animals (e.g., muskrats, mink). About 2 m beyond each fence, I placed a hoop net constructed of 4.7-mm Delta 44 mesh (Nylon Net Company, Nashville, Tennessee, USA) with the throats facing the fence, to collect fish that escaped study reaches. Hoop nets were 2 m long with two 0.5-m-diameter throats supported by 1-m² metal frame openings, and had 3-m long wings. Both fences and hoop nets were installed with a 0.3-m skirt buried in the substrate and secured with sandbags. Hoop nets were anchored by metal stakes and placed so that both throats were submerged. Fences and hoop nets were secured to stream banks and supported with steel posts driven in the stream bed. Structures were inspected daily, cleaned of accumulated debris, and repaired if necessary.

After fences were constructed, fish were collected from each reach to create a population of marked fish with known abundance. Fish were captured by fishing with barbless hooks, minnow traps, and small hoop nets. Fishing was conducted carefully three times in each reach by two people during daylight and dusk hours. Thirty to 50

collapsible minnow traps (20 x 20 x 50 cm; Nylon Net Company, Nashville, Tennessee, USA) were deployed throughout each reach. Additionally, at 6 of the 10 sites, three hoop nets (1.4 m long with four 38-cm hoops, one throat, and two 2-m long wings; Nylon Net Company, Nashville, Tennessee, USA) were set near the head of large pools where the throat was completely submerged. Traps and nets were checked morning and evening. All fish were held temporarily in live wells within the 25-m reach (50 m at Willow Creek) in which they were captured. Fish were anesthetized with tricaine methanesulfonate (MS-222; Argent Chemical Laboratories, Redmond, Washington), measured (fork length [FL], nearest mm), and given both a partial fin clip (lower caudal) and an individual mark. Individual marks were one of three colors (red, green, orange) of visual implant elastomer (VIE; Northwest Marine Technologies, Shaw Island, Washington) injected into either the lower mandible, clear tissue behind the eye, base of the pectoral fin, or a combination of these locations. Fish were allowed to recover in live wells for 1 h, or until able to maintain position in the current, and then released into the reach where they were captured. Any fish unable to maintain position in the current or swim normally were released well downstream of the study reach. Previously marked fish that were recaptured were released immediately. Throughout this sampling, care was taken to minimize impact to the sampling reach and to avoid disturbing fish. Sampling reaches remained undisturbed for a minimum of 12 h before electrofishing.

At each site, I used electrofishing to conduct three-pass nighttime removal estimates of fish abundance. Night electrofishing was initially used in previous research

on similar trout streams to increase capture probabilities (Saunders and Fausch 2007). Comparison of day and night capture probabilities ($\hat{p}$), estimated from sampling the same 10 stream reaches in Wyoming during the day (2004) and at night (2005), suggested that nighttime capture probabilities were, on average, 53% greater than daytime capture probabilities (mean daytime $\hat{p} = 0.55$, mean nighttime $\hat{p} = 0.84$, unpublished data). Therefore, all electrofishing in this study was at night to maximize capture probabilities. A backpack electrofisher (Smith-Root, Inc., Vancouver, Washington; model LR-24) equipped with a 28-cm circular anode and a 5-mm-diameter cable cathode was used, and crews adjusted the voltage and frequency to maximize fish capture probability without causing injury (350 – 600 V, 30 – 45 Hz). Electrofishing began 30 min after complete darkness. Headlamps and a high-powered flood light (Underwater Kinetics, Poway, California, USA) were used to illuminate the area sampled. The 2-m reach between the fence and hoop net at the upstream and downstream ends of the sampling reach was thoroughly sampled, both before and after conducting all removal electrofishing, to evaluate escapement resulting from electrofishing. During each pass, the entire reach was sampled carefully by one person operating the electrofisher and netting fish, and two assistants who also netted and handled fish. Care was taken to ensure that all available habitat was thoroughly electrofished on each pass so that effort remained consistent. However, both the duration and total time that electric current was applied (measured by the electrofishing unit) were greatest for the first pass, and decreased on subsequent passes as fewer fish were encountered. Typically, the first electrofishing pass required about 3 h to complete and the third

about 1.5 h, depending on habitat complexity. Fish captured during each pass were retained in live wells until processed. Fish were anesthetized with MS-222, measured for length (FL; nearest mm) and mass (nearest 0.1 g), held until electrofishing was completed, and then released. During processing, all fish having a partial caudal fin clip were inspected with a VI light (Northwest Marine Technologies, Shaw Island, Washington) by two individuals, to ensure that individual VIE marks were identified accurately.

After the electrofishing estimate, instream habitat and riparian vegetation that could potentially influence electrofishing efficiency were measured during the day. For each study reach, I measured the maximum depths (m) of all pool and run habitats, wetted width (at 5-m intervals; m), total length of undercut banks (m), stream substrate, and streamside vegetation. I also counted all pieces of large woody debris (> 10 cm diameter and > 2 m long) that were at least partly in the wetted channel. I defined pools as habitat units with a >20-cm residual depth (difference between maximum depth and tail-crest depth, the maximum depth along the downstream cross-section; Lisle 1987) and in which there was a substantial visible decrease in water velocity. In contrast, habitat units that were, on average, >20 cm deep but did not have >20-cm residual depth and lacked a substantial decrease in velocity were classified as runs. Runs were common in the moderate-gradient streams I sampled, and were often associated with dense streamside vegetation and undercut banks, which potentially could reduce electrofishing efficiency. The length of undercut banks, defined as at least 20 cm wide and long, with at least 20 cm of water depth beneath them (see Fausch and

Northcote 1992, for similar criteria), was measured throughout the reach. Substrate composition was measured using Wolman pebble counts of 100 bed particles (Wolman 1954; Overton et al. 1997). The presence of streamside vegetation, either overhanging the channel or trailing in the stream to create overhead cover at least 20 cm wide, was recorded for each bank at 5-m intervals throughout the reach. Elevation (m) and gradient (%) of each site were estimated from 7.5-minute USGS topographical maps.

Data analysis

I computed estimates of fish abundance using the Huggins estimator in Program MARK, a closed population estimator that allows incorporating both fish-level and site-level covariates by conditioning unobserved encounter histories (i.e., fish that were never captured) out of the likelihood function (Huggins 1989). As a result, estimates of population abundance are derived parameters, computed based on maximum-likelihood estimates of capture probability. Generally, removal estimates can be analyzed under a closed-population mark-recapture framework by setting the probability of recapture (c in Program MARK) to zero. Additionally, in Program MARK, information contained in multiple similar datasets (here, removal estimates conducted in different streams) can be shared to more accurately estimate parameters (White 2005, 2008), while still providing estimates of capture probability and abundance for individual sites. This was achieved by constructing models to account for factors potentially influencing capture probability across all sites (e.g., heterogeneity in capture probability due to species, fish length, habitat complexity, or stream width), and

evaluating the support of each model under an information theoretic framework (Burnham and Anderson 2002). This allowed me to evaluate more factors potentially affecting capture probability, and obtain better parameter estimates than would be possible by computing estimates separately for each site, where small effective sample size limits the power to detect effects and estimate parameters (White 2005). Finally, model averaging was conducted by computing the weighted averaged model prediction (i.e., $\hat{p}$) for all models that carried AIC_c model weight, to incorporate model uncertainty when multiple models were supported. Model predictions were weighted using Akaike weights (w_i) derived from Akaike's Information Criterion (AIC) scores corrected for small sample sizes (i.e., AIC_c ; Burnham and Anderson 2002, White 2008).

Capture probability modeling and abundance estimation. – To evaluate factors that influenced fish capture probability, I constructed a set of *a priori* models incorporating covariates at either the fish or site level (hereafter, fish and site covariates). To minimize the total number of models evaluated and reduce the potential for detecting spurious effects (Burnham and Anderson 2002), I built models containing only fish or site covariates. Fish covariates were used to account both for heterogeneity among groups of fish from a single site owing to 1) fish species, 2) the electrofishing pass on which fish were captured (i.e., behavioral effects), and 3) whether fish were marked (i.e., indicating previous capture and handled), as well as for heterogeneity among individuals owing to 4) fish length and 5) mass. Site covariates included pool area, maximum pool depth, percentage of bank length that was undercut, substrate diameter, reach width, and percentage of stream bank transects where

vegetation provided overhead cover. Four additional site-level covariates used were: 1) a independent parameter to account for unmeasured differences among sites (a full spatial model with an independent parameter to represent each site), 2) year sampled (2006 or 2009), 3) electrofishing effort applied on the first pass (s/m^2), and 4) a subjective binary classification of sites based on general difficulty of electrofishing (all assessed by Saunders). I anticipated that a model containing both fish and site covariates might be strongly supported because factors at both levels influence electrofishing efficiency, and thus capture probability. Therefore, after ranking *a priori* models based on minimum AIC_c scores, I also conducted a *post hoc* exploratory analysis where I combined the top model with each parameter of the other group, in an additive fashion. For example, if the top model was constructed of fish covariates, I crossed that model with each site covariate to test whether this improved the fit.

To evaluate the support for models and estimate fish abundance separately by species and site, input files contained data for all 10 sites, but each species at each site was defined as a distinct attribute group (terminology in Program MARK). Only data for age-1 and older fish were analyzed, because age-0 fish had low capture probability and many were able to move through the mesh fences owing to their small size (unpublished data), violating the assumption of population closure. Age-0 fish were identified from length-frequency histograms for each site. Individual models were built in the Design Matrix interface in Program MARK (see White 2008), run using a logit link function, and ranked based on AIC_c scores. Ninety-five percent confidence intervals for

abundance estimates were calculated using log-normal 95% confidence intervals for the number of fish never caught (i.e., $\hat{N} - M_{t-1}$; Rexstad and Burnham 1991).

Evaluating removal estimates of abundance. – To evaluate the performance of removal estimators I: 1) compared removal estimates of the number of marked fish (and associated 95% confidence intervals) against the known number of marked fish released in each study reach, minus any escapement; and 2) compared removal versus mark-recapture estimates of the entire enclosed population (i.e., total abundance of marked and unmarked fish). For the mark-recapture estimate, I used the total number of marked fish captured in all three removal passes as the number of recaptures. I modeled capture probability, under a mark-recapture framework, using the Huggins closed capture estimator, which estimates distinct capture probabilities for different sampling occasions (p_i). In the case where two sampling occasions were conducted, the estimation of distinct capture probabilities for each is achieved by solving the partial derivatives of the multinomial log-likelihood, with respect to p_1 and p_2 , at zero for the respective capture probability and making the appropriate substitutions to estimate capture probabilities for both sampling occasions, conditional on the data collected (i.e., the relative frequencies of the three encounter histories). The results of these calculations are provided in the Program MARK output. For the mark-recapture analysis, I evaluated a similar set of *a priori* models as for the removal data, but did not constrain the probability of recapturing fish. Rather, to estimate capture probabilities for both sampling occasions (i.e., marking and electrofishing) I constrained the probability of recapturing a marked individual during electrofishing to be equal to

capturing an unmarked individual. I was unable to evaluate the potential for behavioral effects (e.g., handling effects) in the mark-recapture analysis because I only had one recapture event (i.e., during electrofishing sampling).

Simulating effects of accounting for fish size. – I conducted simulations in Program MARK to evaluate the performance of removal models in which capture probability is constant (Model M_b) versus removal models that incorporate fish length as an individual covariate (Model $M_b + \text{Length}$), for a range of capture probabilities and population sizes frequently observed in studies of wadeable streams. Previous studies have demonstrated that fish length influences susceptibility to electrofishing (Cross and Stott 1975; Anderson 1995) and suggested that the effect may decrease as fish length increases (Dolan and Miranda 2003). Therefore, I modeled the effect of fish size on capture probability as normally distributed around the mean fish length and asymptotically bounded by 0 and 1.0 for the smallest and largest individuals, respectively, using a logit link function in Program MARK. I defined three probability models to describe the relationship between fish size and capture probability (Figure 1), where capture probability for the mean fish length was set at 0.3 (logit parameters: $\beta_0 = -0.847$, $\beta_1 = 1$), 0.5 (logit parameters: $\beta_0 = 0$, $\beta_1 = 1$), and 0.7 (logit parameters: $\beta_0 = 0.847$, $\beta_1 = 1$). These probability models were designed to encompass the range of capture probabilities reported for wadeable streams (e.g., Riley and Fausch 1992; Riley et al. 1993; Anderson 1995; Peterson et al. 2004; Rosenberger and Dunham 2005; Sweka et al. 2006), and to reflect a relationship between fish size and capture probability similar to that observed in the present study. In Program MARK, the individual covariate (fish

length) was randomly generated from a normal distribution (mean = 0, SD = 1) for populations of 100, 200, 300, and 500 individuals. Encounter histories for three sampling occasions were then randomly generated for each individual in a population based on its length and a given probability model. To generate removal data, the probability of recapturing an individual was set to be 0.0. For each probability model and population combination I generated 10,000 datasets from which abundance was estimated using Model M_b and Model $M_b + \text{Length}$. Removal models were evaluated based on bias and 95% log-normal confidence interval coverage, averaged across the 10,000 data sets for each probability model and population size.

Results

I marked 537 salmonids, of which 426 were brook trout, 105 were brown trout, and 6 were rainbow trout. On average, I marked 51 age-1 and older trout per site (Appendix 1), which accounted for an average of 19% of the enclosed population, based on removal estimates (range: 2.5 – 48.1%; see below). The lengths of marked trout spanned the entire range of lengths of all age-1 and older trout captured, estimated from length-frequency histograms for each site (Figure 2).

Fish Escapement

A few fish escaped sampling reaches before or during electrofishing removal estimates and were detected, but the number was generally small. I captured salmonids that escaped at 7 of 10 sites, but only one was marked. Most were captured

in hoop nets beyond the fences, but some were captured by electrofishing between the fence and net. The total number of trout that escaped was, on average, four times greater for age-1 trout than for those age 2 and older (age 1: $n = 4.1$ per stream, 58–117 mm; age 2 and older: $n = 1.0$ per stream, 108–196 mm), but generally accounted for a small portion of the population. Most trout escaped during the 48–72 h before electrofishing, which occurred at 7 of 10 sites and accounted for 1.1% of the population (range: 0–5.2%, $\bar{x} = 3.2$ fish per stream), on average. In contrast, escapement during electrofishing occurred at only 2 of 10 sites and accounted for only 0.4% of the population, on average (range: 0–5.4%, $\bar{x} = 0.8$ fish per stream). Furthermore, the number of age-1 and older trout that escaped study reaches increased with substrate particle diameter (linear regression: $r^2 = 0.48$, $p = 0.05$). Overall, escapement was greatest for age-0 trout ($n = 5.6$ per stream, 39–65 mm), occurring at 8 of the 10 sites sampled, but the number of age-0 trout that escaped was not related to any habitat variable measured.

Capture probability modeling and abundance estimation

Marked sub-population: removal modeling. – Model selection results indicated that there were many top models that were closely ranked, likely resulting from low power to distinguish among competing models owing to small sample size. However, the best fitting models were those incorporating fish covariates for length and behavioral response to successive electrofishing passes, and site covariates for substrate size, year sampled, and first-pass effort (Appendix 2). I evaluated 40 models

constructed to account for heterogeneity in capture probability originating from either fish- or site-level variability, using data from 501 marked salmonids recaptured during removal estimates. I constructed 10 *a priori* models with only fish covariates, 11 with only site covariates, and 19 exploratory models which combined both. Although all *a priori* models ranked relatively closely (maximum $\Delta AIC_c = 14.16$), models with fish covariates had lower average ΔAIC_c than those with site covariates, on average (5.45 vs. 6.19) and accounted for more model weight (72% vs. 26%). The top two models in the *a priori* sets (see Methods), which included p as a function of fish length, and p as a function of fish length + behavioral response to electrofishing, ranked closely ($\Delta AIC_c < 2$), so I added site covariates to each to determine whether models accounting for both fish and site covariates would improve model fit. Incorporating covariates to account for year sampled, substrate diameter, first-pass effort, and unaccounted for variation due to differences between sites resulted in models with lower AIC_c scores than *a priori* models, and were the only models that individually had $\geq 5\%$ model weight. In contrast, there were 18 models that had $\geq 1\%$ model weight.

Overall, six parameters had substantial importance based on cumulative model weights. Fish length, the most important variable, occurred in a set of models that included 95% of the model weight. The behavioral response to electrofishing, year sampled, average substrate diameter, first pass effort, and site appeared in sets of models with 27%, 25%, 18%, 13%, and 13% of the cumulative model weight, respectively. Furthermore, model averaging revealed that, on average, 27% (range: 6–

88%) of the variation associated with abundance estimates (measured with the unconditional standard error) was attributable to model selection uncertainty.

Total trout abundance: removal estimation. – Model selection revealed that fish covariates were more important than site covariates in predicting capture probability for estimates of all trout in study reaches, but that there was variability in capture probability among sites not accounted for by measured habitat parameters. I evaluated 38 candidate models using data from 2,749 salmonids captured during removal electrofishing. Seventeen *a priori* models were constructed with the fish covariates species, size, behavior, and previous handling, and 10 *a priori* models were constructed with the nine site covariates described above. Model selection indicated that models with fish covariates accounted for more variability in capture probability than those with site covariates, as in the analysis of marked fish. Models with fish covariates had ΔAIC_c scores 59.4 units lower than models with only site covariates, on average, and a cumulative model weight of 100%.

Exploratory analysis was based on the top-ranking model with fish covariates, which contained a fish species $\times$ length interaction, and covariates for behavior and previous marking. Five exploratory models had lower ΔAIC_c values than the top *a priori* model (Appendix 3). Although including parameters to account for pool area, difficulty of electrofishing, first-pass effort, and year all improved the fit of the best model with fish covariates, the full spatial model (i.e., allowing p to differ for each site) resulted in the best exploratory model. This top model was far superior to all others ($\Delta AIC_c \geq 47.0$, AIC_c model weight = 1.0), and had an AIC_c score 125 units lower than the model where

capture probabilities were constant, but calculated separately for each site, which corresponds to Model M_b in Program CAPTURE.

Based on this top model, fish length not only had a strong effect on capture probability, but also influenced the effect of other variables. Overall, capture probability increased with fish length, and the magnitude of the effects of all other variables decreased as capture probability for the largest fish approached 1.0 (Figure 3). Moreover, the effect of length was stronger for brook trout than brown trout. Based on models containing only fish-level parameters, there was 247 times more support, based on an AIC_c evidence ratio (used here rather than the cumulative weights used above because the top model contained 99% of the model weight; see Burnham and Anderson 2002) between the top model incorporating a species-by-length interaction and a model with additive species and length effects instead ($\Delta AIC_c = 11.0$). Capture probability for trout encountered on the first pass was also higher than for those encountered on subsequent passes (i.e., a behavioral response), although large trout tended to have high capture probability on all passes (evidence for behavioral response = 50,000; ΔAIC_c for similar model not including behavioral effect = 21.6). Fish previously marked had slightly higher capture probabilities than unmarked fish (evidence for effect of marking = 1571; ΔAIC_c for similar model not including marking effect = 14.7), but this difference also decreased with length. For example, a marked 150-mm brook trout was predicted to have a 0.06 greater probability of being captured on the first pass than an unmarked fish, whereas a 250-mm marked brook trout had only a 0.01 greater capture probability. Similarly, there was greater variability in capture probability among sites for smaller fish

than for large fish. Overall, of the fish-level factors I included in capture probability models, fish length had the greatest effect on capture probability. For example capture probabilities differed by 0.27 and 0.40 between the largest and smallest brown trout and brook trout sampled, respectively. In contrast, the greatest difference in capture probabilities between the first and subsequent electrofishing passes (for a 70 mm trout) was only 0.16 and 0.17 for brown and brook trout, respectively.

Total abundance: mark-recapture estimation. – Model selection results for mark-recapture models were similar to those for removal models (Appendix 4). I constructed 26 models including 4 with fish covariates, 11 with site covariates, and 11 exploratory models. In general, as for removal models, fish-level *a priori* models ranked higher than site-level models, and adding parameters to account for heterogeneity among sites improved the top model with fish covariates (p as a function of a species x length interaction). As when modeling capture probability using removal data, none of the measured habitat variables improved model fit compared using a full spatial model which allowed p to differ for each site. This top exploratory model accounted for 100% of the model weight, and thus no model averaging was necessary.

Evaluation of Removal Estimates

Estimation of marked sub-population. – Removal estimates of marked fish abundance were both unbiased and precise for salmonids. Overall, I recaptured 501 of the 511 (98%) marked age-1 and older trout known to be in the sampling reaches when electrofishing removal estimates began. Abundance estimates were, on average, only

0.5 fish lower than the known marked subpopulation, or biased low by only 2.4% (% bias

$$= \left((\hat{N} - N) / N \right) \times 100, \text{ where } N = \text{known number of marked fish in the study reach}.$$

The 95% log-normal confidence intervals included the known number of marked trout for all but one estimate for brook trout (Colorado Creek), where the upper confidence limit was only two fish below the known abundance (Figure 4A).

Comparison of removal and mark-recapture estimates – In general, removal and mark-recapture estimates of all trout inhabiting study reaches were similar, although 95% confidence intervals varied between the paired estimates. High capture probabilities (median: 0.85 on first pass, 0.75 on second and third passes) resulted in an estimated mean of 97% of trout being captured in three electrofishing passes (Appendix 1). This caused removal and mark-recapture abundance estimates to be similar, and generally have narrow 95% log-normal confidence intervals (Figure 4B). Furthermore, removal and mark-recapture estimates of salmonid abundance differed by less than one fish, on average. Mark-recapture estimates using the Huggins model were, on average, greater than Lincoln-Petersen estimates (Appendix 1), although the differences were generally small (mean = 3 fish).

Incorporating fish length covariates: simulation results – Overall, simulations showed that estimating abundance without accounting for the effect of fish size on capture probability produced negatively biased estimates that had low 95% confidence interval coverage. In contrast, incorporating fish size in the estimation model improved the accuracy and precision of abundance estimates when there was sufficient data to

accurately estimate parameter values (Table 3). Model M_b nearly always underestimated the simulated population size (N), but bias decreased for higher capture probabilities. For example, abundance estimates were biased low by more than 16% for the $p = 0.3$ capture probability function, but only 5% when $p = 0.7$, for all population sizes. In contrast, Model $M_b + \text{Length}$ tended to overestimate the population size for low values of p , but produced accurate estimates of N for both higher values of p and larger population sizes. In addition to underestimating N , Model M_b estimates had small standard errors and 95% log-normal confidence intervals that frequently did not encompass N . Furthermore, confidence interval coverage decreased for larger population sizes, resulting in increasingly precise, but biased, estimates of N . For example, although 79% of confidence intervals included the true population size for $p = 0.7$ and $N = 100$ under Model M_b , only 9% did for $p = 0.7$ and $N = 500$. In contrast, confidence interval coverage for Model $M_b + \text{Length}$ was always $\geq 90\%$, and approached 95% for $N \geq 200$ individuals. Additionally, 95% confidence intervals for Model $M_b + \text{Length}$ were relatively symmetrical with respect to coverage failures. On average, 55% of confidence intervals that did not encompass the true population size had upper bounds below N . In contrast, all confidence intervals for estimates produced by Model M_b that did not include the true population size had upper bounds that were below N , indicating that all these were underestimates. Finally, under combinations of low p and small N , Model $M_b + \text{Length}$ occasionally failed to produce abundance estimates (maximum of 7% failure for $p = 0.3$, $N = 100$).

Removal estimation of non-salmonid populations sampled using night-time electrofishing was also evaluated for catostomids, cottids, and cyprinids encounter at sites while sampling salmonids (Appendices 5 and 6). In general, first pass capture probabilities for large bodied catostomids (ca. $\hat{p} = 0.70$) were similar to those observed for salmonids, where as capture probabilities for small bodied cyprinids (ca. $\hat{p} = 0.60$) and cottids (ca. $\hat{p} = 0.40$), which have strong benthic orientation, were low and resulted in more strongly biased population estimates.

Discussion

Night-time electrofishing proved to be highly effective for sampling salmonid populations in wadeable streams, and three-pass removal estimates using this method were both accurate and precise. Three-pass capture probabilities for salmonids were higher than reported in two recent evaluations where electrofishing was carried out during the day (Peterson et al. 2004; Rosenberger and Dunham 2005), but similar to those reported by other authors who also sampled during the day (Riley and Fausch 1992; Sweka et al. 2006). For example, on average I recaptured 98% of marked salmonids at the 10 study sites sampled. Three-pass removal estimates underestimated the known abundance of marked salmonids by only 2.4%, on average (i.e., less than one fish per reach), and 95% confidence intervals included the number of marked trout for all but one estimate. Furthermore, removal estimates of total salmonid abundance differed from mark-recapture estimates by less than one fish, on average, and

confidence intervals on removal estimates were usually more precise. The similarity of these two estimators is a result of the high capture probability achieved in this study.

The results of this study contrast strongly with two recent evaluations in streams, which reported that electrofishing removal estimates substantially underestimated salmonid abundance. Peterson et al. (2004) found that removal estimates overestimated capture probability by absolute values of 0.40 and 0.25 for bull trout *S. confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisi*, respectively. Rosenberger and Dunham (2005) reported that three-pass removal estimates of marked rainbow trout abundance were biased low by 33%, based on the known number of marked fish in study reaches, and 95% confidence intervals for abundance estimates encompassed the known number of marked fish for only 23% of estimates. Furthermore, Rosenberger and Dunham (2005) demonstrated that removal estimates were consistently lower than mark-recapture estimates, and suggested that the latter were more accurate. Other investigators demonstrated that removal estimates underestimated salmonid abundance less severely (ca. 10 - 20%; Bohlin and Sundstrom 1977; Riley et al. 1993; Sweka et al. 2006), but this bias is still greater than for all but one of my estimates. In contrast, Riley and Fausch (1992) reported low bias (4.2%), similar to my study, based on simulations using data collected with similar methods in similar streams.

Differences in bias among studies suggest that different factors may cause underestimation in different types of streams. For example, streams studied by Peterson et al. (2004) and Rosenberger and Dunham (2005) had higher gradient (> 4%),

more complex habitat due to coarse woody debris, and lower conductivity than my streams, all of which can reduce salmonid capture probability. Additionally, different salmonid species use different microhabitats and respond differently to electrofishing. For example, the bull trout studied by Peterson et al. (2004) use benthic microhabitat, often inhabit interstices in the stream bed (Pratt 1984; Nakano et al. 1998), and generally have low capture probability (e.g., $p \leq 0.46$; Peterson et al. 2004). Furthermore, Peterson et al. (2004) used direct DC (i.e., not pulsed), which is known to be less effective, but which may be necessary when sampling sensitive or threatened fish species. In contrast, my use of pulsed DC at night in streams with higher conductivity and less instream wood, and for primarily brook and brown trout, resulted in much higher capture probabilities, thus enabling accurate removal estimates of trout abundance.

Capture Probability and Underestimation of Fish Abundance

Achieving high capture probability is the most important factor in reducing underestimation of abundance using removal estimates because it reduces the need to address heterogeneity in capture probability. For example, as capture probability approaches 100%, most fish are captured on the first pass, leaving little opportunity for bias from other factors (Riley and Fausch 1992; Sweka et al. 2006) and reducing the need for complex modeling. My simulations demonstrated that underestimation of abundance by Model M_b is minimized at higher capture probabilities, but also that accounting for heterogeneous capture probability further improves estimates across the

range frequently encountered. In the field, I specifically designed sampling to maximize capture probability for brook and brown trout by conducting electrofishing at night and carefully sampling all available habitats. The study streams also had modest habitat complexity, provided primarily by pools and undercut banks. As a result, capture probabilities for 150-mm trout in streams I sampled were approximately three times greater than for westslope cutthroat trout and bull trout of similar size (estimated from Figure 1, Peterson et al. 2004), and capture probabilities for 100-mm trout were 1.9 times greater than for rainbow trout (first-pass capture probability estimated for fish of median length [105 mm] from Figure 1 in Rosenberger and Dunham 2005).

Additional insights from the simulations confirm the value of combining data across estimates to avoid low power due to small sample size. For example, increasing the simulated population sized from 100 (a common abundance for an individual reach), to 500 individuals reduced the bias of Model $M_b + \text{Length}$ by 88%. Although few biologists may sample reaches long enough to contain 500 fish, the effective sample size (ESS , calculated from the frequency of distinct encounter histories for the 2749 brook and brown trout collected during the study), from which I estimated the effect of fish length on capture probability, was $ESS = 3345$, far greater than any I simulated. Thus, pooling data across abundance estimates results in more precise parameter estimates, especially when capture probabilities are relatively low (White 2005). In contrast, larger population sizes did not affect bias under the constant capture probability model (Model M_b). Arguably, the effect of fish length on capture probability in natural populations may be less than I found by simulation (see Price and Peterson 2010 for

non-salmonid examples), in which case the accuracy and precision of both parameter and abundance estimates would improve. My goal was to demonstrate the capability to account for substantial heterogeneity in capture probability using modern analytical tools.

Accounting for Heterogeneity in Capture Probability

Beyond achieving high capture probabilities, analyzing removal data using Program MARK allows testing hypotheses about factors that influence capture probability at both individual and site scales, and accounting for this heterogeneity in estimates. By modeling capture probability using the Huggins estimator, I were able to account for variation due to fish length, the physiological or behavioral response by fish to subsequent electrofishing passes, and characteristics of stream habitat that affect capture. Both Peterson et al. (2004) and Rosenberger and Dunham (2005) suggested that reduced capture probability in successive electrofishing passes is the primary cause for underestimates of abundance. Two mechanisms have been proposed: heterogeneity in capture probability due to fish size (Dolan and Miranda 2003), and behavioral responses to previous exposure to electricity (Mesa and Schreck 1989). If the first occurs, electrofishing can alter the size structure of the population because larger fish are captured on the first pass, thereby reducing the average capture probability for the remaining fish on subsequent passes. If the second occurs, fish seek refuge in complex habitat after initial exposure to electrofishing, or become fatigued by tetany, and are less likely to be captured on subsequent passes.

Heterogeneity owing to fish size –To date, biologists have not used effective methods to account for fish size as a source of heterogeneity in capture probability when estimating abundance. Electrofishing efficiency increases with fish size for salmonids (Anderson 1995; Reynolds 1996). Dolan and Miranda (2003) also demonstrated that electrical power needed to immobilize a variety of non-salmonid species increased rapidly for fish with small volume, but increased more slowly for fish with larger volume. However, they reported that capture probability was similar for fish of all species >150 mm total length, which is similar to my results. Previous solutions include stratifying data based on fish size or age, but this may achieve only limited success in reducing bias (Riley and Fausch 1992; Peterson et al. 2004). This method often concentrates heterogeneous capture probability in small size classes of fish where the influence is greatest, while reducing the effective sample size for all size classes, thereby reducing power to estimate capture probability. Furthermore, variability in the length ranges for a given age class caused by subjectivity, and spatial and temporal variation in growth rates, may cause comparisons through time and among fish populations to be confounded due to inconsistent bias in abundance estimates. In contrast, by modeling capture probability as a continuous function of fish size, biologists can account for heterogeneity in capture probability throughout the entire population without reducing the effective sample size. For example, I estimated size-specific capture probabilities in Program MARK using data from over 2700 fish collected from all 10 sites sampled, and found that using fish length as an individual covariate to model capture probability provided an efficient method to account for the size structure of fish

populations. Dauwalter and Fisher (2007) used logistic regression to model capture probability of smallmouth bass *Micropterus dolomieu* as a continuous function of fish length, and developed more accurate estimates of abundance. However, tools in MARK are more efficient because capture probability can be modeled as a continuous function of individual fish length, thus avoiding subjective definition of size bins and increasing the range of the independent variable on which inference is based.

Heterogeneity owing to behavioral responses and marking – Salmonids can respond to electrofishing both behaviorally (Mesa and Schreck 1989) and physiologically (Schreck et al. 1976), which may reduce subsequent capture probability. To date, it has been difficult to distinguish between fish size versus these responses as the cause of reduced capture probability. For example, the generalized removal model (Model M_{bh}) in Program CAPTURE has been used to account for reduced capture probability caused by either effect (Otis et al. 1978), but the goodness-of-fit test used to detect this has limited power (Peterson et al. 2004) because of small sample sizes and highly variable parameter estimates. *A priori* model selection results reported here indicate that after accounting for species-specific effects of length on capture probability, incorporating a covariate to account for higher capture probabilities on the first pass resulted in far superior model fit ($\Delta AIC_c = 21.6$). In general, reductions in capture probability on subsequent passes were greatest for brook trout <200 mm and brown trout <350 mm, because large fish had consistently high capture probabilities ($p \geq 0.85$). In contrast, Peterson et al. (2004) found significant reductions in capture probability for all age classes of bull trout and westslope cutthroat trout, although they did not account for

variation due to fish length. Dauwalter and Fisher (2007) reported reduced capture probabilities only for large smallmouth bass. In my study, trout length had a greater effect on capture probability than responses to electrofishing, but this may be primarily owing to high first-pass capture probability.

Underestimation of fish abundance can also result from unequal capture probability for marked fish, such as in mark-recapture sampling. I estimated that marked fish were slightly more likely than unmarked fish to be captured during removal estimates (ca. 0.01 to 0.1 increase in absolute capture probability). Although the effect was small, and marked fish made up only 19% of the populations, on average, not accounting for previously handling fish during mark-recapture estimates could result in underestimation of abundance due to inflated capture probability. This effect may be greater if capture probability is lower, or more invasive methods such as electrofishing are used to collect fish during marking passes. Mesa and Schreck (1989) reported greater effects from electrofishing and handling trout in artificial and natural experiments than I found, but generally concluded that a 24-h recovery period was sufficient to restore capture probability to normal. Likewise, Temple and Pearsons (2006) reported that a 3-h recovery period was sufficient for fish to recover from capture and marking. Effects of marking on subsequent recapture probability of fish has rarely been reported in field studies (e.g., Peterson et al. 2004; Rosenberger and Dunham 2005). However, in my study the effect was persistent despite minimally invasive capture methods (angling and trapping), and recovery periods as long as 60 h.

As for the effects of length, combining capture data across 10 sample sites provided sufficient power to detect these small but persistent effects (White 2005).

Site-level Covariates and Modeling Capture Probability

I found that capture probability varied among sites, but that no measured habitat covariates improved the fit of models relative to estimating an independent additive adjustment for each site. This suggests that other unmeasured site-specific factors such as mist that impaired vision when air temperatures dropped below 0°C at night, or perhaps crew fatigue at successive sites, may have reduced capture probability. In several streams, capture probabilities may have been reduced by clay or periphyton that made wading difficult. Riley and Fausch (1992) also reported that measured habitat variables could not explain negative bias in removal estimates. However, others have reported that reach width, depth, and cross-sectional area (Riley et al. 1993; Peterson et al. 2004; Dauwalter and Fisher 2007), amount of undercut banks, substrate composition (Peterson et al. 2004), and amount of coarse woody debris (Rosenberger and Dunham 2005) influenced capture probability or bias for removal estimates. I selected sites similar to those used in a larger study, which may have reduced habitat variability, and I worked hard to maintain high capture probability despite differences in habitat volume and complexity.

Reach Escapement

Underestimates of fish abundance could also be caused by fish escapement, which I measured both before and after conducting removal estimates at each site. Only one marked age-1 and older trout escaped. Overall, escapement of marked and unmarked age-1 and older trout during removal estimates occurred at only 2 of 10 sites, and was very low, similar to other evaluations (Peterson et al. 2004; Rosenberger and Dunham 2005). The most trout escaped at two sites with the largest substrates, where fence skirts were difficult to seal. A few more trout (about 1% total) escaped during the 2–3-d period before electrofishing, even though I buried plastic fences in the substrate as barriers. Others have also reported that escapement through standard block nets increased with time (Peterson et al. 2004; Temple and Pearsons 2006; Dauwalter and Fisher 2007), which may introduce bias in mark-recapture studies of enclosed populations.

Logistics of Night Electrofishing Estimates

Night electrofishing yielded high capture probabilities and accurate abundance estimates for salmonids in small streams, and required similar effort as daytime electrofishing, but may require a few extra safety precautions. I selected night electrofishing because previous research (Saunders and Fausch 2007) indicated that capture probabilities were much higher than during the day. Likewise, others have reported increased sampling efficiency at night, probably because fish are more available for capture due to diel microhabitat selection, activity, or less fright response

(Sanders 1992; Schoenebeck et al. 2005; Hardie et al. 2006). Overall, my night three-pass electrofishing and fish processing required 3.25 h per 100 m of stream, similar to that spent during the day (unpublished data). The gear used was also similar, but good lighting and extra caution is needed to prevent mishaps. Higher gradient streams with more instream wood may pose a greater safety risk. Overall, I have conducted over 70 night-time removal estimates since 2005 with more than 25 technicians, and have had no serious injuries or mishaps.

Conclusions

My results demonstrate that modeling removal data for salmonids using the Huggins estimator for closed populations in Program MARK provides an effective method to account for multiple sources of heterogeneity in capture probability when estimating stream fish abundance. In addition, sample size for estimating effects can be increased by using the design matrix and coding similar data sets as distinct groups (White 2005), thereby improving (or, for small sample sizes, even allowing) estimation of capture probability and abundance (cf. Hickey and Closs 2006). Likewise, simulations reported here and by Sweka et al. (2006) indicated that negative bias was greater for small samples. Furthermore, combined samples can be used with information-theoretic approaches (Burnham and Anderson 2002) to rank competing models describing sources of heterogeneity in capture probability, and model averaging can incorporate variation due to both natural process and model selection uncertainty (i.e., unconditional standard errors). This is superior to basing estimates on a single model

that is deemed "best" only because of lack of fit of more complex models, rather than any direct comparison among models (White 2008). Finally, these analyses can be computed quickly, and incorporate routinely collected data such as fish length and habitat complexity.

In contrast to recent claims of poor performance of removal electrofishing, my results show that these methods can be superior to mark-recapture methods. High capture probability can be achieved, accurate and precise estimates are obtainable, sampling is cost efficient, and violations of assumptions can be minimized with thorough sampling procedures, or accounted for using new analytical methods. I demonstrate that estimates of trout abundance derived from nighttime removal electrofishing were unbiased, based on comparisons with a known population of marked individuals, and estimates of the total abundance of trout were similar to those calculated using mark-recapture methods, but had smaller standard errors, on average. Removal estimates provide an efficient alternative to mark-recapture estimates, because the latter require multiple site visits. Furthermore, mark-recapture estimates of fish abundance are generally computed from a single marking and recapture event (e.g., Lincoln-Petersen type estimators), for which there is little power to account for heterogeneity in capture probability and which are sensitive to violating assumptions. In contrast, flexible mark-recapture models such as those proposed by Huggins (1989, 1991) and Pledger (2000) generally require as many as four sampling occasions for accurate parameter estimation, or to incorporate parameters for heterogeneity in p . Finally, when conducting mark-recapture sampling in streams, there is a tradeoff between the time

required between passes to reduce behavioral and physiological effects of capture and marking (Cross and Stott 1975; Schreck et al. 1976; Mesa and Schreck 1989) and the difficulty of maintaining reach closure as debris collects on block nets (Nordwall 1999; Peterson et al. 2005). These two potential sources of bias can be minimized with removal methods. In general, removal estimates can be an important tool for fish biologists to accurately estimate fish abundance when conducted rigorously and analyzed with modern techniques that account for heterogeneity in capture probability among individuals within a population.

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Table 1. – Characteristics of 10 sites sampled to evaluate electrofishing removal estimates in southern Wyoming and northern Colorado. Sites are ordered by the year sampling was conducted and elevation. Average length of age-1 and older fish, and range of lengths in parentheses, are given for all species (BKT = brook trout, BNT = brown trout, RBT = rainbow trout) for which evaluations of electrofishing removal estimates were conducted.

Site	Location ^a	Year	Elevation (m)	Reach length (m)	Fish species	Mean fish length (mm)
Sheep Creek	Lat: 40°55'12" N Lon: 105°36'37" W	2006	2466	200	BKT	142 (102 - 224)
					BNT	170 (113 - 379)
Lower Hog Park Creek	Lat: 41°01'07" N Lon: 106°50'39" W	2006	2521	215	BKT	116 (76 - 185)
					BNT	104 (63 - 430)
Arapaho Creek	Lat: 40°24'32" N Lon: 106°23'28" W	2006	2705	200	BNT	150 (95 - 318)
Colorado Creek	Lat: 40°28'10" N Lon: 106°36'18" W	2006	2727	200	BKT	133 (88 - 225)
					BNT	163 (94 - 398)
Hinman Creek	Lat: 40°46'07" N Lon: 106°48'57" W	2009	2376	209	BKT	139 (88 - 252)
					RBT	110 (76 - 210)
Lower Rock Creek	Lat: 40°03'00" N Lon: 106°39'19" W	2009	2600	240	BKT	124 (95 - 201)
					BNT	160 (83 - 310)
Upper Hog Park Creek	Lat: 40°58'44" N Lon: 106°50'13" W	2009	2650	208	BKT	116 (53 - 250)
Upper Rock Creek	Lat: 40°05'52" N Lon: 106°37'14" W	2009	2722	200	BKT	132 (93 - 222)
					BNT	129 (85 - 220)
Illinois River	Lat: 40°24'25" N Lon: 106°02'29" W	2009	2778	195	BKT	154 (91 - 248)
					BNT	186 (75 - 380)
Willow Creek	Lat: 40°22'41" N Lon: 106°12'04" W	2009	2786	307	BKT	127 (76 - 226)

^a Data source = WGS 84

Table 2. – Summary of physical habitat for 10 sites sampled in southern Wyoming and northern Colorado to evaluate electrofishing removal estimates. Map gradient was estimated using USGS 7.5' quadrangle maps from a 500-m reach centered on the study reach. Effort exerted on the first pass (Pass 1 effort) was estimated by dividing the total time electricity was applied by reach surface area. Percent undercut bank was calculated as their total length divided by the total length of stream bank, and percent pools was calculated as total pool area divided by reach surface area. Maximum pool depth was the average of the maximum depths of pools in the study reach. Substrate diameter was determined from Wolman pebble counts. Percent streamside vegetation was estimated as the percentage of point estimates on both stream banks at 5-m intervals throughout the reach where streamside vegetation was present. Instream wood represents the number of pieces of large wood (see text) in the study reach normalized per 100 m.

Site	Mean	SE	Range
Wetted width (m)	4.6	0.42	2.9 - 6.6
Map gradient (%)	1.1	0.22	0.2 - 2.5
Pass 1 effort (sec/m ²)	6.7	0.47	3.4 - 8.8
% undercut bank	17	2.4	6 - 30
% pools	39	3.3	15 - 49
Maximum pool depth (m)	0.62	0.039	0.40 - 0.81
Substrate diameter (mm)	70	9.5	21 - 138
% streamside vegetation	47	8.1	13 - 92
Conductivity (μS/sec)	103	12.2	46 - 188
Instream wood	8	1.73	0 - 16

TABLE 2. - Comparison of the two models for estimating the removal rate of the fishery. The model with the best fit is indicated by an asterisk.					
Model	Log-likelihood	AIC	BIC	Adjusted R ²	Adjusted R ² (with 10,000 replicates)
Model 1: $Y = a + b \ln(X)$	10.0	10.0	10.0	0.95	0.95
Model 2: $Y = a + b \ln(X) + c \ln(X^2)$	10.0	10.0	10.0	0.95	0.95
Model 3: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3)$	10.0	10.0	10.0	0.95	0.95
Model 4: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3) + e \ln(X^4)$	10.0	10.0	10.0	0.95	0.95
Model 5: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3) + e \ln(X^4) + f \ln(X^5)$	10.0	10.0	10.0	0.95	0.95
Model 6: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3) + e \ln(X^4) + f \ln(X^5) + g \ln(X^6)$	10.0	10.0	10.0	0.95	0.95
Model 7: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3) + e \ln(X^4) + f \ln(X^5) + g \ln(X^6) + h \ln(X^7)$	10.0	10.0	10.0	0.95	0.95
Model 8: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3) + e \ln(X^4) + f \ln(X^5) + g \ln(X^6) + h \ln(X^7) + i \ln(X^8)$	10.0	10.0	10.0	0.95	0.95
Model 9: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3) + e \ln(X^4) + f \ln(X^5) + g \ln(X^6) + h \ln(X^7) + i \ln(X^8) + j \ln(X^9)$	10.0	10.0	10.0	0.95	0.95
Model 10: $Y = a + b \ln(X) + c \ln(X^2) + d \ln(X^3) + e \ln(X^4) + f \ln(X^5) + g \ln(X^6) + h \ln(X^7) + i \ln(X^8) + j \ln(X^9) + k \ln(X^{10})$	10.0	10.0	10.0	0.95	0.95

Table 3. – Simulation results for constant capture probability removal models (Model M_b) and constant capture probability removal models that incorporate fish length as an individual covariate (Model $M_b + \text{Length}$). Probability models were defined to describe the relationship between fish size and capture probability (see text), and the values given indicated the probability of capturing the mean length fish in the population from which individuals were simulated. Simulation results represent the average of 10,000 replicates for each probability model and population size, from which Model M_b and Model $M_b + \text{Length}$ were used to estimate abundance ($\hat{N}$) and $SE(\hat{N})$ for each replicated dataset. Percent CI Coverage represents the percentage of log-normal based 95% confidence intervals that included the simulated population size. Percent errors represents the percentage of simulated populations from which removal estimates were not possible. Percent bias was calculated as $\% \text{ Bias} = \frac{(\hat{N} - N)}{N} \times 100$, and averaged across the 10,000 replicates.

Model	Probability model	% Errors	$\hat{N}$	$SE(\hat{N})$	% CI coverage	% Bias
Population Size (N) = 100						
M_b	0.3	0.1	84	18.3	73	-16
$M_b + \text{Length}$	0.3	6.7	195	399.8	90	95
M_b	0.5	<0.1	90	5.6	70	-10
$M_b + \text{Length}$	0.5	0.6	135	111.6	92	35
M_b	0.7	0	95	2.3	79	-5
$M_b + \text{Length}$	0.7	0	110	28.4	98	10
Population Size (N) = 200						
M_b	0.3	<0.1	163	18.2	55	-19
$M_b + \text{Length}$	0.3	1.8	277	240.3	92	38
M_b	0.5	0	178	7.4	45	-11
$M_b + \text{Length}$	0.5	0.2	219	53.8	93	9
M_b	0.7	0	191	3.2	54	-5
$M_b + \text{Length}$	0.7	0	205	15.9	94	3
Population Size (N) = 300						
M_b	0.3	0	242	20.9	42	-19
$M_b + \text{Length}$	0.3	0.5	369	192.2	93	23
M_b	0.5	0	267	9.0	27	-11
$M_b + \text{Length}$	0.5	<0.1	316	46.7	94	5
M_b	0.7	0	286	3.9	32	-5
$M_b + \text{Length}$	0.7	0	304	15.5	94	1
Population Size (N) = 500						
M_b	0.3	0	400	25.8	22	-20
$M_b + \text{Length}$	0.3	0.1	556	162.3	94	11
M_b	0.5	0	445	11.4	8	-11
$M_b + \text{Length}$	0.5	0	513	49.4	94	3
M_b	0.7	0	476	5.0	9	-5
$M_b + \text{Length}$	0.7	0	504	18.1	95	1

Figure 1 – Three capture probability models used to define the relationship between fish size and capture probability for generating encounter histories for simulations in Program MARK. The X-axis represents fish sizes normally distributed about the mean length fish. Positive values represent increasingly larger fish and negative values represent increasing smaller fish. Capture probability models were defined by the probability of capturing the mean length fish.

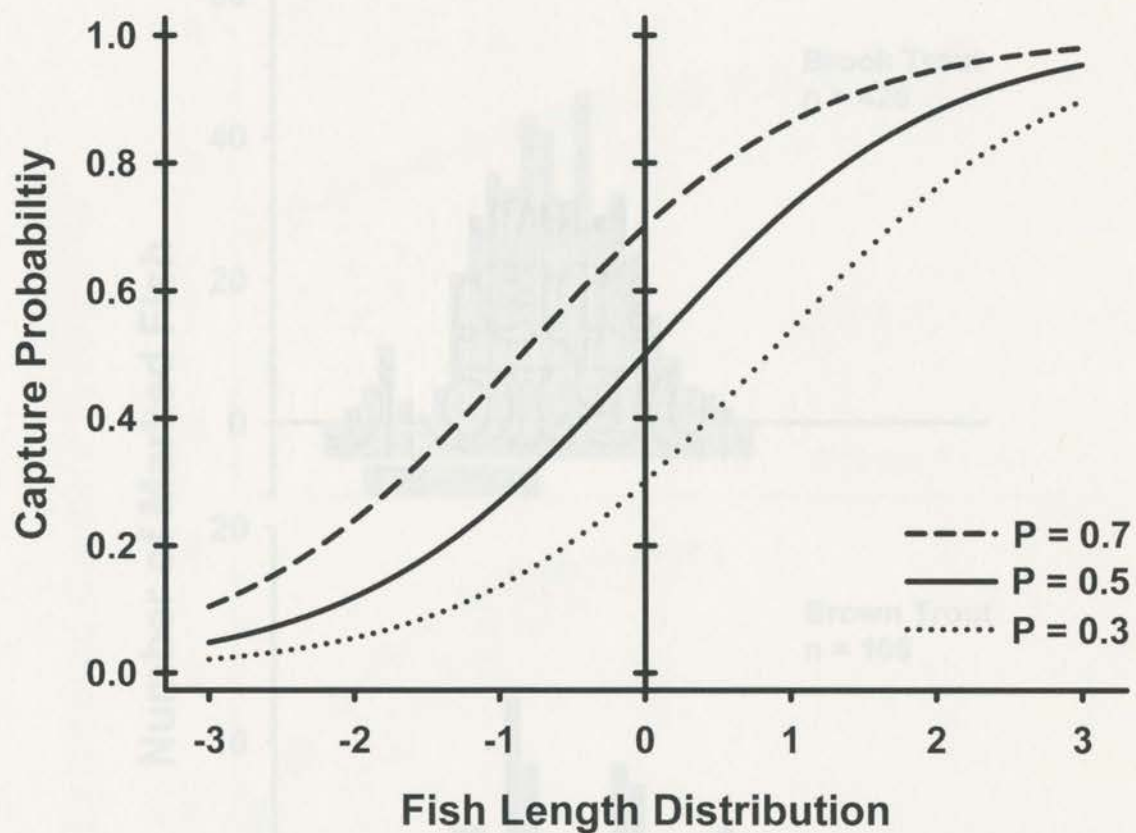


Figure 2 – Length-frequency histograms for brook trout (top) and brown trout (bottom) marked in 2006 and 2009 to evaluate removal estimates. Gray bars below the X-axis represent the range of fish lengths in three age classes from age-0 to age-2 and older (age 2+). These were estimated from individual length-frequency histograms for each site based on three-pass removal electrofishing data, and represent the range of fish lengths in the natural populations. Age-0 fish were not included in the evaluation (see text).

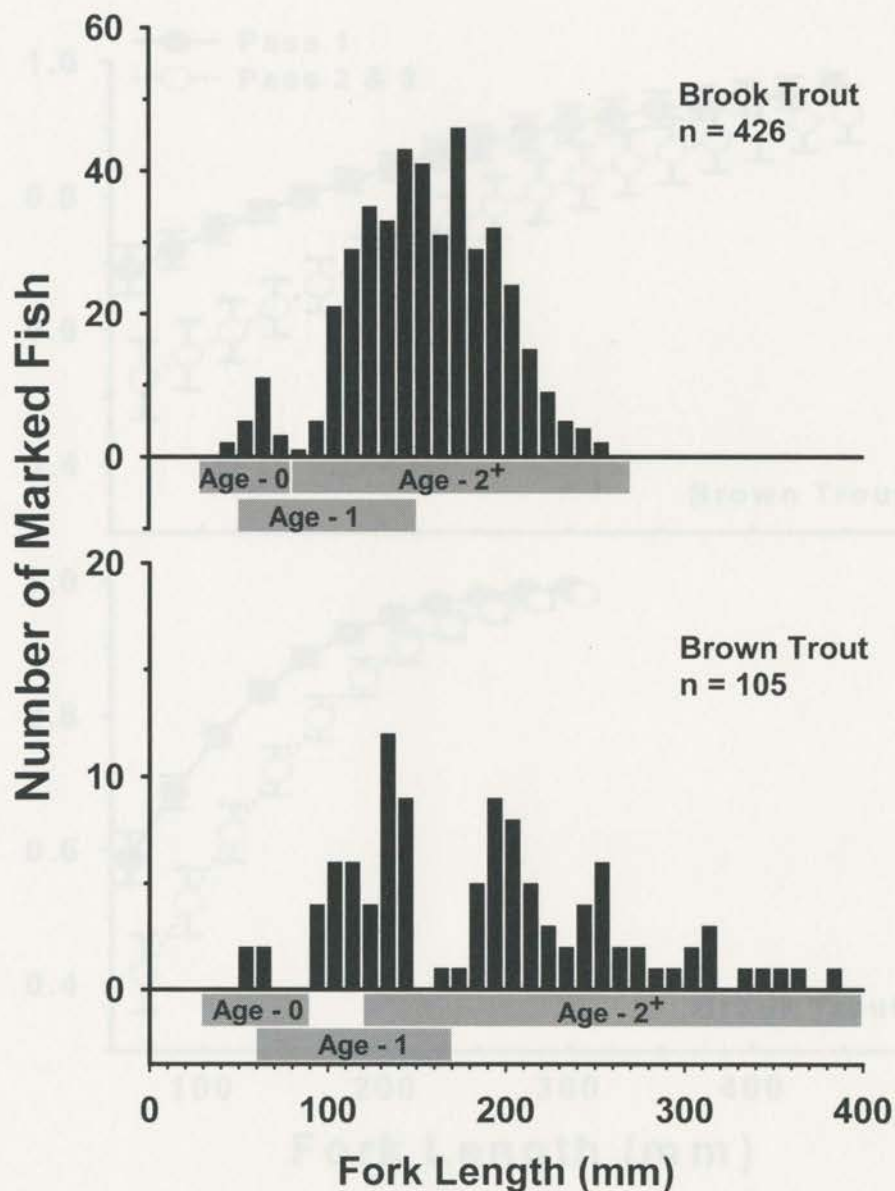
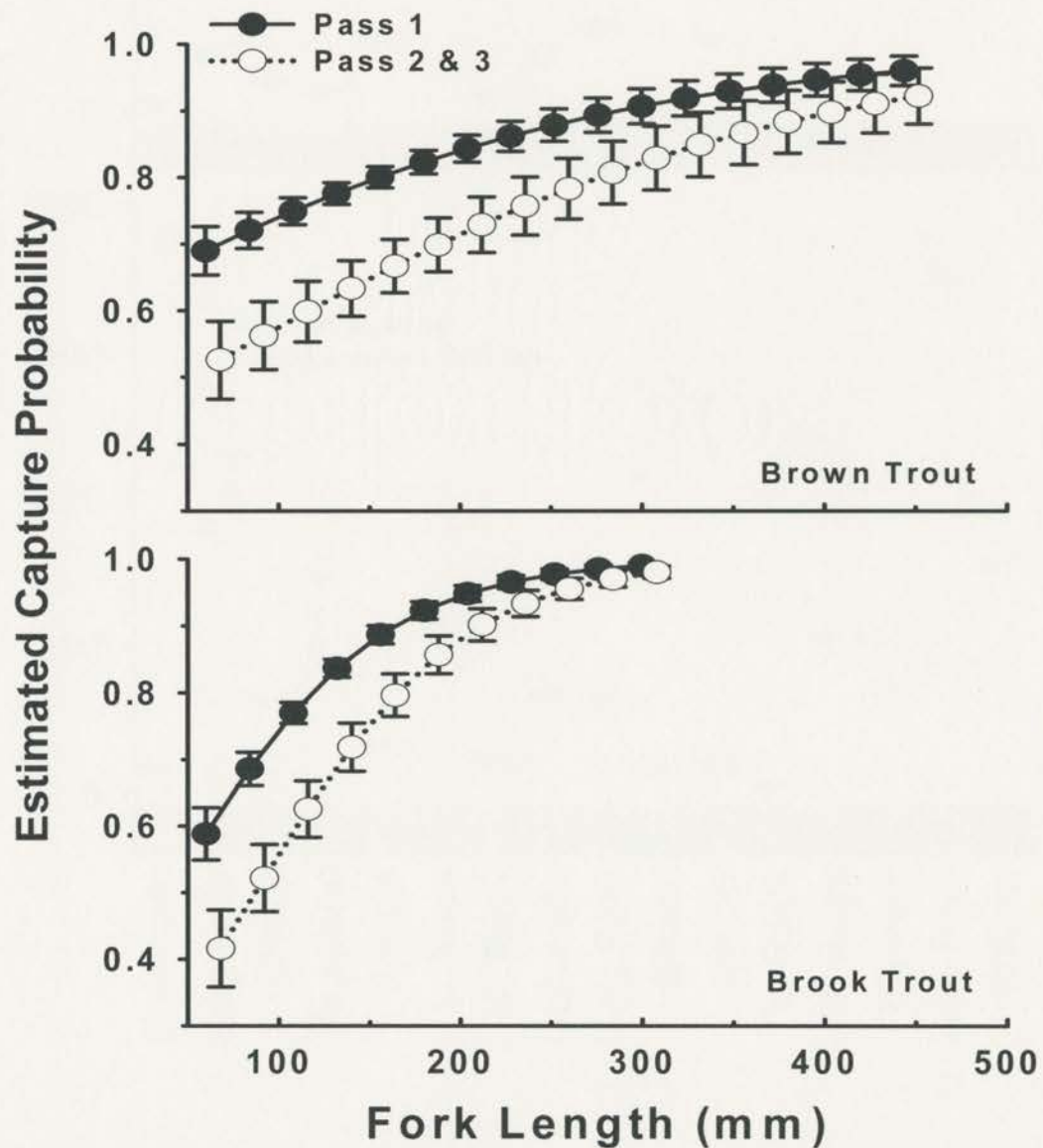


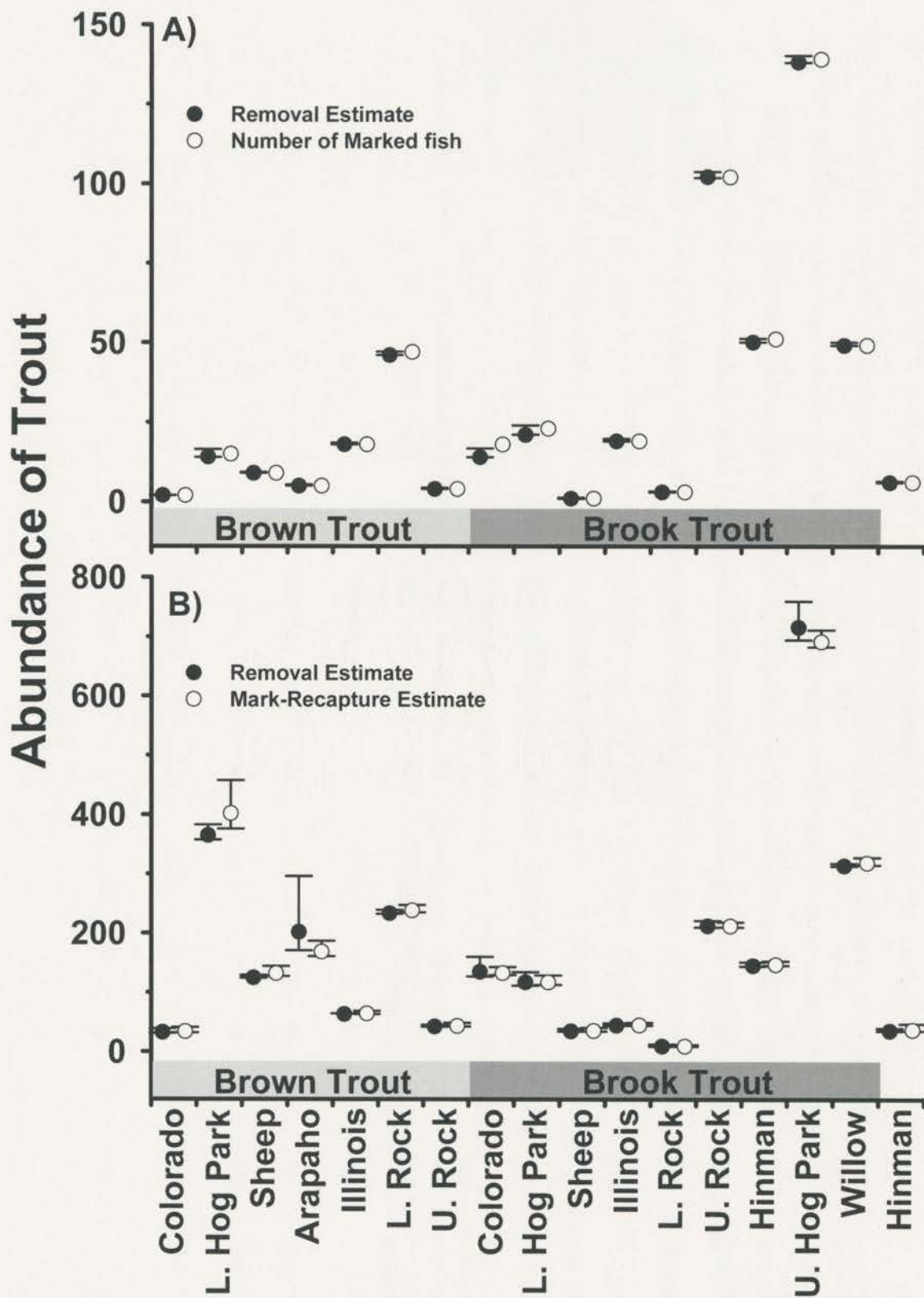
Figure 3 – Estimated capture probability as a function of trout length for fish sampled by electrofishing during 2006 and 2009 from 10 sites in southern Wyoming and northern Colorado. Capture probabilities for unmarked brown trout (top) and brook trout (bottom) were estimated from 1056 and 1658 individuals, respectively. Capture probabilities represent weighted means pooled across sites. Solid circles show capture probabilities for individuals captured on the first electrofishing pass, whereas open circles show capture probabilities for those captured on the second or third passes. Error bars represent 95% confidence intervals.



Abundance of Trout



Figure 4 – Abundance estimates of marked trout (A) and all trout (B), for brown, brook, and rainbow trout in study reaches of 10 streams in southern Wyoming and northern Colorado. Number of marked trout known to be in the study reaches during electrofishing is also shown (A). Removal estimates of marked trout in (A) represent model averaged estimates of abundance. Removal and mark-recapture estimates of total trout abundance in (B) are derived from the top model (see text). Error bars represent 95% log-normal confidence intervals.



Appendix 1. – Removal and mark-recapture estimates of salmonid and non-salmonid abundance at 10 sites in southern Wyoming and northern Colorado. Number of marked fish (N) is the number of age-1 and older fish marked and released into the enclosed study reach, minus the known reach escapement. Abundance estimates ($\hat{N}$) resulting from removal estimates of marked fish represent model-averaged results. Standard errors for model-averaged estimates are unconditional standard errors (un SE) which incorporate both population variability and model selection uncertainty. Removal and mark-recapture estimates for total fish abundance, and their standard errors (SE), represent estimates based on the top model, which had 100% of the AIC_c model weight (see text). Lincoln–Petersen mark-recapture estimates (L–P est.), corrected for small sample size, are given for comparison to estimates derived using the Huggins Model (see text). Capture probabilities (pass-1 $\hat{p}$ and pass-2&3 $\hat{p}$) represent the probability of capturing a 132-mm trout, 141-mm sucker (white and longnose combined), 91-mm creek chub, and 79-mm mottled sculpin (which represent the mean fish length for each taxa) during the first and subsequent electrofishing passes, respectively. Species (Spp) abbreviations are: BKT = brook trout, BNT = brown trout, RBT = rainbow trout, LNS = longnose sucker, WHS = white sucker, CRC = creek chub, and MSC = mottled sculpin.

		Removal estimate of marked fish				Mark – recapture estimate of total fish abundance				Removal estimate of total fish abundance				
Site	Spp	N	N̂	un SE	95% CI	N̂	SE	95% CI	L - P Est.	N̂	SE	95% CI	Pass-1 p̂	Pass-2&3 p̂
Brown Trout														
Arapaho Creek	BNT	5	5	0.07	(5,5)	169	6.19	(161,187)	155	202	28.55	(171,296)	0.47 (0.090)	0.32 (0.095)
Colorado Creek	BNT	2	2	0.01	(2,2)	34	2.01	(32,41)	31	32	1.46	(31,39)	0.74 (0.061)	0.60 (0.088)
Lower Hog Park Creek	BNT	15	14	0.30	(14,16)	402	19.64	(376,457)	377	365	6.05	(358,383)	0.79 (0.026)	0.66 (0.049)
Illinois River	BNT	18	18	0.07	(18,19)	64	1.08	(63,69)	63	63	0.18	(63,64)	0.93 (0.028)	0.88 (0.048)
Lower Rock Creek	BNT	47	46	0.14	(46,47)	238	2.92	(235,248)	237	233	1.40	(232,239)	0.85 (0.026)	0.76 (0.049)
Upper Rock Creek	BNT	4	4	0.07	(4,4)	43	1.25	(42,48)	42	42	0.52	(42,45)	0.87 (0.029)	0.79 (0.049)
Sheep Creek	BNT	9	9	0.05	(9,9)	132	3.98	(127,144)	124	125	0.88	(124,129)	0.86 (0.032)	0.77 (0.055)
Brook Trout														
Colorado Creek	BKT	18	14	0.25	(14,16)	133	3.18	(129,143)	158	135	7.52	(127,160)	0.68 (0.061)	0.54 (0.086)
Hinman Creek	BKT	51	50	0.17	(50,51)	147	1.58	(146,153)	147	145	1.32	(144,151)	0.89 (0.030)	0.82 (0.029)
Lower Hog Park Creek	BKT	23	21	0.30	(21,24)	117	3.72	(113,129)	118	117	5.26	(111,134)	0.74 (0.043)	0.61 (0.067)
Illinois River	BKT	19	19	0.12	(19,20)	45	0.89	(44,49)	44	44	0.66	(44,48)	0.91 (0.035)	0.85 (0.058)
Lower Rock Creek	BKT	3	3	0.05	(3,3)	9	0.42	(9,12)	9	9	0.63	(9,13)	0.82 (0.044)	0.71 (0.069)

Appendix 1. – Continued.

Site	Spp	Removal estimate of marked fish				Mark – recapture estimate of total fish abundance				Removal estimate of total fish abundance				
		<i>N</i>	$\hat{N}$	un SE	95% CI	$\hat{N}$	SE	95% CI	L - P Est.	$\hat{N}$	SE	95% CI	Pass-1 $\hat{p}$	Pass-2&3 $\hat{p}$
Upper Rock Creek	BKT	102	102	0.25	(102,104)	212	1.94	(210,219)	209	212	2.41	(210,221)	0.85 (0.029)	0.75 (0.051)
Sheep Creek	BKT	1	1	0.04	(1,1)	35	1.22	(34,40)	34	35	0.84	(34,39)	0.83 (0.045)	0.72 (0.070)
Upper Hog Park Creek	BKT	139	138	0.34	(138,140)	691	6.88	(682,711)	679	716	15.74	(694,759)	0.82 (0.021)	0.71 (0.043)
Willow Creek	BKT	49	49	0.14	(49,50)	319	2.98	(315,328)	313	314	0.90	(313,318)	0.94 (0.013)	0.90 (0.024)
Rainbow Trout														
Hinman Creek	RBT	6	6	0.07	(6,6)	37	2.29	(35,47)	35	35	0.78	(35,40)	0.94 (0.072)	0.90 (0.120)
Non-salmonid Species														
Sheep Creek	LNS	17	17	0.56	(17,21)	106	6.15	(99,125)	94	99	3.99	(95,114)	0.72 (0.039)	0.52 (0.096)
Colorado Creek	LNS	9	7	0.42	(7,10)	66	5.68	(60,84)	68	58	3.59	(55,72)	0.72 (0.039)	0.52 (0.096)
Lower Rock Creek	LNS	7	7	0.88	(7,13)	125	16.11	(107,177)	97	110	9.32	(101,143)	0.72 (0.039)	0.52 (0.096)
Illinois River	WHS	3	3	0.25	(3,5)	824	389.31	(418,2157)	319	276	21.99	(250,362)	0.72 (0.039)	0.52 (0.096)
Illinois River	CRC	74	60	1.63	(59,68)	354	17.25	(330,400)	360	309	13.73	(295,356)	0.605 (0.039)	0.636 (0.084)
Hinman Creek	MSC	27	6	0.46	(6,9)	2827	1078.8	(1419, 6105)	2531	918	144.75	(744,1361)	0.426 (0.056)	0.337 (0.85)

Appendix 2. – Ninety-five percent confidence set for capture probability models used for removal estimates of the abundance of marked trout at 10 study sites in southern Wyoming and northern Colorado. Parameters for fish length and fish weight are individual fish covariates, whereas the rest are site-level covariates. Behavioral responses are modeled as the difference in capture probability between the first and subsequent electrofishing passes.

Model	AIC _c	Delta AIC _c	AIC _c weights	Number of parameters	Deviance
fish length + year sampled ^a	278.033	0.000	0.165	3	272.0167
fish length + mean substrate diameter ^a	278.634	0.601	0.122	3	272.6176
fish length + study site ^a	279.152	1.120	0.094	11	256.9753
fish length + first pass effort ^a	279.271	1.238	0.089	3	273.2550
fish length + behavioral response + year sampled ^a	279.645	1.612	0.074	4	271.6179
fish length + behavioral response + mean substrate diameter ^a	280.433	2.400	0.050	4	272.4063
fish length	280.955	2.922	0.038	2	276.9471
fish length + behavioral response + first pass effort ^a	281.025	2.992	0.037	4	272.9979
fish length + behavioral response + site ^a	281.051	3.019	0.036	12	256.8419
fish length + % pool habitat ^a	281.298	3.266	0.032	3	275.2824
fish length + general difficulty rating ^a	281.485	3.452	0.029	3	275.4690
fish length + % of stream bank undercut ^a	281.619	3.586	0.027	3	275.6031
fish length + streamside vegetation ^a	281.887	3.854	0.024	3	275.8707
fish length + behavioral response	282.539	4.506	0.017	3	276.5229
fish species [RBT modeled as BKT] + fish length	282.564	4.531	0.017	3	276.5477
fish length + average max pool depth ^a	282.796	4.763	0.015	3	276.7800
fish length + behavioral response + % pool habitat ^a	282.849	4.816	0.015	4	274.8219
fish length + stream width ^a	282.956	4.923	0.014	3	276.9399
fish length + behavioral response + % of stream bank undercut ^a	283.349	5.316	0.012	4	275.3219
year sampled	283.494	5.461	0.011	2	279.4857
fish length + behavioral response + streamside vegetation ^a	283.576	5.543	0.010	4	275.5493
fish species + fish length	283.609	5.576	0.010	4	275.5822
fish weight	283.720	5.688	0.010	2	279.7122
fish species * fish length	283.722	5.690	0.010	6	271.6661

^a – models constructed from top two *a priori* fish-level models (see text)

Model	ΔAIC	Delta AIC	ΔAIC weights	Natural logarithm	Number of respondents	Frequency
species * length + behavioural responses + mark + effort	2625.197	0.000	1	1	28	2273.714
species * length + behavioural responses + mark + pool weighted	2612.855	12.342	0	0	9	2044.763
species * length + behavioural responses + mark + time pool effort	2578.307	46.890	0	0	9	1895.895
species * length + behavioural responses + mark + general difficulty	2574.308	40.889	0	0	9	2266.246
species * length + behavioural responses + mark + 5 pool area	2525.257	99.940	0	0	9	2031.185
species * length + behavioural responses + mark	2546.344	21.147	0	0	9	1936.327
species * length + behavioural responses + mark + dimension	2445.825	81.372	0	0	9	2128.624
vegetation						
species * length + behavioural responses + mark + spatial width	2542.335	81.138	0	0	9	2026.917
species * length + behavioural responses + mark + % of banks covered	2517.234	81.963	0	0	9	2025.872
species * length + behavioural responses + mark + average area pool	2502.912	92.285	0	0	9	2025.381

ΔAIC = difference in AIC values of model and best model; which indicates if only fish with a difference of 2 or less in AIC values are considered.

Species * length + behavioural responses + mark + effort
 Species * length + behavioural responses + mark + pool weighted
 Species * length + behavioural responses + mark + time pool effort
 Species * length + behavioural responses + mark + general difficulty
 Species * length + behavioural responses + mark + 5 pool area
 Species * length + behavioural responses + mark
 Species * length + behavioural responses + mark + dimension
 Vegetation
 Species * length + behavioural responses + mark + spatial width
 Species * length + behavioural responses + mark + % of banks covered
 Species * length + behavioural responses + mark + average area pool

Appendix 3. – Model selection results for exploratory analysis of fish-level and site-level covariates (see text) for capture probability models used for removal estimates of the total trout abundance at 10 study sites in southern Wyoming and northern Colorado. Parameters for fish length, fish weight, and marking are individual fish covariates, whereas the rest are site-level covariates. Behavioral responses are modeled as a difference in capture probability between the first and subsequent electrofishing passes.

Model	AIC _c	Delta AIC _c	AIC _c weights	Model likelihood	Number of Parameters	Deviance
species * length + behavioral response + mark + site	2865.797	0.000	1	1	18	2829.714
species * length + behavioral response + mark + year sampled	2912.805	47.008	0	0	9	2894.783
species * length + behavioral response + mark + first pass effort	2913.107	47.310	0	0	9	2895.085
species * length + behavioral response + mark + general difficulty rating	2914.268	48.472	0	0	9	2896.246
species * length + behavioral response + mark + % pool area	2925.207	59.410	0	0	9	2907.185
species * length + behavioral response + mark ^a	2946.344	80.547	0	0	8	2930.327
species * length + behavioral response + mark + streamside vegetation	2946.826	81.029	0	0	9	2928.804
species * length + behavioral response + mark + wetted width	2946.939	81.142	0	0	9	2928.917
species * length + behavioral response + mark + % of banks undercut	2947.894	82.097	0	0	9	2929.872
species * length + behavioral response + mark + average max pool depth	2948.013	82.217	0	0	9	2929.991

^a – indicates top raking *a priori* model which contained only fish level covariates of capture probability.

Appendix 4. – Model selection results for exploratory analysis of fish-level and site-level covariates (see text) for capture probability models used for mark-recapture estimates of the total trout abundance at 10 study sites in southern Wyoming and northern Colorado.

Parameters for fish length, fish weight, and marking are individual fish covariates, whereas the rest are site-level covariates. For all models the probability of initially capturing fish during electrofishing was fixed equal to recapturing fish during electrofishing.

Model	AIC _c	Delta AIC _c	AIC _c weights	Model likelihood	Number of Parameters	Deviance
species*length + sample site	2192.79	0	0.9891	1	16	2160.69
Species + length + sample site	2213.22	20.42	0.00004	0	14	2185.14
species*length + year sampled	2267.79	74.99	0	0	8	2251.76
species*length + pass 1 effort	2285.86	93.06	0	0	8	2269.83
species*length + % of banks undercut	2295.17	102.38	0	0	8	2279.15
species*length + mean substrate diameter	2320.39	127.59	0	0	8	2304.36
species*length	2325.62	132.82	0	0	7	2311.59
species*length + streamside vegetation	2325.71	132.91	0	0	8	2309.68
species*length + average maximum pool depth	2325.80	133.00	0	0	8	2309.77
species*length + stream width	2326.27	133.48	0	0	8	2310.25
species*length + % pool habitat	2327.60	134.81	0	0	8	2311.58
Species + length	2344.80	152.01	0	0	5	2334.79
Species + sample site	2486.89	294.09	0	0	13	2460.82
species*sample site	2492.72	299.92	0	0	24	2444.49
Sample site	2522.82	330.02	0	0	11	2500.77
Length	5430.09	3237.29	0	0	2	5426.08

Appendix 5. – Summary of results and discussion for evaluation of night-time electrofishing and removal estimation of population abundance for non-salmonid species sampled in streams in northern Colorado and southern Wyoming. The methods used to sample fish and evaluate population estimates are the same as for salmonid species (see text).

Results

Fish marking. – In addition to marking salmonids, I marked all nonsalmonid species captured that were large enough to mark (≥ 50 mm, see Appendix 6 for population size structure), including 33 longnose suckers *Catostomus catostomus* at 3 sites, and 3 white suckers *Catostomus commersoni*, 27 mottled sculpin *Cottus bairdi*, and 74 creek chub *Semotilus atromaculatus* at one site each.

Reach escapement. – At 9 of 10 sites, only two nonsalmonid fishes escaped study reaches. At the last site, the only one where mottled sculpin were present, I captured 30 age-0 and 42 age-1 and older sculpin beyond the fences. The age-1 and older sculpins accounted for 1.5% of the mark-recapture population estimate.

Non-salmonid capture probability modeling. – Fish covariates also were generally more important in modeling capture probabilities for non-salmonids, but account for the percent pool habitat improved the top *a priori* fish-scale model. Models that included a species X length interaction, either a species-specific or additive behavioral response,

and an additive response to previous capture ranked higher than all other *a priori* models. For both removal and mark-recapture models, length had a positive, non-linear effect similar to that for salmonids, which was strongest for mottled sculpin. For both sucker species and mottled sculpin, but not creek chub, capture probability decreased on passes two and three. Site-scale covariates for the percent area in pool habitat and the average maximum pool depth improved the fit of top *a priori* models, and both had negative effects on capture probability. Combining fish and site covariates resulted in superior models compared to the *a priori* model set, including five models that ranked close to the top model ($\Delta AIC_c \leq 4$) for both removal and mark-recapture estimates. Therefore, I used model averaging, and found that model selection uncertainty accounted for, on average, 12%, 17%, and 31% of the variability in abundance estimates resulting from removal estimates of marked fish, mark-recapture estimates, and removal estimates of total non-salmonid abundance, respectively.

Removal and mark-recapture estimates of catostomid abundance also were generally similar, but mark-recapture estimates of creek chub and sculpin were greater than removal estimates and had wider confidence limits (Appendix 1). The two estimates for longnose suckers differed by 10 fish, on average. In contrast, the mark-recapture estimate for white sucker was much greater than the removal estimate, probably because only three fish were marked. Likewise, mark-recapture estimates for both creek chub and mottled sculpin were greater than removal estimates, and the 95 % log-normal confidence interval for the removal estimate of sculpin abundance did not include the mark-recapture estimate.

Discussion

In contrast to the results for salmonids, removal estimates were inconsistent for non-salmonids. Estimates of the abundance of suckers, particularly longnose sucker, were generally accurate, whereas those for creek chub and mottled sculpin underestimated the known number of marked fish and were smaller than mark-recapture estimates of total abundance. Site selection and sampling were optimized for salmonids, not non-salmonids, so evaluation of removal estimates of non-salmonid abundance were frequently based on small numbers of marked individuals, or were unreplicated. Therefore, results for non-salmonids should not be considered a thorough evaluation of removal estimates for these species.

	91 (52 - 129)
CP	169.3 (105 - 219)
WH	121.7 (65 - 432)
Lower Rock Cr.	129 (68 - 220)
Johnson Cr.	192 (57 - 140)

Appendix 6. – Size structure of non-salmonid populations at sites sampled to evaluate electrofishing removal estimates in southern Wyoming and northern Colorado. Average length of Age 1 and older fish, and range of lengths in parentheses, is given for all species (LNS = longnose sucker, WHS = white sucker, CRC = creek chub, and MSC = mottled sculpin) for which evaluations of electrofishing removal estimates were possible.

Site	Fish Species	Fish Length (mm)
Colorado Cr.	LNS	153 (64 – 289)
Sheep Cr.	LNS	144.9 (80 – 189)
Lower Illinois Rv.	CRC	91 (62 – 193)
	LNS	169.3 (105 – 215)
	WHS	121.3 (66 – 432)
Lower Rock Cr.	LNS	118.2 (68 – 232)
Hinman Cr.	MSC	79.2 (57 – 142)

Abstract

Research on forest and grassland ecosystems indicates that terrestrial invertebrates that fall into streams can be an important prey resource for fish, providing about 50% of their annual energy and having strong effects on growth and abundance. During summer 2007, I conducted a large-scale field study to evaluate the effects of three commonly used grazing systems, continuous season-long grazing and two types of rotational grazing systems, on terrestrial invertebrate inputs to streams in northern

CHAPTER 2:

Grazing Management Influences Terrestrial Invertebrate Prey Subsidies that Feed Trout

in Central Rocky Mountain Streams

with little or no livestock grazing. Grazing management (either simple or intensive) resulted in more riparian vegetation, greater inputs of terrestrial invertebrates, greater biomass of terrestrial invertebrates prey in trout diets, and more trout biomass than season-long grazing. However, these differences were frequently inconsistent owing to high variability, especially for trout diets and biomass. Furthermore, riparian vegetation and terrestrial invertebrates growing directly on stream banks at sites managed for total exclusion were similar to sites managed for selective grazing only. These results suggest that rotational grazing systems can be effective for maintaining levels of terrestrial invertebrate subsidies to stream predatory fish support robust trout populations, but that the factors influencing the effect of riparian grazing on stream subsidies are both complex, owing to variability in microclimate and invertebrate and plant populations, and spatially variable.

Abstract

Research in forest and grassland ecosystems indicates that terrestrial invertebrates that fall into streams can be an important prey resource for fish, providing about 50% of their annual energy and having strong effects on growth and abundance. During summer 2007, I conducted a large-scale field study to evaluate the effects of three commonly-used grazing systems, traditional season-long grazing and two types of rotational grazing systems, on terrestrial invertebrate inputs to streams in northern Colorado and their use by trout. I also compared these effects to sites grazed only by wildlife (i.e., no livestock use). Overall, rotational grazing management (either simple or intensive), resulted in more riparian vegetation, greater inputs of terrestrial invertebrates, greater biomass of terrestrial invertebrate prey in trout diets, and more trout biomass than season-long grazing. However, these differences were frequently inconsistent owing to high variability, especially for trout diets and biomass. Furthermore, riparian vegetation and terrestrial invertebrates entering streams and in trout diets at sites managed for rotational grazing were similar to sites managed for wildlife grazing only. These results indicate that rotational grazing systems can be effective for maintaining levels of terrestrial invertebrate subsidies to streams necessary to support robust trout populations, but that the factors influencing the effect of riparian grazing on stream subsidies are both complex, owing to variability in microclimate and invertebrate and plant populations, and spatially variable.

Introduction

Habitat degradation is the leading cause of biodiversity loss worldwide (Vitousek et al. 1997; Dirzo and Raven 2003; Fahrig 2003), and humans have now modified more than 75% of the ice-free land surface (Ellis and Ramankutty 2008). Effects of habitat degradation on plant and animal populations may result directly from habitat loss, but also indirectly from the decoupling of important linkages among habitats and communities (Foley et al. 2005; Hooper et al. 2005). These habitat linkages are especially important in streams, which have small area but long boundaries with the adjacent riparian areas, so they are strongly influenced by fluxes from the terrestrial habitats they drain (Wallace et al. 1997; Nakano and Murakami 2001; see reviews by Baxter et al. 2005; Fausch et al. 2010). These fluxes are an alternate pathway through which land-use practices can influence food webs and ecosystem processes in recipient habitats, but the extent to which land use affects fluxes of terrestrial materials to streams is poorly understood.

Livestock grazing is one of the dominant land uses globally, and can have strong negative direct effects on aquatic habitats if poorly managed. More than half of all agricultural land is used for grazing (22% of the land surface, Ramankutty et al. 2008), including >344 million hectares in the U.S. (GAO 1988; NRCS 2002), primarily in the West. Livestock grazing influences ecological functions directly by trampling and compacting soils, adding manure, and removing vegetation, which can alter plant productivity and community composition. Although riparian zones make up <1% of rangelands, cattle congregate in these sensitive areas to find forage, shade, and water

(Armour et al. 1991). High densities of cattle, or cattle poorly distributed across the landscape, can overgraze and trample stream banks, and reduce bank stability. This leads to bank erosion, increased turbidity, siltation of streambed gravel, infilling of pools, and reduced habitat complexity (Platts 1981; Kauffman and Krueger 1984; Belsky et al. 1999). In turn, this can reduce aquatic invertebrate production, growth and reproduction of trout, and ultimately trout abundance and production.

Current grazing management is primarily designed to protect stream bank stability and instream habitat by maintaining sufficient aboveground plant biomass to sustain roots that bind banks, and to prevent cattle from over-browsing riparian shrubs (Clary and Webster 1989; Meehan 1991; Clary and Kruse 2004). The guiding principle has been that maintaining a minimum level of riparian vegetation (e.g., 10 cm of grass stubble, Clary and Leininger 2000) prevents erosion that destroys habitat for aquatic invertebrates and trout (Wyman et al. 2006). This logic has been supported by demonstration projects in which cattle grazing was eliminated from riparian zones altogether. These have showed large increases in both streamside vegetation (Rickard and Cushing 1982; Platts and Wagstaff 1984; Kauffman et al. 1997; Dobkin et al. 1998; Holland et al. 2005) and abundance or biomass of trout (Keller and Burnham 1982; Knapp and Matthews 1996; see Platts 1991 for review) within five years after no livestock use. However, full recovery of stream habitat, including stream bank stabilization, lateral scour that creates deep pools with overhead cover, cleaning of stream gravel needed for invertebrate production and trout spawning, and input of woody debris that creates habitat complexity, often requires more than these short

periods to achieve (Kondolf 1993; Magilligan and McDowell 1997; see Sarr 2002 for review). Therefore, it is likely that other mechanisms in addition to direct habitat loss from erosion and siltation are important in influencing trout populations in rangeland streams

Two indirect pathways by which improved grazing practices that increase riparian vegetation may influence trout are increased inputs of terrestrial insects, and of detritus that fuels secondary production of aquatic insects. In addition to invertebrates produced within the stream, terrestrial invertebrates that fall, crawl, or blow into streams from riparian vegetation are important for sustaining trout (Baxter et al. 2005). These prey account for 50 – 85 % of trout diets during summer months (e.g., Dineen et al. 2007; Utz and Hartman 2007) and provide about 50% of their annual energy budget (Kawaguchi and Nakano 2001; Nakano and Murakami 2001; Sweka and Hartman 2008). Moreover, experimental reduction of terrestrial prey using mesh greenhouses in a Japanese stream reduced growth of salmonids by 25% compared to a control (Baxter et al. 2007), and caused half the biomass of salmonids to emigrate in response (see Kawaguchi et al. 2003; Fausch et al. 2010 for review). Bioenergetic simulations yielded similar conclusions about the importance of terrestrial prey (Sweka and Hartman 2008).

Although this research highlights the importance of riparian vegetation in supplying terrestrial invertebrates that help sustain stream salmonids, we have yet to fully evaluate how actual land uses alter these prey subsidies so that managers can apply the results. Several recent studies have reported that terrestrial prey inputs were strongly influenced by cattle grazing. Edwards and Huryn (1996) found that streams

traversing New Zealand grasslands used for livestock grazing received less terrestrial invertebrate biomass than ungrazed native tussock grasslands. Moreover, Saunders and Fausch (2007) showed that terrestrial invertebrate inputs to Wyoming streams with riparian zones under a high-density short-duration grazing system were more than double that for paired streams under season-long grazing, and that terrestrial invertebrates made up about half the biomass of summer afternoon trout diets. Furthermore, trout biomass in the streams under improved grazing management was also more than double that in the streams under season-long grazing. However, what is needed now are comparative studies in other regions of the most common prescribed grazing management systems and their effects on these indirect pathways by which livestock may influence trout populations.

The goals of this study were to: 1) evaluate whether terrestrial invertebrates that enter western U.S. rangeland streams provide important prey resources for trout, and 2) evaluate the potential for four commonly-used grazing management systems and livestock exclusion to support terrestrial prey inputs and trout populations. I conducted a large-scale field study of three common grazing systems in northern Colorado, and compared their effects to those resulting from allowing grazing only by wildlife. I show that sites under rotational grazing systems and those grazed only by wildlife had more riparian vegetation and provided more terrestrial prey that sustained trout than sites managed for season-long grazing. However, high variability among sites limited the consistency of some differences among contrasting grazing management systems.

Methods

Study reaches.-- To address these goals, I selected 16 study reaches on 14 streams in the North Platte and Colorado river drainages of north-central Colorado (Figure 1), 3 to 5 under each of four grazing management systems on a mixture of private, state, and federal lands (Table 1; Appendix Table 1). Livestock grazing is believed to have the strongest effects on fish populations in lower-gradient channels with extensive riparian zones (Wyman et al. 2006), so all were second to fourth order streams with relatively low gradient ($1.7\% \pm 0.18\%$ [mean $\pm$ 1 SE]), moderate width (6.4 ± 0.7 m), in mid-elevation shrublands ($2,552 \pm 26$ m elevation), where mean summer temperatures were suitable for trout ($15.1 \pm 0.7^\circ\text{C}$ during July and August). All streams had gravel substrate, mixed with either cobble or fine materials, and consisted primarily of long runs and short pools, with few riffles. All had naturally-reproducing populations of brook trout *Salvelinus fontinalis* or brown trout *Salmo trutta*, and four streams also had low densities of wild rainbow trout *Oncorhynchus mykiss* or cutthroat trout *O. clarkii*.

Grazing management. -- I compared the effects of traditional season-long cattle grazing to two rotational grazing systems and cattle exclusion (wildlife grazing only [WO]). Under season-long grazing (SLG), cattle are put in large pastures for the entire grazing season (about 120 d in north-central Colorado) to achieve a certain stocking rate. In contrast, under prescribed rotational grazing, management is tailored to range conditions, and managers determine the timing, intensity, and duration of grazing. Under simple rotational grazing (SRG), cattle grazed individual pastures for 35-45 d, and

were rotated among 3-5 pastures with the order changing each year. Intensive rotational grazing (IRG) is more variable, but cattle are rotated through pastures at 10-20-d intervals (total grazing pressure = 17 – 21 d) which allow managers to mimic aspects of the historical grazing of large herds of native ungulates like, elk *Cervus canadensis*, and bighorn sheep *Ovis Canadensis*. These ungulates typically move from lower to higher elevation as the season progresses, and graze on new vegetation growth as it appears (Burkhardt 1996). Data on stock density was not available, because many private operations did not have information on pasture size or were unwilling to disclose the number cattle having access to each pasture. Therefore, timing of use (Table 1) and estimated utilization of herbaceous vegetation (see below) were the best available measures of cattle use of streamside vegetation. Moreover, estimates of utilization of streamside vegetation likely provide a better estimate of riparian grazing pressure because they integrate the effects of stocking rate, cattle distribution, and vegetation regrowth at sites under rotational grazing management.

Suitable sites managed for WO were rare because cattle exclosures usually were too small (Bayley and Li 2008), so only three of sufficient size were found, and these were either in headwaters or surrounded by heavily grazed riparian zones. Additionally, sites managed for intensive rotational grazing (IRG) were most common in a portion of the region and, as a result, four of five sites were located in a 15 by 18 km area of the North Platte drainage. A fifth site was selected 80 km to the west in the Colorado River drainage, on a lake tributary, to increase the spatial distribution of sites under IRG management. Four sites each were under SLG or SRG regimes, and were well

distributed across the region. All pastures had been managed under the same grazing system for at least 7 years. However, managers responsible for implementing grazing systems regularly adjust the timing, duration, or intensity of grazing to account for range conditions at the local scale, so grazing systems do not represent uniform or static grazing treatments. In each pasture, a 200-m study reach was selected to maximize distance to changes in geomorphology and grazing management. In each reach, I sampled riparian vegetation, terrestrial prey input, fish diets, and fish abundance during summer 2007, using the same methods as previous research (Saunders and Fausch 2007), except where described below.

Riparian vegetation sampling. – Riparian vegetation measurements included clipped biomass, estimates of utilization for herbaceous species, overhead cover, and community composition and ground cover. Most measurements were made during July at peak standing crop biomass, before plant maturation. The standing crop of aboveground biomass was estimated separately for graminoids (hereafter grasses) and forbs by clipping all plants to ground level within four randomly-located 0.25-m² circular plots placed 1.5 m from the bankfull channel. Utilization of herbaceous vegetation by ungulate grazers was estimated using two 1-m² exclosures (13 x 20-cm cattle panel), each placed at a randomly-selected distance along one bank. Paired 0.25-m² circular plots inside and outside of the exclosure were clipped in late August or early September. Use of streamside vegetation by ungulates (i.e., utilization by both cattle and wildlife) was estimated as the difference in biomass of vegetation between clippings exposed to herbivory and those protected (i.e., clippings taken within exclosures) divided by the

potential vegetation production for the sample period (biomass from clippings in exclosures). All clipped vegetation was dried at 55°C for 48 hours, and weighed (nearest 0.1 g). Exclosures were constructed before livestock grazing in all but three cases. At two sites, the North Fork North Platte River and Shafer Creek (both SLG), cattle grazing began three weeks before exclosures were built, and no exclosures were built at Lower Trout Creek (SRG) because the pasture had already been grazed for 35 of the 40 days planned.

Overhead cover was measured using hemispherical photographs. Images were taken at 10-m intervals along each reach, with random starting points (0-10 m), using a Nikon D200 with an AF DX Fisheye-NIKKOR 10.5mm f/2.8G ED lens positioned 50 cm above the ground or stream surface. Images were taken each 2 m along a transect perpendicular to the channel that extended 4 m into the riparian zone on each bank. Percent overhead cover was estimated by placing a 100-point sampling grid over the digital images, after fisheye distortion had been corrected using program Capture NX (Nikon Corporation). Each grid point was identified as either open (no vegetation) or as covered by grasses, forbs, shrubs, or trees.

During 16 July through 10 August 2007, plant community composition was characterized by identifying all species present and estimating ground cover class by species along two 30-m Daubenmire transects placed 1.5 m from each stream bank. Transects started at a randomly chosen distances to fit within the 200-m study reach, and followed the stream bank. Visual estimates were made of ground cover classes for all plant species in 10 equally-spaced 20-cm x 50-cm quadrats (Stohlgren et al. 1998).

Invertebrate sampling. – Inputs of terrestrial and adult aquatic invertebrates were measured using plastic pan traps filled with 5 cm of filtered stream water, to which 5 mL of unscented, biodegradable surfactant was added to reduce surface tension (Mason and MacDonald 1982; Wipfli 1997; Nakano et al. 1999b). Overhead vegetative cover was classified as either high or low (> 35% or < 35% cover) at 5-m intervals using a convex densitometer and five clear pan traps (100 cm x 41 cm x 15 cm deep) were randomly allocated to locations in proportion to the size of these two strata. Three were randomly selected and deployed next to the bank and the other two were located mid-channel, to sample both invertebrates that tumble in from the banks or fall in from above (e.g., from vegetation, or when flying).

Invertebrates falling into study reaches were sampled during middle and late summer (2-16 July and 9-16 August 2007), when terrestrial inputs to temperate streams are greatest (Cloe and Garman 1996; Kawaguchi and Nakano 2001; Allan et al. 2003). Falling invertebrates were collected for a 6-d period divided into two 3-d samples, to optimize sampling effort based on a variance analysis of previous samples (see Saunders and Fausch 2007). Invertebrates in traps were sieved with a 250- μ m net and preserved in 70% ethanol.

Sampling fish diets and fish population characteristics. – Stomach contents were collected from salmonids in each reach during July and August 2007 to estimate the biomass and proportion of terrestrial invertebrates in fish diets. Diets were collected from 10 - 20 fish captured by electrofishing just after the period of peak terrestrial invertebrate input (ca. 1500-1900 h; Young et al. 1997a; Nakano et al. 1999a; Hieber et

al. 2003). Gastric lavage was used to collect diets from fish of 110-350 mm fork length (FL), because diets could not be sampled effectively from smaller fish, and larger fish become piscivorous. Stomach contents were sieved through 333- μ m mesh and preserved in 70% ethanol. On average, gastric lavage removed 98% (SE = 0.9) of the invertebrate biomass in trout diets, based on stomachs removed from 19 trout euthanized after lavage (average length = 221 mm, SE = 17.1).

To determine how terrestrial inputs influence fish populations, abundance and biomass of trout were estimated in each 200-m reach at baseflow in August 2007. Fish abundance was estimated using three-pass depletion electrofishing (Riley and Fausch 1995) conducted at night to improve accuracy (Saunders and Fausch 2007; Saunders et al. *in review* [Chapter 1]). High-output LED headlamps and hand held dive lights were used to illuminate the area electrofished. Two backpack electrofishing units (LR-24, SmithRoot Inc., Vancouver, WA) were used in wide streams (≥ 7 m) to increase efficiency. Mass (nearest 0.1 g) and length (nearest 1 mm FL) were recorded for all trout. Biomass was estimated by multiplying population abundance by mean fish mass, and the finite population variance (Riley and Fausch 1995) was used to calculate variances. Age-0 fish are not sampled efficiently and were not measured. Removal estimates of capture probability and fish abundance were calculated using the Huggins closed population estimator in Program MARK (White and Burnham 1999, see Saunders et al. *in review* review for details), where the probability of recapture was set at zero and fish size was used as an individual covariate. Additionally, estimates of individual

capture probabilities were improved by pooling capture data across the 16 sites sampled (see White 2005).

Invertebrate identification and biomass estimation. – Invertebrates were sorted to the taxonomic level necessary to identify their origin as terrestrial versus aquatic (generally Family, see Saunders and Fausch 2007 for details). Biomass (nearest 0.3 mg) of invertebrates found in pan trap and diet samples was measured after drying at 60°C for 48 h. Fish consumption of invertebrates could not be accurately estimated using models based on laboratory gastric evacuation rates (Elliott 1972; Hayward and Weiland 1998; Sweka et al. 2004) because water temperatures were higher and trout diets more complex at the study sites than those on which models were based. Instead, biomass of prey items in trout diets was estimated and reconstructed using published length-mass regressions based on total invertebrate length or head capsule width (Rogers et al. 1977; Smock 1980; Meyer 1989; Burgher and Meyer 1997; Benke et al. 1999; Johnston and Cunjak 1999; Sabo et al. 2002). Lengths were measured for up to 15 items of each taxon in each fish diet. When more than 15 individuals of the same taxa were encountered, the mean mass of the 15 measured individuals was used to estimate biomass for the total number counted.

Stream habitat characteristics. – Several characteristics of stream habitat were measured for each 200-m reach, for use as covariates in models, including stream width, fish habitat (pool and run area), water temperature, and map gradient. Wetted and bankfull widths were measured at 10-m intervals. The dimensions of each pool and run (length and width) were measured (nearest 0.1 m). HOBO WaterTemp Pro temperature

loggers (Onset Computer Corporation, Pocasset, MA), programmed to record water temperature hourly from June through September, were deployed in the middle of each reach. Loggers were deployed in shaded locations that were not vulnerable to physical disturbance by grazing animals. Stream gradient for a 500-m stream segment containing each study reach was estimated from U.S. Geological Survey 7.5-minute topographical maps.

Data analysis

Linear mixed models were used to investigate the factors influencing grazing utilization, vegetation biomass, overhead cover, invertebrate input, fish diets, and fish biomass, and were evaluated using an Information Theoretic approach (Anderson et al. 2001; Burnham and Anderson 2001, 2002). A priori, I hypothesized that site level habitat and vegetation measurements would be better predictors of terrestrial invertebrate input to streams and in fish diets than the four categorical grazing systems. Therefore, models were developed following two themes, one with categorical variables for the four grazing systems only, and another with only site-level covariates such as stream width and overhead cover. The goal was to assess 1) how much variance could be explained by the two sets of covariates, and 2) whether mechanistic variables (e.g., vegetation characteristics) would be supported by model selection. For each model theme, I fit models with all combinations of covariates to allow model averaging across a balanced set of models (Doherty et al. *in review*). Afterwards, exploratory analysis was conducted to assess whether the top model using grazing system covariates could be

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improved by adding site-level covariates. Models were ranked using the Akaike Information Criterion corrected for small sample sizes (AIC_c). Multi-model inference was conducted by model-averaging either parameter estimates or model predictions using Akaike weights (w_i) to account for model selection uncertainty when multiple models were supported (Burnham and Anderson 2004).

Models for invertebrate input and fish diets. – Several *a priori* hypotheses were used to select covariates for models. I hypothesized that cattle grazing would influence input of terrestrial invertebrates to streams and in trout diets by altering aboveground herbaceous biomass, total vegetation cover, and vegetation community composition. For the last, I used the minimum number of plant species that accounted for 85% of vegetation ground cover as a surrogate. I also hypothesized that terrestrial input would decrease with increasing wetted width (e.g., Cloe and Garman 1996). When analyzing data for July and August for both terrestrial input and trout diets, I also included month, but made separate predictions by month (see below) only when the confidence interval on this parameter did not overlap zero. To reduce heterogeneous variance, data on invertebrate input were transformed using natural logarithms, and data on the biomass in trout diets was transformed using the square root. Standard errors for back-transformed data were estimated using the Delta Method (DeGroot and Schervish 2002).

Trout diets are also potentially influenced by trout species and relative size, so additional covariates for these were included in models. Salmonids in streams form distinct size-based dominance hierarchies (Fausch 1984; Nakano 1995), which

determine foraging positions and access to large, profitable prey. Therefore, relatively larger fish within populations become dominants, and are expected to ingest a greater biomass of prey compared to subordinate fish. Relative length was defined as the length of the fish from which the diet was taken divided by the length of the fish at the 90th percentile for the site, determined from the electrofishing sample. Individuals $\geq 90^{\text{th}}$ percentile were assigned a relative length of 1.

The response variables of terrestrial invertebrate input and invertebrate biomass in trout diets had multiple samples per site, which were likely not independent of each other, so I first used model selection to select a variance structure for the random effects. Models with four variance structures were evaluated for each of the two global models that included all system or site covariates (the fixed effects): 1) no random effect, 2) homogeneous variances among sites managed under different grazing management, 3) heterogeneous variances among sites under different grazing management, and 4) homogeneous variance within two sets of grazing systems (SL and WO vs. SRG and IRG) but heterogeneous variance between the sets. All were compared using AIC_C derived from optimizing the restricted maximum likelihood (REML). Models with random effects were fit using the lme4 package in Program R (Bates and Maechler 2010; R Development Core Team 2010). The result of this analysis was that the best approximating model of variance structure was the last (homogeneous within two sets of grazing systems) for both global models and for both response variables, so this was used in further analyses. The amount of variation associated with sites managed for

both types of rotational grazing was approximately double that of sites managed for either SLG or WO.

Having chosen an appropriate variance structure, the next step was to fit two sets of models (with system vs. site covariates) for invertebrate input and fish diets, and evaluate their support using the full maximum likelihood. Model selection has rarely been used to evaluate differences among multiple levels of a categorical variable (e.g., grazing systems), because parameters are conditioned on a given model and rarely have consistent interpretations among all models in a set. Therefore, models with categorical covariates were developed with a standard intercept, which represents the mean value of the response variable across all sites, and the sum of each column of the design matrix associated with categorical variables equaled zero (Appendix 2). This allows a consistent interpretation of parameters for categorical covariates across all models while facilitating model averaging to account for model uncertainty (D. R. Anderson, personal communication). An artifact of this constraint was that the value for the "effect" of one level of each categorical variable was a derived estimate. In contrast, all models with site-level covariates, which were continuous, were fit and evaluated using standard methods. In a final step, I conducted a *post hoc* exploratory analysis where I combined the top model (minimum AIC_c) with grazing system parameters, and the global system model, with each site-level parameter in turn, to assess whether adding any site-level covariates resulted in a superior model.

After fitting all models in each set, parameters for each covariate were determined by model-averaging over the set of models including the covariate

(Burnham and Anderson 2002; Burnham and Anderson 2004), and unconditional standard errors were calculated that included model selection variance. Because parameters for grazing systems were deviations from the global mean (intercept), the final parameters presented in figures were estimated from the sum of these two, and the standard error and confidence intervals estimated by summing appropriate variances and covariances of the intercept and model parameters. Likewise, contrasts between parameters (e.g., between different grazing systems) were estimated as the difference between two model averaged parameters, and the unconditional standard error of this difference was also estimated by summing appropriate variances and covariances. Because this is the first study to evaluate effects of a broad variety of grazing systems, I used 90% confidence intervals to avoid Type II statistical error (failing to detect real effects). Confidence intervals that do not include zero indicated that the observed effects (e.g., differences between grazing systems) were consistent across the study sites an estimated $\geq 90\%$ of the time. Therefore, this level of effect is considered biologically important, and is described throughout as a "consistent" difference.

Models for vegetation characteristics and trout biomass. – A similar modeling strategy was used for the response variables that were measured only once at each site. However, each response variable was measured during a single sampling event at each site, and so values were considered independent and random effects were not evaluated. For models of riparian vegetation characteristics (utilization, aboveground biomass, and overhead cover) only grazing system covariates were included. For models of trout biomass, covariates hypothesized to influence trout in addition to

grazing system were wetted channel width, stream gradient, proportion of surface area made up by pool and run habitats, mean July water temperature, the terrestrial and total invertebrate biomass that entered the study site (considered separately), and the proportion of brown trout inhabiting the site (because brown trout grow to larger sizes than brook trout). Additionally, two variables were used to account for the spatial context of study sites: 1) the product of the total length of stream under consistent management (km) and the shortest distance from the study site to a change in grazing management (km), and 2) the distance from the study site to the nearest confluence with a stream of equal or higher stream order. All models for trout biomass were fit and compared in one model set.

Results

Riparian Vegetation

Utilization of herbaceous vegetation was greatest at SLG sites and decreased with both increasing management (SLG to IRG) and exclusion of cattle from riparian areas (WO sites). On average, utilization of herbaceous vegetation was 30%, which represents the intercept common to all models (Table 2). Sites managed for SLG had 3.3 times the total percent utilization of herbaceous vegetation measured at sites managed for IRG, and 6.5 times that at WO sites (Figure 2). Non-overlapping 90% CI indicated these two differences were consistent throughout the study region. Other differences were not consistent owing to high variability among sites within each grazing system. At two SLG sites, exclosures were constructed after about three weeks of grazing, which

makes these estimates conservative (i.e., had the exclosures been built earlier, utilization would have been even higher).

Sites managed for rotational and WO grazing tended to have more riparian vegetation than sites managed for SL grazing, and this pattern was most obvious for the percent overhead vegetative cover. On average, sites had 135 g/m² of aboveground herbaceous biomass and 55% overhead vegetative cover (Table 3). Sites managed for either rotational or WO grazing had, on average, 3.1 times the percentage of overhead cover measured at sites managed for SLG (Figure 3a), and these differences were consistent throughout the study region. Woody vegetation was the predominant vegetation functional group contributing to overhead cover at all sites, although tall grasses and forbs contributed about 5-10% of the overhead cover at IRG and WO sites. Sites managed for IRG also had, on average, 2.9 times the aboveground herbaceous biomass of sites managed for SL grazing, and 1.8 times that at sites managed for SRG (Figure 3b). In contrast, there was no evidence that sites managed for rotational grazing differed in these vegetation characteristics from those grazed by wildlife only.

Overall, there were small differences among vegetation communities at sites under each of the four types of grazing management, but these were generally inconsistent owing to high variability among study sites. On average, green vegetative cover was highest at sites managed for SLG (78%), lowest at WO sites (63%), and intermediate at sites managed for SRG (66%) and IRG (71%; Table 4). In contrast, the amount of ground covered by plant litter was higher at SRG, IRG, and WO sites (average = 22%) than at SLG sites (14%). In general, forbs accounted for more vegetative ground

cover (range: 23 – 31%) than other functional groups, except at IRG sites where grasses accounted for 33% and were more abundant than forbs. Woody vegetation provide the least percentage of ground cover (range: 9 – 15%) and also tended to be the most variable, although these estimates do not account for overhead cover contributed by woody vegetation that was not rooted in the sample plots. White clover (see Table 4 for scientific names), dandelion, field horsetail, and wild strawberry were the most common forbs at sites grazed by cattle. The most common grasses at sites grazed by cattle were tufted hairgrass, Kentucky bluegrass, timothy, sandberg bluegrass, fowl bluegrass, and beaked sedge. In contrast, at WO sites white clover and cow parsnip were relatively common forbs and tufted hairgrass, timothy, and fowl bluegrass were relatively common grasses, but in general there were fewer species that contributed $\geq 2\%$ to the ground cover at WO sites than for the other grazing systems. Willows were the most common woody vegetation at all sites.

Falling Invertebrate Input

Terrestrial invertebrate biomass falling into streams during July and August 2007 was greatest at SRG and WO sites, and lowest at SLG sites. Terrestrial invertebrate biomass entering streams was similar during July and August 2007, so the data were pooled. On average, sites received $25.0 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ input of terrestrial invertebrate biomass (estimate back-transformed from Table 5). Sites managed for SRG received, on average, 5.4 times the invertebrate biomass measured at SLG sites, and 3.0 times that at sites managed for IRG (Figure 4). Sites managed for WO received 3.1 times the

invertebrate biomass as SLG sites, but no consistent differences could be detected compared to sites managed for either type of rotational grazing. Twelve orders of terrestrial invertebrates were collected in common among sites managed for all four grazing systems, whereas Orthoptera were collected only at sites managed for rotational grazing. Averaged across all the study sites, Diptera (34%), Heteroptera (17%), Lepidoptera (14%, adults and larvae combined), Coleoptera (12%), Hymenoptera (9%), and Homoptera (8%, Auchenorrhyncha and Sternorrhyncha combined) accounted for 94% of terrestrial invertebrate biomass entering streams (Appendix 3).

In contrast to terrestrial invertebrates, the input of adult aquatic insects was variable among grazing systems, but was greater during July than August 2007. In general, sites received 4.0 times the biomass of adult aquatic insects during July (average input = $26.1 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, SE = 6.9) as August ($6.5 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, SE = 0.89), and this difference was consistent among all grazing systems. In contrast, the biomass of adult aquatic insects falling into streams during summer 2007 did not consistently differ among grazing systems, owing to high variability among sites during July and low levels of input across all sites during August. However, during July sites managed for SLG ($12.9 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, SE = 7.14) or SRG ($17.5 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, SE = 9.61) tended to receive less adult aquatic insect biomass than sites managed for either IRG ($30.7 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, SE = 15.08) or WO ($43.4 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, SE = 27.54). Overall, the most common adult aquatic insects found entering streams were Trichoptera, Chironomidae, Ephemeroptera, Ceratopogonidae, Tipulidae, and Coleoptera (Appendix 4).

Continuous site variables, in general, performed poorly in explaining variability in the biomass of terrestrial invertebrates entering streams. On average, terrestrial input was less in wider streams (Table 5), whereas the three vegetation characteristics measured had small and inconsistent effects. Comparison between the best-approximating model constructed of system versus site covariates using an AIC_c evidence ratio (Burnham and Anderson 2002), indicated that there was 52 times more support for the best model with only grazing system covariates.

Invertebrate Biomass in Trout Diets

During both July and August 2007, trout at sites managed for SRG had more terrestrial invertebrate biomass in their diets than trout at sites under other grazing systems, and this difference was consistent during August (Figure 5A). In general, the biomass of terrestrial invertebrates in trout diets increased between July and August at SRG and WO sites, whereas it remained constant at SLG sites and decreased at IRG sites. These differences were consistent, based on the importance of the model that included a grazing system by month interaction (AIC_c model weight = 99.4%, Table 6). During July, trout at SRG sites had 7.4 times the biomass of terrestrial prey as those at WO sites. Differences between SRG and SLG or IRG were not consistent even though they were 2-3 times, due to high variability among sites. Differences among grazing systems were greater in August, when fish at SRG sites had, on average, 4.7 times the terrestrial invertebrate prey in their stomachs as trout at SLG sites, 15.2 times that at IRG sites, and 5.2 times that at WO sites. On average, terrestrial invertebrate prey made up 31% of

the biomass in trout diets during July, and 43% in August (range 21% [IRG July] – 52% [SRG August]). In general, the trout sampled (length range: 105 – 365 mm) consumed few vertebrate prey items. Only 23 of 507 diets collected (4.5%) contained vertebrate prey remains. Small fish, primarily salmonids, cyprinids (minnows), and catostomids (suckers), were the most prevalent, but small mammals and amphibians were also found (10% of all vertebrate prey items).

In contrast to terrestrial invertebrates, trout at sites under all grazing systems had similar amounts of aquatic invertebrate biomass in their diets, but had more during July than August (Figure 5B). Of the biomass of aquatic invertebrates, on average, 42% was adult aquatic insects, 41% was immature and pupating macroinvertebrates, and 17% was other aquatic invertebrates (e.g., snails, bivalves, and annelids). On average, trout consumed 1.8 times more aquatic invertebrate biomass during July than August 2007 (Table 7), but fish at IRG sites had 3.3 times more aquatic invertebrate biomass in their diet during July than August (i.e., the model incorporating a grazing system x month interaction ranked highest with 43% of the AIC_c weight). During July, trout diets at sites under all grazing systems had similar amounts of aquatic invertebrate biomass. Although during August fish at sites managed for IRG tended to have the least aquatic invertebrate biomass in their diets, differences among grazing systems were not consistent.

As for invertebrate input, models constructed of site-level covariates performed poorly in explaining variability in the biomass of terrestrial invertebrates in trout diets, in general. Overall, there was >2500 times more support, based on an AIC_c evidence

ratio, for the best system model than any model that included site covariates (based on $\Delta AIC_c \geq 15.6$). However, adding vegetation and stream width parameters to the best model constructed of grazing system parameters resulted in models < 2 AICc units from this top model, indicating that these parameters may have been weakly associated with the biomass of aquatic invertebrates in trout diets. Nevertheless, large standard errors associated with these parameter estimates suggest that the predictive power of these models is small (Table 6).

There was considerable variation in the biomass of terrestrial and aquatic invertebrates in diets among individual fish, and part of this could be explained by trout species and fish length. In general, rainbow and cutthroat trout (hereafter ONCH) and brook (BKT) tended to have greater invertebrate biomass (both terrestrial and aquatic) in their diet than brown trout (BNT) of similar size (Figure 6, Table 8). On average, ONCH had 57.8 mg of terrestrial invertebrate biomass (making up 52% to their diet), whereas BKT had 31.2 mg (44%) and BNT had 19.1 mg (30%). Additionally, the invertebrate biomass in trout diets increased with relative fish length for both terrestrial and aquatic prey, although the relative length of BNT had little effect on the biomass of terrestrial prey in their diets.

Trout Density and Biomass Estimates

Density and biomass of adult trout less than 350 mm was greatest at SRG and IRG sites, but these differences were not consistent due to high variability among sites within grazing regimes. In general, biomass of trout less than 350 mm varied

considerably both among sites under the same grazing system (average CV among grazing systems = 0.36) and among different grazing systems. Trout biomass at sites managed for SRG and IRG were, on average, 1.7 and 1.5 times that at sites under SLG, but these differences were not consistent (Figure 7). Furthermore, trout biomass at sites receiving no livestock grazing (WO) tended to be lower than at sites grazed by cattle. However, these results were strongly influenced by low trout abundance at Grizzly Creek, a site adjacent to heavily grazed reaches upstream and downstream. Trout density under the different grazing systems showed a similar pattern as trout biomass, but tended to be even more variable (average CV among grazing systems = 0.41). The trout in Floyd Creek (an IRG site) had migrated out of Steamboat Lake to spawn and were not resident fish, so this site was excluded. Large trout (> 350 mm), mostly brown trout, were also excluded because they tend to be mobile among different reaches (Clapp et al. 1990; Young et al. 1997b), and influenced estimates of total trout biomass. Large trout were present at 10 of 15 sites and contributed, on average, 3% (SE = 1.1%) of the biomass, but more at SLG sites where the majority of trout were small.

Incorporating site characteristics as covariates failed to improve model fit, although incorporating covariates for stream temperature, the proportion of brown trout, and average input of terrestrial invertebrate biomass all produced models with at least 5% AIC_c model weight, and some with $\Delta\text{AIC}_c \leq 1.9$. Similarly, incorporating spatial covariates for the amount of potential habitat under similar grazing management or distance to the confluence with an equal or larger sized stream produced models with

$\Delta AICc \leq 3.7$. In general, average summer water temperature (range: 10.9 – 18.4 °C), proportion of brown trout (range: 0 – 1), and terrestrial invertebrate input (range: 3.3 – 99.8 mg • m⁻² • day⁻¹) had positive effects on fish biomass, although 90% CI on these parameters overlapped zero substantially.

Discussion

Overall, rotational grazing management (either simple or intensive) usually resulted in greater aboveground vegetation biomass and more overhead vegetative cover, greater inputs of terrestrial invertebrates, greater biomass of terrestrial invertebrate prey in trout diets, and more trout biomass than traditional season-long grazing. Furthermore, sites managed for SLG usually supported the lowest levels of these response variables of all the grazing systems I evaluated. However, these differences were frequently inconsistent owing to high variability, especially for trout diets and biomass. Furthermore, riparian vegetation and terrestrial invertebrates entering streams and in trout diets at sites managed for rotational grazing were similar to sites with wildlife grazing only (i.e., livestock were excluded). The input of terrestrial invertebrates, and their biomass in trout diets, was greater than initially hypothesized at sites managed for SRG relative to the other types of grazing management, whereas sites managed for IRG had unexpectedly low levels of both response variables. The results presented here, and those reported by Saunders and Fausch (2007), indicate that rotational grazing systems can be effective for maintaining levels of terrestrial

invertebrate inputs necessary to support trout, but that the factors influencing the effect of riparian grazing on these subsidies are complex and highly variable.

Riparian Vegetation

In general, grazing pressure, measured as percent utilization, decreased with increasing management intensity, and was lowest at sites managed for wildlife grazing only. Sites where cattle grazed throughout a 120-d season (SLG) had both the highest percent utilization values and lowest aboveground vegetation biomass and vertical vegetation structure, measured as percent overhead cover. Saunders and Fausch (2007) reported similar differences for riparian areas managed for high-density short-duration (a type of intensive rotational grazing) versus season-long grazing in west central Wyoming. These consistent results indicate that rotational grazing management, when applied to riparian areas which typically have longer periods favorable to plant growth than uplands, results in both greater herbaceous vegetation biomass and more complex vegetation communities than season-long grazing.

Differences in utilization of herbaceous vegetation, and conversely the remaining biomass aboveground, among sites grazed by cattle resulted from different periods of grazing (duration), different stocking rates (intensity), different vegetation regrowth after cattle were removed (timing, which could not be controlled in this study), and different historical grazing management. Under IRG in particular, vegetation had a higher potential for regrowth because grazing bouts were shorter, totaling about 20 d. In contrast, under SLG, any regrowth was likely to be regrazed later in the summer when

upland vegetation dried and cattle focused on riparian areas. Greater vegetation biomass and vertical structure at more intensively managed sites likely provides more food and cover for terrestrial invertebrates, thereby supporting greater densities. A greater variety of common plant species may also support a greater diversity of invertebrate species (Morris 2000; Soderstrom et al. 2001; Zurbrugg and Frank 2006). Additionally, increased structural complexity increases the probability that terrestrial invertebrates, and recently emerged aquatic insects, fall into streams (Wipfli 1997; Baxter et al. 2005; Saunders and Fausch 2007).

High variability in the biomass of aboveground vegetation among sites within grazing systems also may have resulted from site-specific grazing management, or variation in vegetation communities throughout the study area. Additionally, study sites were distributed over a large area, so more variation could be introduced by different regional weather patterns, annual precipitation, and vegetation communities. Despite these two factors that increased variation and limited the ability to detect differences among grazing systems, two clear patterns were that vegetation biomass and structural complexity increased with increasing management intensity.

Invertebrate Input

Overall, differences in the biomass of invertebrates entering streams under different grazing management systems were greatest during August and driven more by inputs of terrestrial invertebrates than aquatic invertebrates. In general, sites managed for rotational grazing (both SRG and IRG) received about two to five times more

terrestrial invertebrate biomass than sites managed for SLG, although pairwise differences between different grazing systems were frequently inconsistent owing to high variability within grazing systems. Nevertheless, this pattern is consistent with that reported by Saunders and Fausch (2007) for rangeland streams managed under an intensive rotational grazing system, which received 2.3 times more input of terrestrial invertebrates than sites under season-long grazing. Finally, the biomass of terrestrial invertebrates entering streams grazed only by wildlife was 3.1 times that at SLG sites, but no consistent differences could be detected compared to rotational grazing.

One paradox was that sites managed under intensive rotational grazing, on average, had the highest aboveground vegetation biomass and overhead cover of all grazing systems, yet received low levels of invertebrate input relative to either SRG or WO sites. One reason may be that simple metrics of aboveground vegetation production and stream-side vegetation height are insufficient to predict invertebrate inputs from riparian areas to streams. This argument is strengthened by the poor performance of site-level variables in predicting terrestrial invertebrate input. In contrast, invertebrate subsidies may depend on particular attributes of the riparian vegetation, not simply the absolute amount. A second reason is that the flux of invertebrates to streams is likely to be highly variable (Kawaguchi and Nakano 2001; Nakano and Murakami 2001; Saunders and Fausch, unpublished data), both through time and spatially, owing to local weather, insect phenology, and their interaction, all of which drive insect development and delivery to streams.

Comparisons with published literature show that streams in northern Colorado received similar amounts of terrestrial invertebrate subsidies as streams in other regions. Summer inputs of terrestrial invertebrates to northern Colorado rangeland streams ($25 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) were less than observed in similar-sized streams in eastern U.S. deciduous forests (ca. $145\text{--}450 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$; Cloe and Garman 1996), but were similar to those in Scotland (ca. $25\text{--}30 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$; Bridcut 2000) and a deciduous forest in northern Japan during a cool wet year (ca. $40 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$; Baxter et al. 2005). Furthermore, the terrestrial invertebrate input entering grassland streams in northern Colorado was similar to that measured for a grassland reach in Japan ($30 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$; Kawaguchi and Nakano 2001) and Wyoming (ca. $20\text{--}46 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$; estimated from data in Saunders and Fausch 2007, using wet-weight:dry-weight regression for invertebrate orders [Kawaguchi and Nakano 2001, C.V. Baxter unpublished data]), but greater than grazed and ungrazed grassland streams in New Zealand (ca. $4 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$; Edwards and Huryn 1995, 1996). In fact, rangeland streams in northern Colorado under all grazing systems received 2.7 to 14.7 times more terrestrial invertebrate biomass than streams grazed by livestock in New Zealand (average input to pasture streams reported by Edwards and Huryn 1995, 1996).

These results indicate that terrestrial invertebrate prey are as important a resource for salmonids in western U.S. grassland streams as in many other regions worldwide, but that levels may vary considerably in grasslands of semi-arid regions like Colorado and New Zealand. Moreover, the overall importance of this resource to trout foraging, growth, and density has been amply demonstrated in regions with similar

levels of inputs through both comparative studies (Wipfli 1997; Dineen et al. 2007; Sweka and Hartman 2008) and experiments (Kawaguchi and Nakano 2001; Kawaguchi et al. 2003; Baxter et al. 2004; 2007; see Fausch et al. 2010 for review).

Fish Diets

Overall, terrestrial invertebrates contributed 30 – 40% to the biomass of invertebrate prey in trout diets, but trout diets were highly variable during summer 2007 both among sites under the same grazing management and among trout collected from the same stream. The biomass of terrestrial invertebrates in trout diets generally reflected the biomass of terrestrials entering streams, in that fish at sites managed for SRG had more terrestrial invertebrate biomass in their diets than fish at sites under the other types of grazing management. However, trout at IRG and WO sites had less terrestrial invertebrate biomass in their diets, relative to fish at SLG sites, than would have been expected solely based on the amount of terrestrial invertebrates entering these sites. In contrast, there was more aquatic invertebrate biomass (including both adult and larval aquatic insects) in trout diets during July than August, as would be expected based on the early summer emergence peak characteristic of many taxa, but there were no consistent differences in diets among sites under different grazing management. On average, 42% of the aquatic invertebrate biomass in trout diets (24% of the total invertebrate biomass) was contributed by adult aquatic insects, but these may also rely heavily on streamside vegetation for shelter and resting sites (Wallace et al. 1997; Huryn et al. 2008). Although the input of terrestrial invertebrates and adult

aquatic insects were similar in Colorado and Wyoming, trout sampled in Colorado during summer 2007 tended to have more invertebrate biomass their diets than trout sampled in Wyoming rangeland streams in 2004 and 2005 (ca. 20 – 46 mg•fish⁻¹ terrestrial, 8-23 mg•fish⁻¹ aquatic invertebrate biomass; estimated from Saunders and Fausch 2007).

It is possible that the invertebrate biomass in trout diets as a function of riparian grazing management may have been influenced by the spatial arrangement of sample sites used in this study, or different composition of salmonid communities among sites with different grazing management. Weather conditions and insect phenology are likely to be spatially autocorrelated among sites in close proximity and could result in similarly low invertebrate availability at these sites by chance alone. For example, owing to the more intensive nature of intensive rotational grazing systems and thus less frequent use of this grazing system relative to both SLG and SRG, four of the five IRG sites were located in a relatively small area in the North Platte River drainage, relative to the overall distribution of study sites. These sites were sampled during 12-15 August 2007, which was a relatively short period of cool and calm weather that could have resulted in reduced terrestrial prey availability at four of the five IRG sites. Alternatively, sampling of different trout species at sites may confound the ability to estimate the effects of riparian grazing management on use of terrestrial invertebrates by trout. For example, diet samples from the same four sites under IRG management mentioned above were collected from brown trout only (which use terrestrial invertebrate prey less than brook trout or *Oncorhynchus* spp.; Figure 6). In contrast, diet samples from sites under the three other types of grazing management were collected primarily from brook and

brown trout, and samples from rainbow and cutthroat trout were also collected at sites under WO and SRG management. Although the models presented here account for differences in diets among species, inconsistencies in trout assemblages among sites under different grazing management limit the extent to which species differences are able to be held constant statistically while evaluating the effects grazing management. Ideally, sites would be selected with the same species (or similar trout communities) under different grazing management to account for their different foraging behaviors, but this was impossible owing to the limited number of riparian areas under IRG and WO management that were suitable for study.

High variability in the biomass of prey in trout diets and the composition of trout diets limited my ability to detect consistent differences among grazing systems for all but the most extreme difference (e.g., > 4.5 times different). High variability in trout diets, especially in terrestrial prey, is common (Hunt 1975; Saunders and Fausch 2007; Utz and Hartman 2007), and likely results from variability in prey inputs owing to insect phenology, spatial variability of streamside vegetation, and local weather. Furthermore, fish dominance hierarchies typically allow a few large fish to usurp most terrestrial prey, which are large and conspicuous, while smaller fish are excluded from optimal foraging positions and subsist on drifting aquatic invertebrates or those they pick them from the substrate (Nakano and Furukawa-Tanaka 1994; Nakano 1995; Fausch et al. 1997).

Furthermore, age-1+ salmonids tend to have more terrestrial invertebrate biomass in their diets than age-0 individuals (Furukawa-Tanaka 1985; Dineen et al. 2007), although

this may be owing to gape-limitation or lower foraging success of age-0 fish (Gustafsson et al. 2010).

The data reported here show that the largest fish occurring at each study site tended to consume more terrestrial invertebrates than smaller fish, for all species present, but that this relationship was strongest for brook trout, and rainbow and cutthroat trout (the last two pooled for analysis owing to small sample size). These results suggest that larger trout, particularly brook, rainbow and cutthroat, were selectively foraging on terrestrial invertebrate prey, which tend to be larger than aquatic prey (Furukawa-Tanaka 1985; Nakano et al. 1999a). In contrast, brown trout appeared to forage primarily on aquatic prey items, which contributed 70% to their diets. Additionally, in northern Colorado some individual fish of all trout species fed primarily on terrestrial invertebrates, while others ate almost exclusively aquatic prey. Many were cased caddisfly larvae and snails which rarely enter the drift (W.C. Saunders, personal observation), which has also been reported by Furukawa-Tanaka (1985) and Lepori et al. (*In review*). These patterns suggest that fish occupying the same habitat may use different prey resources or forage differently, resulting in the high variability in invertebrate biomass in trout diets such as I found. However, these diverse foraging strategies also may be a mechanism by which streams receiving substantial terrestrial invertebrate inputs support healthy trout populations.

Trout Density and Biomass

Overall, fish density and biomass tended to be higher at sites managed for either type of rotational grazing system, although high variability among sites within grazing

systems rendered these differences inconsistent. In general, the higher biomass of trout at sites under rotational management than SLG sites was similar to differences reported by Saunders and Fausch (2007), although the average fish biomass was greater in Colorado and differences between grazing systems were smaller. The high variability among sites within grazing systems suggests that either fish populations were able to compensate for local effects of grazing, or larger-scale processes also influenced fish populations and reduced local effects. Research evaluating the effects of livestock exclosures on fish populations has produced inconsistent results (Platts 1991; Sarr 2002), probably because many livestock exclosures are too small to provide the diversity of habitats necessary for salmonids to complete their life history (Fausch et al. 2002; Bayley and Li 2008). This was especially likely for wildlife-only grazing exclosures, which were difficult to find, and often either located on small headwater streams or bounded on both ends by season-long grazing.

These spatial factors are likely most important for large trout, which tend to be highly mobile and need large home ranges to find adequate prey resources (typically other fish) and critical habitats (Fausch and Young 1995; Young et al. 1997b; Young 1999). Therefore, these fish are less likely to depend on invertebrates at the reach scale than specific food and habitat resources that are dispersed across the riverscape (Fausch et al. 2002). As a result, these large trout may be found only temporarily in a given habitat while they use specific resources there, which is why I did not include them in the fish biomass estimates.

Conclusions

The data presented here indicate that differences in streamside vegetation in riparian areas under different grazing management resulted in different invertebrate inputs, and influenced trout diets and trout biomass to varying degrees. However, high variability among sites within grazing systems limited the ability to detect consistent differences among grazing systems. Variability in the availability and importance of terrestrial invertebrates for trout populations may result from inherent natural variability in the processes by which riparian vegetation and local weather patterns influence invertebrate populations and the flux of invertebrates to streams, factors governing foraging behavior and prey selection by trout, and the diverse habitat and life history requirements of trout populations. This variability is reflected in the increase in the average coefficient of variation (CV) associated with response variables measuring increasingly indirect effects of grazing on trout. These CVs were smaller for the direct effect of grazing on riparian vegetation ($\overline{CV} = 0.22$ for all vegetation measurements) and the biomass of terrestrial invertebrates entering streams ($\overline{CV} = 0.21$) than for the biomass of terrestrial invertebrates in fish diets ($\overline{CV} = 0.37$) or trout biomass ($\overline{CV} = 0.37$).

Despite this variability, the results presented here, and those of Saunders and Fausch (2007), show that rotational grazing systems support more riparian vegetation, and can increase terrestrial invertebrate inputs to streams and the biomass of these prey in trout diets, relative to sites managed for season-long grazing. However, it is unlikely that a single type of grazing management will be universally best suited for

maintaining terrestrial subsidies for trout. For example, the more consistent results reported by Saunders and Fausch (2007) indicate that in more arid rangelands such as those studied in Wyoming (which average 355 mm annual precipitation and 17°C summer air temperature; data from weather stations near Lander, WY, data obtained from NCDC 2010) more intensive grazing management (e.g., intensive rotational grazing) may be necessary to support terrestrial subsidies for trout because growing seasons are shorter and riparian vegetation more sensitive to adequate recovery periods after defoliation. In contrast, in more mesic rangelands, such as those in northern Colorado (475 mm, 11°C summer temperature, data from weather stations near Walden and Steamboat Springs, CO, NCDC 2010), riparian vegetation may support a greater variety of grazing systems, including less management-intensive rotational systems like the SRG I studied. Although in this study only two rotational grazing systems were evaluated, there is a great diversity of rotational systems that operators can tailor to vegetation and conditions in specific pastures. Armed with the knowledge here, specific systems could be designed to favor subsidies for trout. This may be of substantial benefit because trout angling is often an important goal for large ranches in Colorado and elsewhere that attempt to optimize income from both cattle production and angling recreation.

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Table 1. — Characteristics of physical habitat in the 16 study sites in northern Colorado. Data were collected at five sites managed for Intensive Rotational Grazing (IRG), four sites managed under Simple Rotational Grazing (SRG), four sites managed under Season-Long Grazing (SLG), and three sites grazed by Wildlife Only (WO, see text). Mean summer water temperature was calculated from hourly water temperatures recorded during July and August 2007. Trout species present (BNT: brown trout, BKT: brook trout, RBT: rainbow trout, CUT: cutthroat trout) are listed in order of abundance.

Site name	Location	Land ownership ^a	Bankfull width (m)	Mean summer temperature (°C)	Trout species	Cattle Use
Intensive Rotational Grazing						
Lower Canadian	Lat: 40°37'58" N Lon: 106°01'45" W	Private	5.4	^b	BNT, RBT	early June (10 d) Sep. (10 d)
Upper Canadian	Lat: 40°38'32" N Lon: 106°02'21" W	Private	5.2	16.3	BNT	mid July (17 d)
Michigan	Lat: 40°37'42" N Lon: 106°06'27" W	Private	13.0	16.4	BNT, RBT	Sep. (21 d)
Illinois	Lat: 40°32'01" N Lon: 106°13'22" W	Private	8.3	17.5	BNT	late July (19 d)
Floyd	Lat: 40°47'53" N Lon: 106°59'16" W	Private	2.0	15.7	BKT, RBT, CUT	Mid June, July, Aug. (6 d each)
Simple Rotational Grazing						
Arapaho	Lat: 40°24'32" N Lon: 106°23'28" W	USFS	3.1	^b	BNT	July – mid Aug. (42 d)
Northern Rock	Lat: 40°23'58" N Lon: 106°12'47" W	USFS	3.0	11.2	BKT	mid July – Aug (40 d)
Southern Rock	Lat: 40°02'10" N Lon: 106°39'27" W	USFS	6.3	16.6	BNT	Aug. (35 d)
Lower Trout	Lat: 40°16'00" N Lon: 107°03'38" W	Private	6.3	15.3	BNT, BKT, RBT, CUT	June – July (43 d)

Table 1-- continued

Site name	Location	Land ownership ^a	Bankfull width (m)	Mean summer temperature (°C)	Trout species	Cattle Use
Season Long Grazing						
North Fork North Platte	Lat: 40°52'56" N Lon: 106°32'59" W	Private	5.0	15.9	BNT, BKT	June - Oct. (150 d)
Shafer	Lat: 40°51'49" N Lon: 106°33'00" W	Private	4.6	10.5	BNT, BKT	June - Oct. (150 d)
East Fork Troublesome	Lat: 40°11'26" N Lon: 106°13'30" W	USFS	7.3	^b	BNT	1 July - 15 Sep. (77 d)
Newcomb	Lat: 40°35'43" N Lon: 106°36'05" W	USFS	11.2	14.9	BNT, BKT	July - Oct. (123 d)
Wildlife Only						
Hinman	Lat: 40°46'07" N Lon: 106°48'57" W	USFS	6.6	13.5	BKT, RBT	-
Upper Trout	Lat: 40°13'45" N Lon: 106°06'00" W	USFS	6.4	14.1	BKT, CUT	-
Grizzly	Lat: 40°26'10" N Lon: 106°29'00" W	Private	8.5	18.4	BNT	-

^a Sites were on lands owned privately, or by the U.S. Forest Service (USFS) or Bureau of Land Management (BLM).

^b No temperature data were available for 2007.

Table 2. – Model-averaged parameter estimates for models predicting utilization of vegetation (percentage of herbaceous vegetation removed by ungulates) along 16 rangeland streams in northern Colorado managed for season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Parameter standard errors (SE) represent the unconditional standard error, which accounts for both process variance and model selection uncertainty. Cumulative model weight represents the sum of the individual AIC_c model weights for all models including a given parameter. CL = confidence limit.

Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL	Cumulative model weight
Intercept	0.295	0.082	0.159	0.430	^a
SLG	0.276	0.143	0.040	0.511	0.87
SRG	0.043	0.146	-0.197	0.283	0.20
IRG	-0.156	0.115	-0.345	0.034	0.39
WO	-0.222	0.126	-0.429	-0.015	0.54

^a parameter included in all models

Table 3. – Model-averaged parameter estimates for models predicting aboveground biomass of herbaceous vegetation ($\text{g}\cdot\text{m}^{-2}$) and overhead vegetative cover (%) along 16 rangeland streams in northern Colorado managed for season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Unconditional standard errors (SE) are shown for parameter estimates. Cumulative model weight represents the sum of the individual AIC_c model weights for all models including a given parameter. CL = confidence limit.

Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL	Cumulative model weight
Aboveground herbaceous biomass					
Intercept	135.3	16.56	108.0	162.5	^a
SLG	-67.6	26.47	-111.1	-24.0	0.83
SRG	-24.4	34.06	-80.4	31.7	0.25
IRG	76.4	34.80	19.1	133.6	0.97
WO	3.7	44.61	-69.7	77.1	0.16
Overhead vegetative cover					
Intercept	55.0	7.00	43.5	66.5	^a
SLG	-35.0	15.72	-60.8	-9.1	0.99
SRG	11.3	14.80	-13.0	35.7	0.15
IRG	17.2	13.50	-5.1	39.4	0.29
WO	14.1	17.79	-15.2	43.3	0.17

^a parameter included in all models

Table 4. – Mean percentage ground cover of prevalent plant species at study sites along 16 rangeland streams in northern Colorado managed for season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Prevalent species contributed at least 1% to the total ground cover.

Plant taxa	SLG		SRG		IRG		WO	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Total forb cover	31.2	1.06	31.6	3.71	23.0	1.91	26.5	8.79
White clover <i>Trifolium repens</i> L.	8.8	4.87	2.3	1.07	4.1	1.25	3.3	3.24
Dandelion <i>Taraxacum officinale</i> F.H. Wigg.	4.4	1.73	6.1	2.57	4.9	1.15	0.9	0.55
Field horsetail <i>Equisetum arvense</i> L.	1.4	0.95	3.4	2.19	2.1	1.40	1.7	0.85
Wild strawberry <i>Fragaria virginiana</i> Duchesne	2.5	1.40	3.0	1.91	1.3	0.75	0.6	0.28
Cow parsnip <i>Heracleum maximum</i> Bartram	1.3	1.31					3.3	1.89
American vetch <i>Vicia americana</i> Muhl. ex Willd.	0.7	0.43	1.6	0.91	0.7	0.27	0.5	0.47
Canada thistle <i>Cirsium arvense</i> (L.) Scop.	0.9	0.91	0.7	0.28	1.5	0.97		
Western yarrow <i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC.	0.9	0.26	1.5	0.77	0.3	0.25	0.2	0.12
Locoweed <i>Oxytropis lambertii</i> Pursh	0.4	0.24	2.3	2.30				
Bedstraw <i>Galium</i> spp.			0.1	0.11	0.6	0.58	1.3	1.08
Monks head <i>Aconitum columbianum</i> Nutt.			0.1	0.09			1.9	1.90
Total graminoid cover	31.4	3.75	23.2	2.20	33.4	2.77	19.9	4.39
Grasses	14.9	1.74	12.4	4.43	22.2	2.58	12.7	0.51
Tufted hairgrass <i>Deschampsia cespitosa</i> (L.) P. Beauv.	2.6	1.14	2.7	0.59	4.9	2.39	2.2	1.47
Kentucky bluegrass <i>Poa pratensis</i> L.	6.6	2.43	2.8	0.61	2.2	1.35	0.4	0.24
timothy <i>Phleum pratense</i> L.	2.2	1.22	1.0	0.98	4.8	0.79	2.7	1.00
Sandberg bluegrass <i>Poa secunda</i> J. Presl	2.9	2.94	2.8	2.12	3.2	0.82	1.6	0.79
Fowl bluegrass <i>Poa palustris</i> L.	0.5	0.54			0.7	0.46	2.0	1.55
Blue wildrye <i>Elymus glaucus</i> Buckley	0.1	0.11			0.1	0.10	1.9	1.88
Bluejoint Reedgrass <i>Calamagrostis canadensis</i> (Michx.) P. Beauv.			0.8	0.56	1.0	0.75	0.3	0.31

Table 4 – continued.

Plant taxa	SLG		SRG		IRG		WO	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Nuttall's alkaligrass <i>Puccinellia nuttalliana</i> (Schant.) Hitchc.	0.2	0.21			1.2	0.36		
Jones Reedgrass <i>Calamagrostis scopulorum</i> M.E. Jones					1.2	1.25		
Sedges <i>Carex</i> spp.	12.9	3.55	8.9	4.03	10.4	2.55	5.7	2.97
Beaked sedge <i>Carex rostrata</i> Stokes	1.6	1.24	5.6	4.76	8.3	2.54	0.9	0.53
Water sedge <i>Carex aquatilis</i> Wahlenb.			2.0	2.01	0.5	0.52		
Rush <i>Juncus</i> spp.	1.2	0.48	1.0	0.58	0.9	0.52	1.6	1.61
Swordleaf rush <i>Juncus ensifolius</i> Wikstr.			1.0	0.58	0.3	0.34		
Total shrub cover	13.5	4.96	8.6	3.46	13.7	3.09	15.0	6.16
<i>Salix</i> spp.	7.7	4.13	6.1	2.71	11.0	2.49	13.6	5.82
Plainleaf willow <i>Salix planifolia</i> Pursh	2.7	1.85	2.2	0.72	3.4	1.46	0.2	0.15
Booth Willow <i>Salix boothii</i> Dorn	0.1	0.11			0.8	0.77	7.0	7.04
Geyer willow <i>Salix geyeriana</i> Andersson	5.1	4.04	0.7	0.46	1.6	1.12		
Mountain Willow <i>Salix monticola</i> Bebb	0.6	0.56	1.7	1.18	0.6	0.42	0.2	0.18
Whiplash willow <i>Salix lucida</i> Muhl. ssp. <i>lasiandra</i> (Benth.) E. Murray			0.6	0.58	1.7	1.21	4.2	4.22
Alder <i>Alnus incana</i> (L.) Moench			0.6	0.57	1.3	0.75	1.4	0.89
Gooseberry <i>Ribes oxycanthoides</i> L.	1.0	0.86	0.8	0.82	0.1	0.10		
Shrubby cinquefoil <i>Dasiphora fruticosa</i> (L.) Rydb.	1.5	1.06	0.3	0.26				
Wood's rose <i>Rosa woodsii</i> Lindl.	0.1	0.12			1.2	1.25		
Bare Ground	6.6	0.49	12.4	5.00	7.1	2.30	13.4	3.44
Litter	14.4	2.88	21.4	3.54	21.4	1.25	23.5	5.05
Livestock manure	1.2	0.42			0.1	0.07		

Table 5. – Model-averaged parameter estimates for models predicting terrestrial invertebrate input ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) to 16 rangeland streams in northern Colorado managed for either season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Models were constructed with either grazing system or continuous site-level covariates (see text). The parameter estimate for the biomass of terrestrial invertebrate input to sites during August = $-1(\text{July parameter})$. Data were log transformed prior to analysis, so parameter estimates reflect the transformed scale. Unconditional standard errors (SE) are shown for parameter estimates. Cumulative model weight represents the sum of the individual AIC_c model weights for all models including a given parameter. CL = confidence limit.

Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL	Cumulative model weight
Grazing system models					
Intercept	3.218	0.175	2.931	3.506	^a
July	-0.122	0.159	-0.383	0.140	^a
SLG	-0.848	0.258	-1.272	-0.423	0.93
SRG	0.861	0.266	0.423	1.298	0.95
IRG	-0.269	0.257	-0.693	0.154	0.29
WO	0.291	0.331	-0.254	0.836	0.27
Site covariates					
Intercept	2.914	0.755	1.672	4.157	^a
July	-0.122	0.179	-0.416	0.173	^a
overhead cover	0.011	0.009	-0.003	0.026	0.40
wetted width	-0.168	0.076	-0.294	-0.042	0.65
species composition	0.066	0.049	-0.015	0.147	0.64
herbaceous biomass	-0.001	0.025	-0.042	0.040	0.22

^a parameter included in all models

Table 6. – Model-averaged parameter estimates describing site-level variability for models predicting terrestrial invertebrate biomass in trout diets ($\text{mg} \cdot \text{fish}^{-1}$) at 16 rangeland streams in northern Colorado managed for season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. All site-level models were evaluated with a global parameterization at the fish level (among fish variation, see text). Models were constructed with either grazing system or continuous site-level covariates (see text). The parameter estimate for the biomass of terrestrial invertebrates in trout diets during August (including interaction parameters) = $-1(\text{July parameter})$. Data were square root transformed prior to analysis, so parameter estimates reflect the transformed scale. Unconditional standard errors (SE) are shown for parameter estimates. Cumulative model weight represents the sum of the individual AIC_c model weights for all models including a given parameter. CL = confidence limit.

Table 7. Model-averaged parameter estimates describing the variability for models predicting annual insecticide biomass in 1998. Models that included the parameter were evaluated with a χ^2 test of model fit.

Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL	Cumulative model weight
Grazing system models ^a					
Intercept	1.381	1.059	-0.361	3.122	
July	-0.220	1.290	-2.342	1.903	
IRG	3.548	1.338	1.347	5.749	
SLG	-1.769	1.212	-3.762	0.225	
SRG	-1.560	1.452	-3.949	0.829	
WO	-0.454	0.200	-0.782	-0.125	
July × IRG	0.594	0.293	0.112	1.077	
July × SLG	-1.208	0.469	-1.979	-0.436	
July × SRG	1.129	0.281	0.666	1.591	
July × WO	-0.515	0.313	-1.030	-0.001	
Site covariates					
Intercept	2.875	2.931	-1.946	7.697	^b
July	-0.099	0.170	-0.378	0.181	^b
overhead cover	0.045	0.032	-0.008	0.097	0.47
wetted width	-0.313	0.318	-0.835	0.210	0.39
species composition	-0.071	0.133	-0.290	0.148	0.34
herbaceous biomass	-0.082	0.042	-0.151	-0.012	0.61

^a Model averaging was not conducted for grazing system parameters, because the top model including a month by grazing system interaction had 99.4% of the AIC_c model weight.

^b Parameter included in all models

Table 7. – Model-averaged parameter estimates describing site-level variability for models predicting aquatic invertebrate biomass in trout diets ($\text{mg} \cdot \text{fish}^{-1}$) at 16 rangeland streams in northern Colorado managed for season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. All site-level models were evaluated with a global parameterization at the fish level (among fish variation, see text). The parameter estimate for the biomass of terrestrial invertebrates in trout diets during August (including interaction parameters) = $-1(\text{July parameter})$. Data were square root transformed prior to analysis, so parameter estimates reflect the transformed scale. Unconditional standard errors (SE) are shown for parameter estimates. Cumulative model weight represents the sum of the individual AIC_c model weights for all models including a given parameter. CL = confidence limit.

Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL	Cumulative model weight
Intercept	2.114	0.850	0.716	3.512	^a
July	0.940	0.164	0.670	1.209	^a
IRG	0.967	0.747	-0.262	2.197	0.71
SLG	0.820	0.696	-0.324	1.964	0.72
SRG	-0.867	0.685	-1.993	0.259	0.72
WO	-0.929	0.798	-2.242	0.384	0.71
July $\times$ IRG	-0.365	0.397	-1.017	0.288	0.43
July $\times$ SLG	-0.003	0.150	-0.250	0.245	0.43
July $\times$ SRG	0.538	0.489	-0.266	1.343	0.43
July $\times$ WO	-0.179	0.250	-0.590	0.231	0.43

^a parameter included in all models

Table 8. – Model-averaged parameter estimates describing fish-level variability for models predicting terrestrial and aquatic invertebrate biomass in trout diets ($\text{mg} \cdot \text{fish}^{-1}$) at 16 rangeland streams in northern Colorado managed for season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Fish-level models were evaluated with respect to the top ranking system parameterization (see text). Data were square root transformed prior to analysis, so parameter estimates reflect the transformed scale. Unconditional standard errors (SE) are shown for parameter estimates. Cumulative model weight represents the sum of the individual AIC_c model weights for all models including a given parameter. CL = confidence limit.

Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL	Cumulative model weight
Terrestrial invertebrate biomass ^a					
Intercept	-1.566	1.669	-4.311	1.180	
BKT	-2.610	1.637	-5.303	0.084	
BNT	1.981	1.502	-0.491	4.452	
ONCH	1.629	5.473	-7.374	10.632	
r.length	7.464	1.780	4.536	10.391	
BKT $\times$ r.length	3.514	2.035	0.167	6.862	
BNT $\times$ r.length	-4.263	1.863	-7.328	-1.198	
ONCH $\times$ r.length	0.749	7.039	-10.831	12.328	
Aquatic invertebrate biomass					
Intercept	1.580	0.995	-0.057	3.217	^b
BKT	-0.607	0.759	-1.856	0.642	0.44
BNT	0.130	1.316	-2.034	2.295	0.46
ONCH	0.606	1.285	-1.508	2.720	0.91
r.length	5.326	1.381	3.053	7.598	1.00
BKT $\times$ r.length	0.092	0.681	-1.029	1.212	0.15
BNT $\times$ r.length	-1.130	1.659	-3.859	1.600	0.15
ONCH $\times$ r.length	1.038	1.818	-1.953	4.029	0.15

^a Model averaging was not conducted for terrestrial biomass parameters because the model including a species by relative length interaction had 95% of the AIC_c model weight.

^b Parameter included in all models.

Figure 1. — Map of the 16 study sites in northern Colorado. Data were collected at five sites managed for Intensive Rotational Grazing (circles), four sites managed under Simple Rotational Grazing (squares), four sites managed under Season-Long Grazing (triangles), and three sites grazed by Wildlife Only (stars, see text).

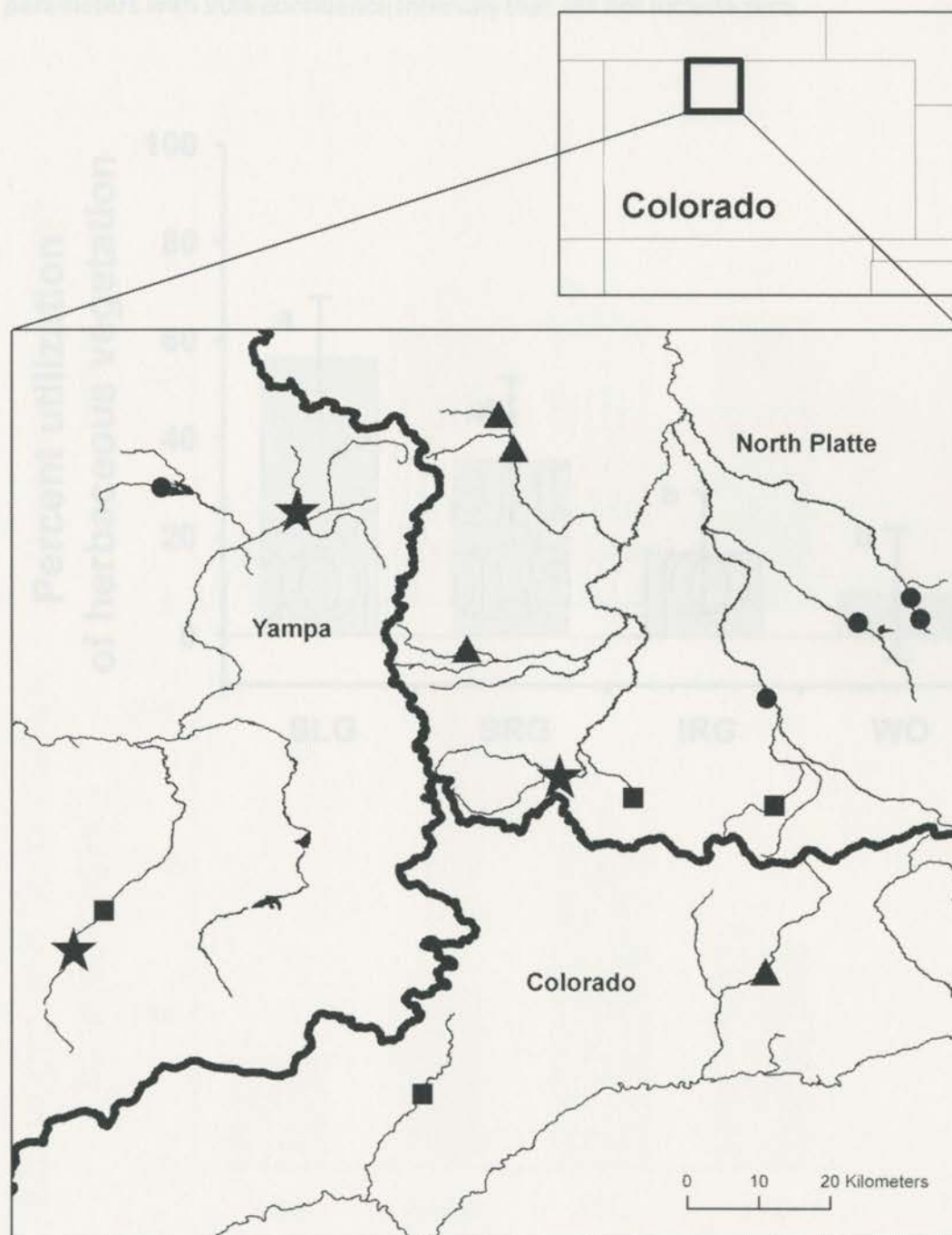


Figure 2. — Predicted average percent utilization of herbaceous riparian vegetation at 15 sites in northern Colorado under season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing (no estimates could be made for one Simple Rotation site, see text). Error bars show $\pm$ SE. Different letters indicate consistent differences between sites, based on mean differences between model parameters with 90% confidence intervals that did not include zero.

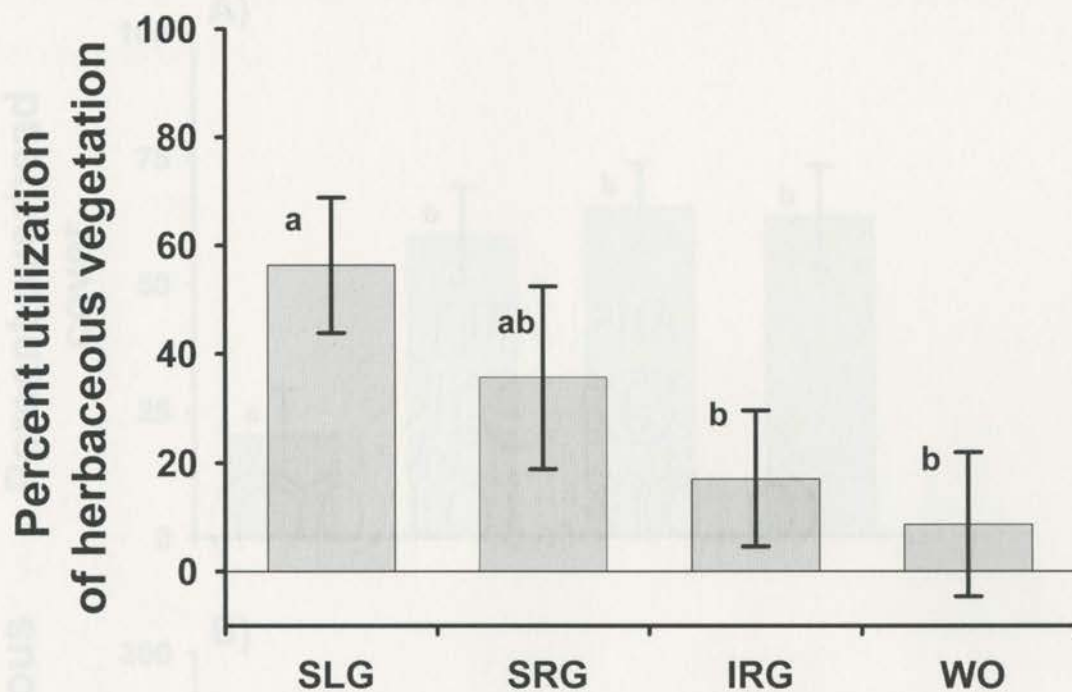


Figure 3. — Predicted average percent overhead vegetative cover (A) and aboveground dry biomass (B) of herbaceous vegetation at 16 riparian sites under season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Error bars show $\pm$ SE. Different letters indicate consistent differences between sites based on the differences between model parameters with 90% confidence intervals that did not include zero. Biomass estimates reflects 64 vegetation clippings.

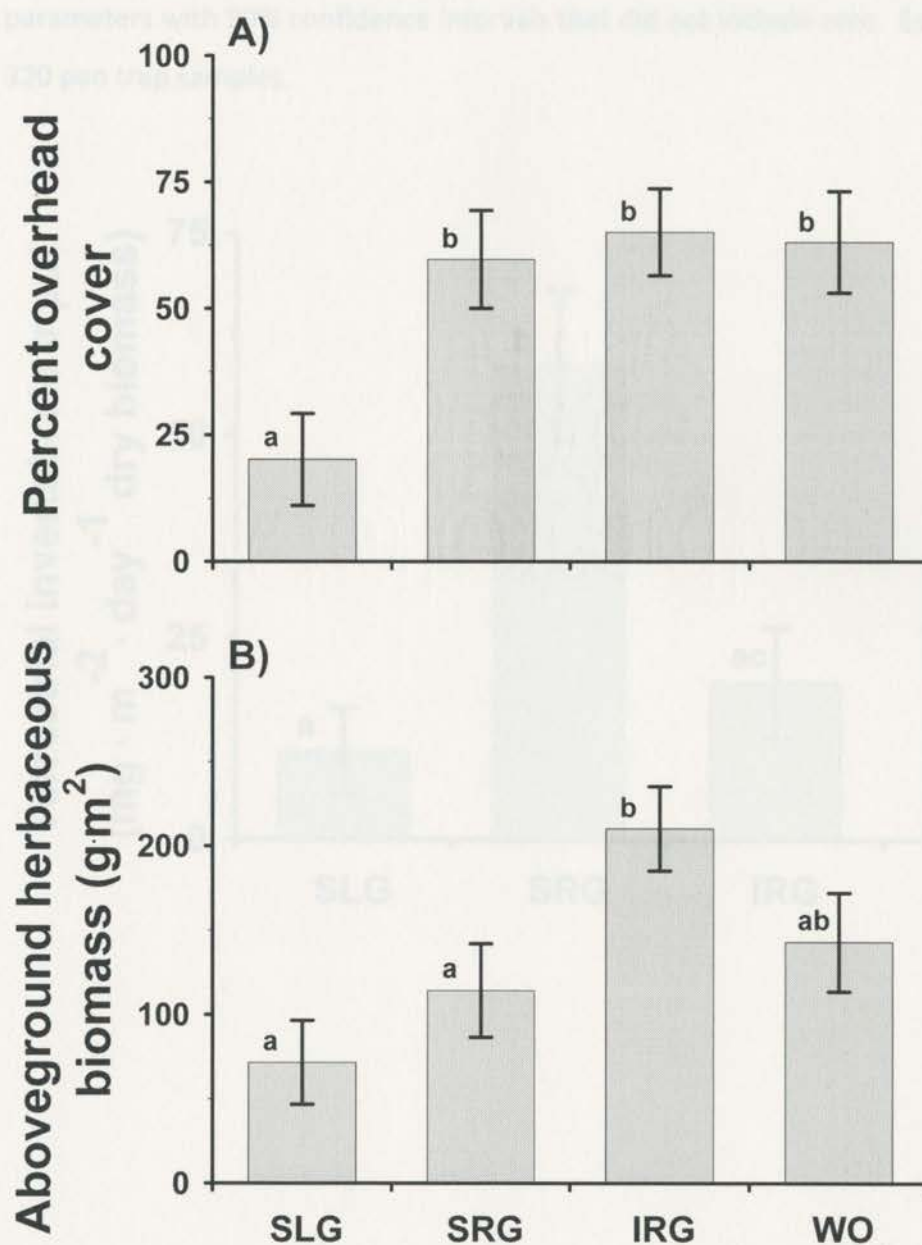


Figure 4. — Predicted average terrestrial invertebrate input to 16 streams in northern Colorado under season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Error bars show ± 1 SE. Values reflect estimates computed using natural log transformed data which were subsequently back-transformed to show the average input of invertebrate biomass on the original (i.e., untransformed) scale. Standard errors were estimated using the Delta Method. Different letters indicate consistent differences between sites based on the differences between model parameters with 90% confidence intervals that did not include zero. Estimates reflect 320 pan trap samples.

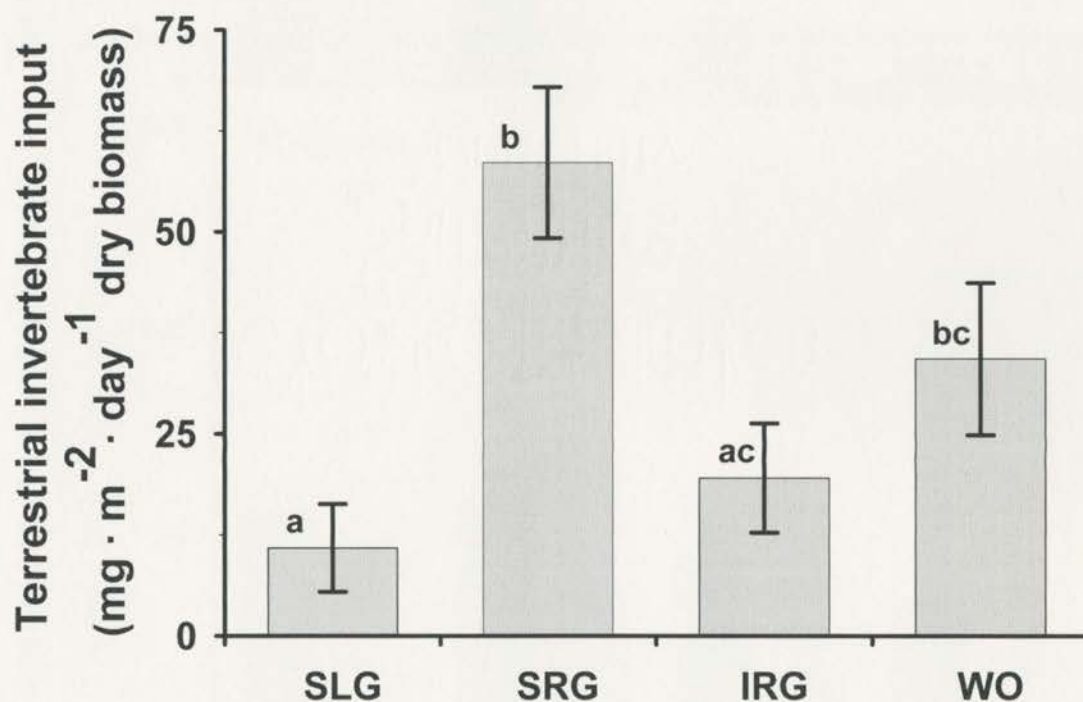




Figure 5. — Predicted average terrestrial (A) and aquatic invertebrate biomass (B) in mid-afternoon trout diets for 16 streams in northern Colorado under season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Data represent invertebrate biomass in the average trout diet (relative length = 0.73) and account for species differences. Error bars show ± 1 SE in both panels, which represents the variation in the amount of invertebrate input among sites within each type of grazing management. Values reflect estimates computed using square-root transformed data which were subsequently back transformed to show the average biomass of invertebrate in trout diets on the original (i.e., untransformed) scale. Standard errors were estimated using the Delta Method (see text). Different letters above estimates indicate consistent differences between different grazing systems, but comparisons are valid only within months (shown by upper and lower case letters). Estimates reflect data collected from 507 trout.

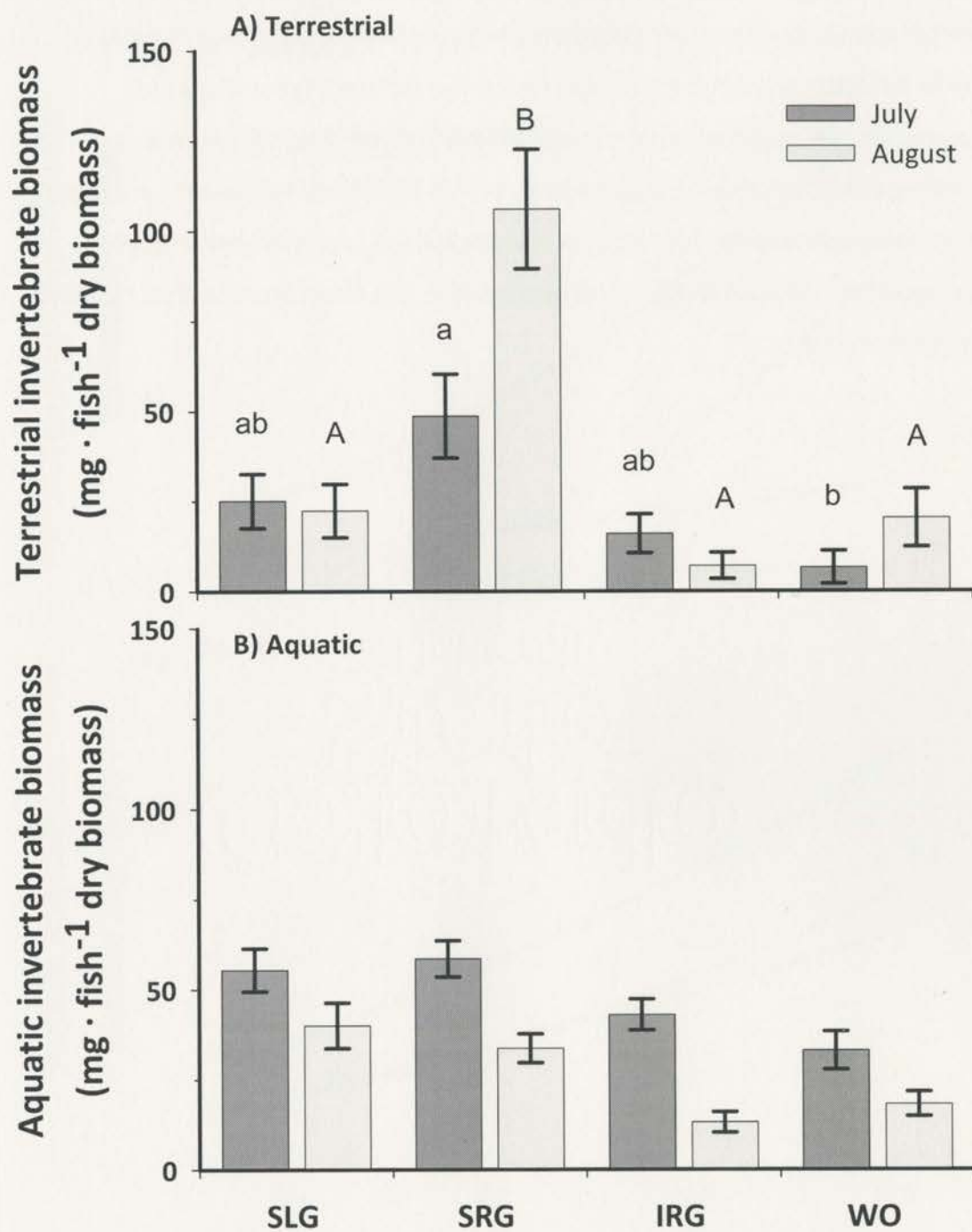




Figure 6. – Relationship between relative fish length (see text) and biomass of (A) terrestrial and (B) aquatic invertebrate prey in trout diets sampled in 16 streams in northern Colorado averaged across sites under four different types of grazing management. Values reflect model predictions estimated using square-root transformed data, which were subsequently back-transformed to show the average biomass of invertebrate in trout diets on the original (i.e., untransformed) scale. Estimates reflect data collected on 318 brown trout, 151 brook trout, and 38 rainbow and cutthroat trout.

Figure 7 — Predicted average trout biomass for Age-2 and older fish >350 mm
 presented at 15 streams in northern Colorado under various long
 single rotational (SLO), intensive rotational (ISO), or wildlife only grazing
 systems. The ISO system is considered as a buffer system between
 the SLO and WO systems. The SLO and WO systems are considered as
 the extremes under a given grazing system.

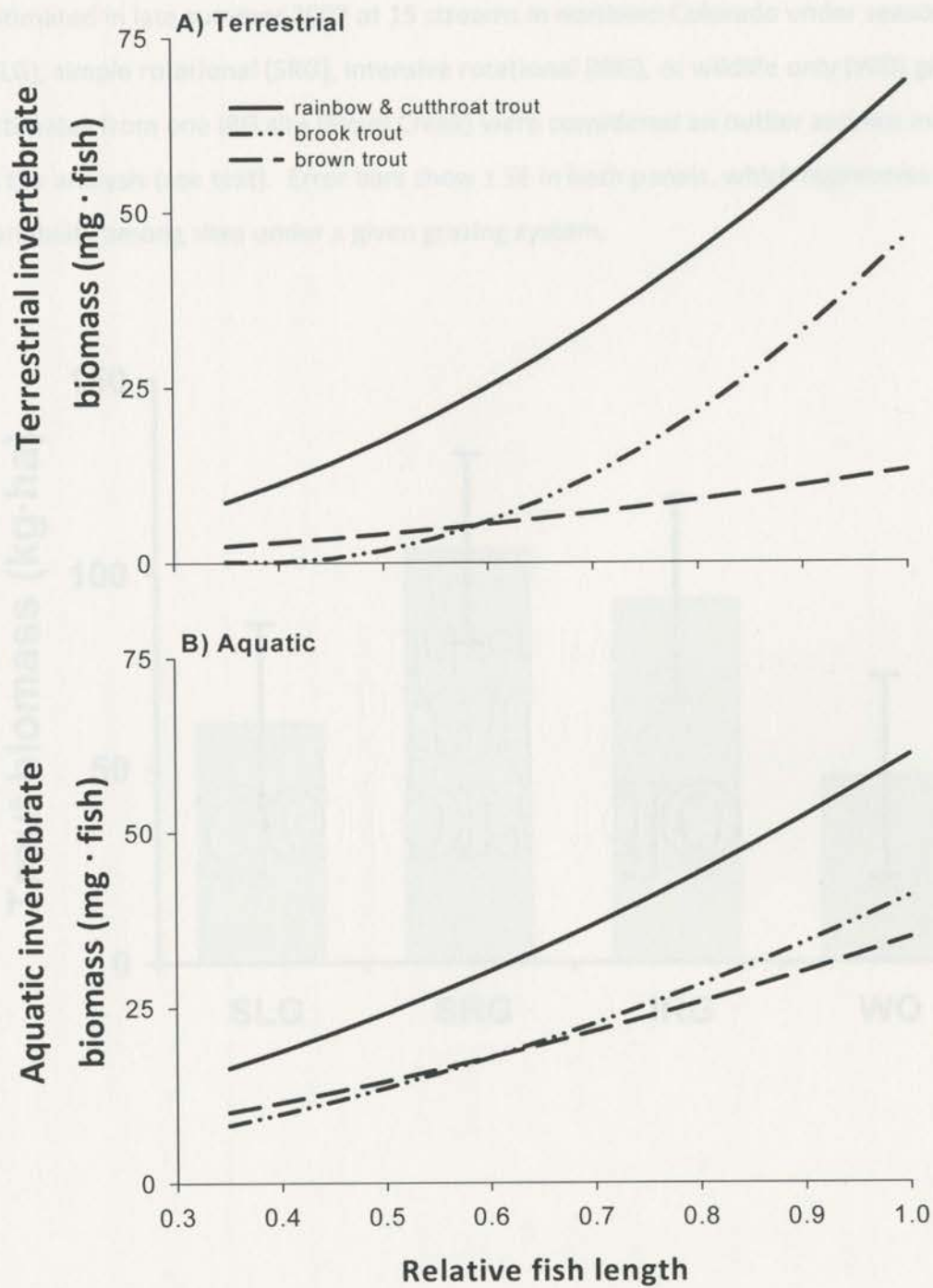
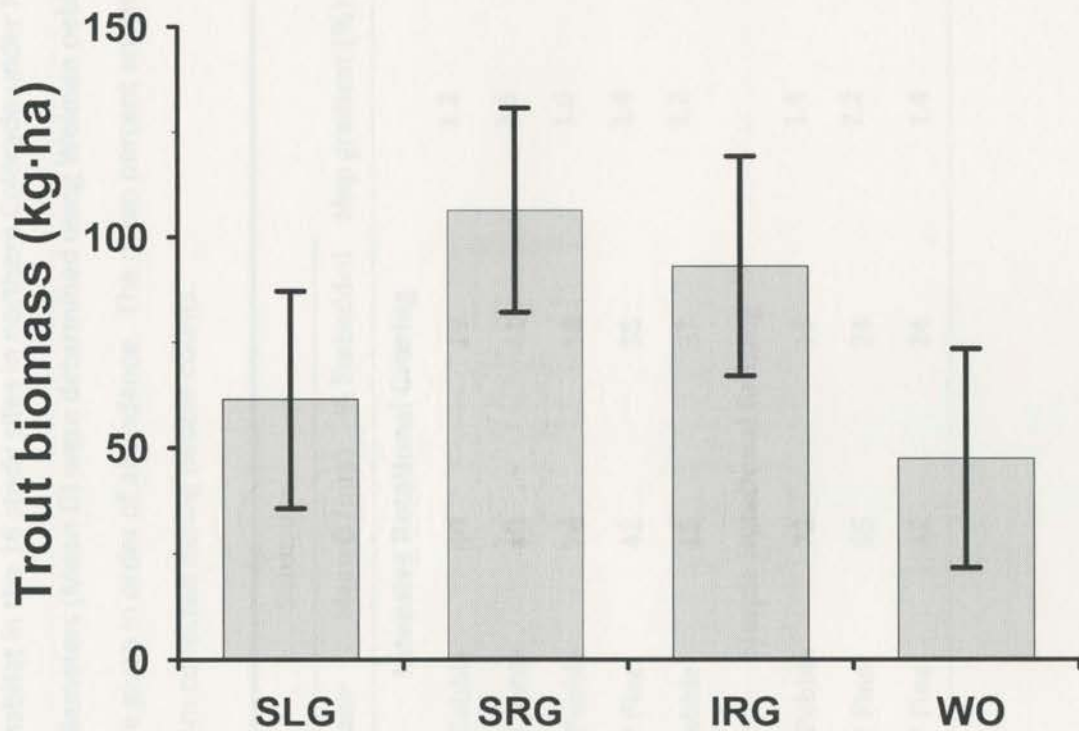


Figure 7. — Predicted average trout biomass for age-1 and older fish <350 mm estimated in late summer 2007 at 15 streams in northern Colorado under season long (SLG), simple rotational (SRG), intensive rotational (IRG), or wildlife only (WO) grazing. Estimates from one IRG site (Floyd Creek) were considered an outlier and not included in the analysis (see text). Error bars show $\pm$ SE in both panels, which represents the variability among sites under a given grazing system.



Appendix 1. — Characteristics of physical habitat in the 16 study sites in northern Colorado under four different types of grazing management (see text). Mean substrate diameters (Mean D) were determined using Wolman pebble counts (Overton et al. 1997). The two most prevalent substrate types are given in order of abundance. The mean percent embeddedness (% Embedded) was estimated for all substrate particles ≥ 15 mm collected during pebble counts.

Site Name	Elevation (m)	Substrate			Map gradient (%)	Pool and run area (m²)
		Dominant ^a	Mean D (mm)	% Embedded		
Intensive Rotational Grazing						
Lower Canadian	2,564	Pebble / Cobble	49	19	1.2	397
Upper Canadian	2,555	Pebble / Cobble	48	41	2.6	463
Michigan	2,580	Cobble / Pebble	76	18	1.0	1490
Illinois	2,564	Pebble / Fine	42	35	1.4	1114
Floyd	2,458	Fine / Pebble	15	37	1.2	311
Simple Rotational Grazing						
Arapaho	2,683	Cobble / Pebble	73	15	1.4	173
Northern Rock	2,751	Cobble / Fine	55	24	2.2	175
Southern Rock	2,600	Pebble / Fine	42	24	1.4	997

Appendix 1.-- continued

Site Name	Elevation (m)	Substrate			Map gradient (%)	Pool and run area (m ²)
		Dominant ^a	Mean D (mm)	% Embedded		
Lower Trout	2,343	Cobble / Pebble	108	12	2.8	391
Season Long Grazing						
N.F. North Platte	2,591	Pebble / Gravel	28	48	1.2	907
Shafer	2,576	Pebble / Cobble	50	13	2.4	622
East Fork Troublesome	2,475	Cobble / Pebble	78	45	0.8	971
Newcomb	2,656	Pebble / Fine	45	36	1.2	895
Wildlife Only						
Hinman	2,375	Cobble / Pebble	78	21	1.4	441
Upper Trout	2,508	Cobble / Fine	101	36	3.2	541
Grizzly	2,554	Pebble / Fine	28	27	1.2	1154

^a Substrate categories are based on the Wentworth classification (Wentworth 1922).

Appendix 2. – Example of model structure and parameter derivation for analysis of categorical data using a model selection framework.

The objective of analyzing response variables using categorical variables was primarily to evaluate the influence of different types of grazing management on riparian habitat and the availability and use of terrestrial invertebrate subsidies to streams. This was accomplished by evaluating models with all combinations of the four types of grazing systems, including a grazing system by collection period interaction. For each model, I constructed a design matrix (see below) in which the columns associated with all categorical variables summed to 0 such that the intercept was constrained to equal the global average of the response variable.

Example design matrix for analysis of data using parameters for 4 levels of grazing system

	Intercept	Parameter_2	Parameter_3	Parameter_4	Parameter_5
System_1-July	1	1	0	0	1
System_1-August	1	1	0	0	-1
System_2-July	1	0	1	0	1
System_2-August	1	0	1	0	-1
System_3-July	1	0	0	1	1
System_3-August	1	0	0	1	-1
System_4-July	1	-1	-1	-1	1
System_4-August	1	-1	-1	-1	-1

The design matrix above depicts the parameterization for the model:

$y \sim \alpha + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \beta_5 x_5$; such that α = model intercept, $\beta_2 : \beta_4$ = parameters for grazing systems 1 through 3, and β_5 = parameter for sampling period. It follows that the estimate for grazing system 4 is a derived parameter (γ) such that

$$\gamma = -1(\beta_2 + \beta_3 + \beta_4), \text{ and}$$

$$\begin{aligned}
 \text{var}(\gamma) &= (-1)^2 \text{var}(\beta_2 + \beta_3 + \beta_4) \\
 &= \text{var}(\beta_2) + \text{var}(\beta_3) + \text{var}(\beta_4) + 2 \times [\text{cov}(\beta_2, \beta_3) + \text{cov}(\beta_2, \beta_4) \\
 &\quad + \text{cov}(\beta_3, \beta_4)]
 \end{aligned}$$

In total, I designed 16 matrices such as that above: 1 to model the interaction of the four levels of grazing system and sampling period, 1 to model the additive effects of each of the four levels of grazing system and sampling period (shown in the example above), 4 to model the "effects" of three grazing systems with the fourth set equal to the intercept (i.e., regional mean), 6 to model 2 grazing systems as being different than the intercept, and 4 to model a single grazing system as being different than the mean. Examples of one of each of these matrices are provided below although the equations for derived parameters are not provided as they follow logically from those provided above.

Design matrix for model with three levels of grazing system (i.e., systems 1, 2, and 4)

	α	β_2	β_3	β_5
Sys_1-Jul	1	1	0	1
Sys_1-Aug	1	1	0	-1
Sys_2-Jul	1	0	1	1
Sys_2-Aug	1	0	1	-1
Sys_3-Jul	1	0	0	1
Sys_3-Aug	1	0	0	-1
Sys_4-Jul	1	-1	-1	1
Sys_4-Aug	1	-1	-1	-1

Design matrix for model with only one level of grazing system (i.e., systems 1)

	α	β_2'	β_5
Sys_1-Jul	1	1	1
Sys_1-Aug	1	1	-1
Sys_2-Jul	1	0	1
Sys_2-Aug	1	0	-1
Sys_3-Jul	1	0	1
Sys_3-Aug	1	0	-1
Sys_4-Jul	1	0	1
Sys_4-Aug	1	0	-1

Design matrix for model with two levels of grazing system (i.e., systems 1 and 4)

	α	β_2	β_5
Sys_1-Jul	1	1	1
Sys_1-Aug	1	1	-1
Sys_2-Jul	1	0	1
Sys_2-Aug	1	0	-1
Sys_3-Jul	1	0	1
Sys_3-Aug	1	0	-1
Sys_4-Jul	1	-1	1
Sys_4-Aug	1	-1	-1

After calculating the derived parameters for each of the 16 models, model averaged parameter estimates ($\bar{\beta}_i$) were calculated from the nine models containing β_i (i.e., using the non-shrinkage type model averaging presented in Burnham and Anderson 2002) using the AIC_c weights obtained by maximizing the full log-likelihood. This model structure provides inference as to the regional mean value of the response variable (i.e., model-averaged intercept), as well as the effect each grazing system has on the response variable as determined by the size of the parameter estimate and its variability as estimated using the unconditional standard error. Further inference can be gained by estimating the difference between model-averaged parameter estimates and evaluating whether the confidence interval around this value does not include zero, which would indicate that there was a consistent difference between sites managed under the two types of grazing systems in question. This type of inference is similar to that gained by conducting preplanned comparisons under an analysis of variance framework, but allows incorporating model selection uncertainty when making comparisons.

Calculation of the variance of the difference between two model-averaged parameter estimates requires a model-averaged estimate of the sampling correlation or covariance (see Burnham and Anderson 2002), which must also be derived when γ is one of the two parameters of interest. In the case where the difference of interest is between grazing system 1 (β_2) and grazing system 4 ($\gamma = -1[\beta_2 + \beta_3 + \beta_4]$, following the example above), the covariance was calculated as follows.

$$\begin{aligned} cov(\beta_2, \gamma) &= cov(\beta_2, -1[\beta_2 + \beta_3 + \beta_4]) = -1\{cov(\beta_2, \beta_2 + \beta_3 + \beta_4)\} \\ cov(\beta_2, \gamma) &= -1\{var(\beta_2) + cov(\beta_2, \beta_3) + cov(\beta_2, \beta_4)\} \end{aligned}$$

Appendix 3. – Dry biomass ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) of major terrestrial invertebrate taxa entering 16 study sites in northern Colorado during July and August 2007. Major taxa were identified as those which contributed greater than 1% to the total invertebrate biomass entering streams, averaged across July and August for all sites, or contributed more than 5% to the biomass of terrestrial invertebrates collected at a single site. For each taxon collected at each site, the percentage contribution to the terrestrial invertebrate input is shown in parentheses. Samples were collected using pan traps set for two 3-d sampling periods during July and August (see text). Samples were collected at five sites managed for Intensive Rotational Grazing (IRG), four sites managed under Simple Rotational Grazing (SRG), four sites managed under Season-Long Grazing (SLG), and three sites grazed by Wildlife Only (WO, see text). Other taxa sampled included Neuroptera, Siphonaptera, mites, earthworms, immature Coleoptera, and immature Neuroptera.

Site	Grazing System	Month	Total Biomass	Coleoptera	Collembola	Hemiptera	Homoptera	Hymenoptera	Lepidoptera	Orthoptera	Spiders
East Fork Troublesome	SLG	July	3.3087	0.6814 (21)		0.3777 (11)	0.3941 (12)	0.2217 (7)			0.353 (11)
Newcomb	SLG	July	22.5616	1.1987 (5)	0.0411 (0)	4.1544 (18)	1.3629 (6)	0.3859 (2)	0.2874 (1)		0.0657 (0)
North Fork North Platte	SLG	July	21.2863	2.2386 (11)		3.2512 (15)	2.173 (10)	2.6163 (12)	0.3339 (2)		0.2737 (1)
Shafer	SLG	July	8.9374	1.9059 (21)	0.0117 (0)	1.0908 (12)	1.0321 (12)	0.4574 (5)	1.5541 (17)		0.1525 (2)
Arapaho	SRG	July	33.5632	5.4433 (16)		0.5665 (2)	1.5435 (5)	0.2217 (1)	15.6897 (47)	5.5665 (17)	0.0739 (0)
Lower Trout	SRG	July	59.0476	6.9622 (12)	0.0246 (0)	2.2742 (4)	2.6847 (5)	2.9475 (5)	7.6273 (13)		1.2151 (2)
Northern Rock	SRG	July	21.3383	2.6108 (12)	0.0246 (0)	2.9639 (14)	0.5255 (3)	2.734 (13)	0.936 (4)		1.2315 (6)
Southern Rock	SRG	July	34.9343	0.9278 (3)	0.0328 (0)	0.7964 (2)	1.0427 (3)	2.3153 (7)	1.3793 (4)		0.936 (3)
Floyd	IRG	July	50.4433	6.4204 (13)	0.1232 (0)	1.4532 (3)	8.4072 (17)	2.9557 (6)	0.5172 (1)		1.2315 (2)
Illinois	IRG	July	5.7964	0.1724 (3)	0.0246 (0)	0.3448 (6)	0.6568 (11)	0.1478 (3)		0.9524 (16)	0.1724 (3)
Lower Canadian	IRG	July	22.2113	1.9157 (9)	0.1204 (1)	0.9743 (4)	2.1073 (10)	2.4193 (11)	0.6513 (3)	0.4324 (2)	0.5364 (2)
Michigan	IRG	July	17.7559	1.6092 (9)	0.0109 (0)	1.1877 (7)	2.6601 (15)	0.8539 (5)	0.4817 (3)		0.4981 (3)
Upper Canadian	IRG	July	32.775	1.1932 (4)	0.0219 (0)	0.7608 (2)	1.8719 (6)	2.1565 (7)	2.6163 (8)		0.4324 (1)
Grizzly	WO	July	26.8473	1.6585 (6)	0.0411 (0)	3.9409 (15)	3.7274 (14)	0.8128 (3)	3.1199 (12)		0.312 (1)
Hinman	WO	July	99.803	3.9573 (4)	0.0164 (0)	2.3235 (2)	7.9967 (8)	2.4056 (2)	24.9589 (25)		3.1609 (3)
Upper Trout	WO	July	14.9918	1.2726 (9)	0.0328 (0)	1.289 (9)	2.0772 (14)	1.1494 (8)	4.2447 (28)		0.1888 (1)

Appendix 3. – Continued

Site	Grazing System	Month	Total Biomass	Coleoptera	Collembola	Hemiptera	Homoptera	Hymenoptera	Lepidoptera	Orthoptera	Spiders
East Fork Troublesome	SLG	August	11.0427	0.2668 (2)		0.3284 (3)	2.3974 (22)	2.4754 (22)	0.0287 (0)		0.0164 (0)
Newcomb	SLG	August	4.0148	0.1314 (3)	0.0328 (1)	0.156 (4)	0.1806 (5)	2.7094 (68)			
North Fork North Platte	SLG	August	12.9844	0.3489 (3)	0.0246 (0)	1.0673 (8)	1.1494 (9)	1.7549 (14)	0.3695 (3)		0.0431 (0)
Shafer	SLG	August	26.2993	2.1162 (8)	0.0308 (0)	2.5226 (10)	1.2397 (5)	8.0152 (31)	4.2221 (16)		0.5603 (2)
Arapaho	SRG	August	273.0378	1.1494 (0)	0.1314 (0)	83.4483 (31)	2.1429 (1)	8.0049 (3)	4.0969 (2)		0.0082 (0)
Lower Trout	SRG	August	125.8621	0.0274 (0)	0.0109 (0)	0.2381 (0)	0.5446 (0)	6.5709 (5)		44.7674 (36)	6.3684 (5)
Northern Rock	SRG	August	33.908	2.3317 (7)	0.1533 (1)	0.9031 (3)	2.5233 (7)	7.2742 (22)	1.4888 (4)		0.9414 (3)
Southern Rock	SRG	August	94.7017	87.8243 (93)	0.0164 (0)	0.3229 (0)	0.3831 (0)	1.9239 (2)	0.1423 (0)		0.0109 (0)
Floyd	IRG	August	11.6502	0.6076 (5)	1.2726 (11)	0.5419 (5)	1.7323 (15)	1.6585 (14)			0.0164 (0)
Illinois	IRG	August	2.7176	0.1724 (6)	0.1149 (4)	0.2053 (8)	0.9852 (36)	0.3777 (14)	0.0657 (2)		0.0821 (3)
Lower Canadian	IRG	August	59.8166	1.1166 (2)	0.494 (1)	0.6349 (1)	2.303 (4)	1.6804 (3)	0.0219 (0)		0.4885 (1)
Michigan	IRG	August	27.7217	0.5665 (2)	0.0616 (0)	0.5973 (2)	2.0074 (7)	2.6355 (10)	0.5788 (2)	13.4052 (48)	0.9544 (3)
Upper Canadian	IRG	August	26.6913	0.4926 (2)	0.1204 (1)	0.4899 (2)	2.4795 (9)	3.191 (12)	4.8495 (18)		0.6294 (2)
Grizzly	WO	August	126.7462	1.0004 (1)	0.0411 (0)	96.3938 (76)	5.4074 (4)	3.5992 (3)	0.0189 (0)		0.6701 (1)
Hinman	WO	August	25.6212	11.7077 (46)	0.1715 (1)	1.7296 (7)	0.9305 (4)	2.8407 (11)			1.1002 (4)
Upper Trout	WO	August	20.546	0.0493 (0)	0.0534 (0)	1.3218 (6)	1.1946 (6)	1.757 (9)	0.0246 (0)		0.0123 (0)

Appendix 3. – Continued

Site	Grazing System	Month	Ticks	Thrips	Psocoptera	Adult Diptera	Immature Diptera	Immature Lepidoptera	Other Taxa
East Fork Troublesome	SLG	July		0.0575 (2)	0.0575 (2)	1.1658 (35)			
Newcomb	SLG	July	0.0328 (0)	0.6897 (3)		14.3268 (64)			0.0164 (0)
North Fork North Platte	SLG	July	0.0383 (0)	0.3229 (2)		8.9546 (42)		1.0837 (5)	
Shafer	SLG	July	0.0235 (0)	0.0411 (1)		2.5158 (28)	0.0352 (0)	0.0352 (0)	0.0821 (1)
Arapaho	SRG	July	0.0575 (0)	0.0985 (0)	0.0082 (0)	3.1527 (9)		1.1412 (3)	
Lower Trout	SRG	July	0.1888 (0)	0.0739 (0)	0.1724 (0)	34.2857 (58)	0.0246 (0)	0.4598 (1)	0.1067 (0)
Northern Rock	SRG	July	0.0903 (0)	0.0985 (1)		8.4811 (40)	0.0164 (0)	1.6256 (8)	
Southern Rock	SRG	July	0.0903 (0)	0.0821 (0)		27.2989 (78)		0.0328 (0)	
Floyd	IRG	July	9.0805 (18)	0.1642 (0)	0.1149 (0)	18.2594 (36)		1.5764 (3)	0.1396 (0)
Illinois	IRG	July		0.0575 (1)	0.0082 (0)	3.2512 (56)			0.0082 (0)
Lower Canadian	IRG	July	0.0438 (0)	0.0985 (0)	0.0383 (0)	8.8725 (40)	3.7165 (17)	0.2846 (1)	
Michigan	IRG	July	0.1314 (1)	0.0766 (0)	0.3065 (2)	8.7958 (50)	0.0219 (0)	1.1221 (6)	
Upper Canadian	IRG	July	0.0219 (0)	0.0438 (0)	0.1314 (0)	21.0947 (64)	0.0109 (0)	1.5326 (5)	0.8867 (3)
Grizzly	WO	July	0.0739 (0)	0.0985 (0)	0.0657 (0)	12.2003 (45)	0.0246 (0)		0.7718 (3)
Hinman	WO	July	0.0328 (0)	0.1232 (0)	0.0164 (0)	51.3054 (51)		2.4877 (3)	1.0181 (1)
Upper Trout	WO	July		0.1642 (1)	0.1314 (1)	4.22 (28)	0.0082 (0)	0.2135 (1)	

Appendix 3. – Continued

Site	Grazing System	Month	Ticks	Thrips	Psocoptera	Adult Diptera	Immature Diptera	Immature Lepidoptera	Other Taxa
East Fork Troublesome	SLG	August	1.7077 (16)	0.9031 (8)	1.0304 (9)	1.8637 (17)			0.0246 (0)
Newcomb	SLG	August		0.0082 (0)	0.312 (8)	0.197 (5)		0.2874 (7)	
North Fork North Platte	SLG	August	0.0493 (0)	0.7225 (6)	0.2278 (2)	7.0587 (54)		0.0575 (0)	0.1108 (1)
Shafer	SLG	August	0.3879 (2)	0.1314 (1)	0.0616 (0)	6.5353 (25)			0.4762 (2)
Arapaho	SRG	August	0.1724 (0)	0.2463 (0)	82.3563 (30)	3.6207 (1)		87.3481 (32)	0.312 (0)
Lower Trout	SRG	August	0.0985 (0)	0.0301 (0)	66.0482 (53)	0.9278 (1)			0.2299 (0)
Northern Rock	SRG	August	0.3886 (1)	0.2737 (1)	0.7444 (2)	15.7033 (46)		0.7006 (2)	0.4817 (1)
Southern Rock	SRG	August	0.2956 (0)	0.0821 (0)	0.5884 (1)	3.0296 (3)			0.0821 (0)
Floyd	IRG	August	0.9934 (9)	0.0985 (1)	0.9031 (8)	2.6108 (22)		1.2151 (10)	
Illinois	IRG	August	0.0821 (3)	0.1067 (4)	0.1806 (7)	0.3038 (11)		0.0164 (1)	0.0246 (1)
Lower Canadian	IRG	August	0.2313 (0)	0.1574 (0)	47.7408 (80)	4.2269 (7)	0.0479 (0)	0.5255 (1)	0.1478 (0)
Michigan	IRG	August	0.5172 (2)	0.1047 (0)	0.4002 (1)	5.7204 (21)		0.1355 (1)	0.0369 (0)
Upper Canadian	IRG	August	0.2436 (1)	0.1533 (1)	0.3257 (1)	10.4981 (39)		3.1773 (12)	0.0411 (0)
Grizzly	WO	August	0.7623 (1)	3.1988 (3)	6.474 (5)	5.9821 (5)	0.0082 (0)	1.8947 (2)	1.2953 (1)
Hinman	WO	August	0.8411 (3)	0.0274 (0)	0.0566 (0)	5.0593 (20)		0.7006 (3)	0.4561 (2)
Upper Trout	WO	August	0.0903 (0)	0.0411 (0)	14.5156 (71)	0.6158 (3)		0.8621 (4)	0.0082 (0)

Appendix 4. – Dry biomass ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) of major adult aquatic insect taxa collected at 16 study sites in northern Colorado during July and August 2007. Major taxa were identified as those which contributed greater than 1% to the total invertebrate biomass entering streams, averaged across July and August for all sites, or contributed more than 5% to the biomass of adult aquatic insects collected at a single site. For each taxon collected at each site, the percentage contribution to the adult aquatic insects input is shown in parentheses. Samples were collected using pan traps set for two 3-d sampling periods during July and August (see text). Samples were collected at five sites managed for Intensive Rotational Grazing (IRG), four sites managed under Simple Rotational Grazing (SRG), four sites managed under Season-Long Grazing (SLG), and three sites grazed by Wildlife Only (WO, see text). Other taxa sampled included Dixidae, Culicidae, Ptychopteridae, Stratiomyidae, and Lepidoptera.

Site	Grazing System	Month	Total Biomass	Chironomidae	Ceratopogonidae	Tipulidae	Psychodidae	Simuliidae	Tabanidae
East Fork Troublesome	SLG	July	0.7143	0.4023 (56)	0.0575 (8)			0.0575 (8)	0.0164 (2)
Newcomb	SLG	July	44.3021	8.7192 (20)	1.0263 (2)	1.1494 (3)	0.2791 (1)	0.2463 (1)	1.8309 (4)
North Fork North Platte	SLG	July	13.9956	2.0416 (15)	0.4707 (3)	0.509 (4)	0.093 (1)	0.1533 (1)	2.8352 (20)
Shafer	SLG	July	64.2623	2.076 (3)	0.0997 (0)	0.3519 (1)	58.7204 (91)	0.1232 (0)	0.4516 (1)
Arapaho	SRG	July	6.6831	0.4433 (7)	0.1067 (2)	0.1724 (3)	0.0164 (0)	0.0821 (1)	3.4729 (52)
Lower Trout	SRG	July	38.202	3.4729 (9)	0.4187 (1)	2.2742 (6)	0.8621 (2)	0.0903 (0)	
Northern Rock	SRG	July	17.4631	4.3678 (25)	0.156 (1)	0.9524 (6)	0.0985 (1)	0.3284 (2)	
Southern Rock	SRG	July	20.8949	2.3645 (11)	0.2135 (1)	2.0279 (10)	0.2381 (1)	0.9195 (4)	
Floyd	IRG	July	33.6535	3.2184 (10)	0.2135 (1)	6.2233 (19)	0.0821 (0)	0.4269 (1)	
Illinois	IRG	July	8.67	0.4598 (5)	0.1314 (2)	3.0378 (36)		0.0821 (1)	0.2545 (3)
Lower Canadian	IRG	July	54.8112	5.0958 (9)	0.1806 (0)	1.8993 (4)	0.1204 (0)	5.8128 (11)	
Michigan	IRG	July	66.4806	6.0372 (9)	0.3941 (1)	5.8894 (9)	0.4707 (1)	0.4871 (1)	
Upper Canadian	IRG	July	25.4735	4.231 (17)	0.2791 (1)	3.1144 (12)	0.0274 (0)	0.9031 (4)	
Grizzly	WO	July	100.8046	19.1051 (19)	4.532 (5)	3.3908 (3)	0.0246 (0)	0.8128 (1)	
Hinman	WO	July	33.1691	5.2217 (16)	1.6256 (5)	3.358 (10)	2.8571 (9)	0.4023 (1)	2.2167 (7)
Upper Trout	WO	July	24.3924	3.7521 (15)	0.2463 (1)	1.0837 (4)	3.1856 (13)	0.7635 (3)	

Appendix 4. – Continued

Site	Grazing System	Month	Total Biomass	Chironomidae	Ceratopogonidae	Tipulidae	Psychodidae	Simuliidae	Tabanidae
East Fork Troublesome	SLG	August	6.8719	1.2069 (18)	0.0821 (1)				
Newcomb	SLG	August	1.3793	0.2299 (17)	0.156 (11)				
North Fork North Platte	SLG	August	20.3551	10.9154 (54)	1.6892 (8)	0.1252 (1)	0.1539 (1)	0.0944 (1)	
Shafer	SLG	August	15.8846	5.5686 (35)	0.7184 (5)	0.0369 (0)	0.1847 (1)	0.0431 (0)	
Arapaho	SRG	August	1.8062	0.2874 (16)	0.0411 (2)	0.5419 (30)	0.1149 (6)	(0)	
Lower Trout	SRG	August	3.2321	1.393 (43)	0.1861 (6)			0.0109 (0)	
Northern Rock	SRG	August	13.0104	0.8155 (6)	0.3612 (3)	0.4598 (4)	0.093 (1)	0.0219 (0)	
Southern Rock	SRG	August	3.2266	0.2545 (8)	0.093 (3)	0.0411 (1)		0.0547 (2)	
Floyd	IRG	August	5.6486	1.8555 (33)	1.5764 (28)	0.0411 (1)	0.0164 (0)		
Illinois	IRG	August	2.3727	0.2545 (11)	0.1396 (6)				
Lower Canadian	IRG	August	15.0698	1.4888 (10)	0.2477 (2)	0.0616 (0)	0.379 (3)	0.2573 (2)	
Michigan	IRG	August	7.7894	1.2869 (17)	0.3202 (4)	0.1232 (2)	0.2586 (3)	0.1786 (2)	
Upper Canadian	IRG	August	8.2841	0.8402 (10)	0.1587 (2)	1.0427 (13)	0.2573 (3)	0.1149 (1)	
Grizzly	WO	August	30.3006	5.9315 (20)	5.3922 (18)				
Hinman	WO	August	2.9484	0.5127 (17)	0.2937 (10)	0.0493 (2)		0.0456 (2)	
Upper Trout	WO	August	5.4475	0.3489 (6)	0.1806 (3)		0.0164 (0)	0.0493 (1)	

Appendix 4. – Continued

Site	Grazing System	Month	Ephemeroptera	Trichoptera	Plecoptera	Odonata	Coleoptera	Hemiptera	Other
East Fork Troublesome	SLG	July	0.0903 (13)	0.0411 (6)			0.0493 (7)		
Newcomb	SLG	July	7.8161 (18)	21.5353 (49)	0.8703 (2)		0.7389 (2)		0.0903 (0)
North Fork North Platte	SLG	July	3.0542 (22)	3.3716 (24)	0.0712 (1)		1.3848 (10)		0.0109 (0)
Shafer	SLG	July	0.7682 (1)	1.0439 (2)	0.4516 (1)		0.1232 (0)		0.0528 (0)
Arapaho	SRG	July	1.33 (20)	0.6076 (9)	0.0903 (1)		0.3284 (5)		0.0328 (1)
Lower Trout	SRG	July	2.4877 (7)	26.798 (70)	1.7323 (5)				0.0657 (0)
Northern Rock	SRG	July	5.3284 (31)	0.0164 (0)	4.9836 (29)		1.0181 (6)		0.2135 (1)
Southern Rock	SRG	July	2.8571 (14)	11.3547 (54)	0.8128 (4)		0.0821 (0)	0.0246 (0)	
Floyd	IRG	July	1.4039 (4)	16.7077 (50)	0.1232 (0)	1.9787 (6)	2.7915 (8)		0.4844 (1)
Illinois	IRG	July	1.3054 (15)	2.4548 (28)	0.6897 (8)		0.0411 (1)	0.2053 (2)	0.0082 (0)
Lower Canadian	IRG	July	2.5506 (5)	34.1708 (62)	4.2365 (8)		0.2846 (1)	0.3777 (1)	0.0821 (0)
Michigan	IRG	July	2.5014 (4)	48.139 (72)	2.1128 (3)		0.2627 (0)		0.1861 (0)
Upper Canadian	IRG	July	5.1888 (20)	9.8522 (39)	1.5161 (6)		0.0602 (0)		0.301 (1)
Grizzly	WO	July	2.1675 (2)	48.7356 (48)	2.578 (3)	19.0558 (19)	0.3777 (0)		0.0246 (0)
Hinman	WO	July	3.6782 (11)	9.335 (28)	3.5386 (11)				0.936 (3)
Upper Trout	WO	July	3.711 (15)	10.6486 (44)	0.9442 (4)		0.0164 (0)		0.0411 (0)

Appendix 4. – Continued

Site	Grazing System	Month	Ephemeroptera	Trichoptera	Plecoptera	Odonata	Coleoptera	Hemiptera	Other
East Fork Troublesome	SLG	August	3.4565 (50)	0.2381 (4)			1.8883 (28)		
Newcomb	SLG	August		0.0657 (5)			0.9031 (66)		0.0246 (2)
North Fork North Platte	SLG	August	0.9298 (5)	5.0883 (25)	0.0431 (0)		0.9955 (5)	0.2956 (2)	0.0246 (0)
Shafer	SLG	August	3.9594 (25)	1.2911 (8)	0.6014 (4)		0.938 (6)	2.3399 (15)	0.2032 (1)
Arapaho	SRG	August	0.1067 (6)	0.0985 (6)	0.1149 (6)		0.2791 (16)	0.1396 (8)	0.0821 (5)
Lower Trout	SRG	August	0.0794 (3)	1.0564 (33)	0.0219 (1)		0.3421 (11)		0.1423 (4)
Northern Rock	SRG	August	2.9776 (23)	4.8385 (37)	2.7313 (21)		0.5802 (5)	0.104 (1)	0.0274 (0)
Southern Rock	SRG	August	1.9787 (61)	0.4844 (15)	0.145 (5)		0.1423 (4)		0.0328 (1)
Floyd	IRG	August	0.0246 (0)	1.3629 (24)			0.7718 (14)		
Illinois	IRG	August	1.0509 (44)	0.0246 (1)			0.7553 (32)	0.1478 (6)	
Lower Canadian	IRG	August	2.2099 (15)	7.1798 (48)	0.8456 (6)		2.3727 (16)		0.0274 (0)
Michigan	IRG	August	0.5172 (7)	3.6207 (47)	0.117 (2)		1.367 (18)		
Upper Canadian	IRG	August	0.7827 (9)	3.856 (47)	0.5145 (6)		0.6787 (8)		0.0383 (1)
Grizzly	WO	August	9.5585 (32)	1.3711 (5)			4.9722 (16)	1.3073 (4)	1.7677 (6)
Hinman	WO	August	0.6149 (21)	0.0547 (2)	0.3339 (11)		1.0327 (35)		0.0109 (0)
Upper Trout	WO	August	0.0246 (1)	4.0558 (75)			0.7718 (14)		

Abstract

Research in forest and grassland ecosystems indicated that terrestrial invertebrates that fall into streams can be an important prey resource for fish, providing about 50% of their annual energy, and having strong effects on growth and abundance. However, there had been no explicit studies of the effects of grazing by livestock on terrestrial invertebrate subsidies to trout.

CHAPTER 3:

Effects of a Single Grazing Event by Cattle on Terrestrial Invertebrate Subsidies to Trout:

Results of a Field Experiment

Field experiments to test whether grazing and manual removal of streamside woody vegetation affects trout populations by reducing terrestrial invertebrate prey input in central Wyoming streams. I tested three grazing treatments: 1) moderate intensity grazing (heights 10-25 cm stubble height), 2) high intensity grazing (5-7.5 cm stubble height), 3) high intensity grazing plus manual removal of streamside woody vegetation, and 4) a control with no livestock grazing. All treatments were applied with cow/calf pairs with 12 of each grazing treatment or 6 cow/calf pairs to aquatic habitat for fish. Overall, short duration of moderate and high intensity cattle grazing that occurred midsummer in 3 single years, which rapidly reduced both riparian vegetation biomass and vegetative cover by 50-70%, had no detectable effect on the biomass of terrestrial invertebrates entering streams. However, high intensity grazing plus removal of streamside woody vegetation resulted in reductions in terrestrial invertebrate input to streams, although these effects were variable. In contrast, all experimental treatments reduced the biomass of terrestrial invertebrates in trout diets in late summer. Although experimental treatments reduced terrestrial prey resources for trout to varying extents, neither trout biomass nor density was reduced during the

Abstract

Research in forest and grassland ecosystems indicates that terrestrial invertebrates that fall into streams can be an important prey resource for fish, providing about 50% of their annual energy and having strong effects on growth and abundance. However, there has been no experimental test of whether riparian grazing by livestock reduces this important prey resource for trout. During summer 2008, I conducted a field experiment to test whether cattle grazing alone, or grazing and manual removal of streamside woody vegetation, affects trout populations by reducing terrestrial invertebrate prey input in central Wyoming streams. I tested three grazing treatments: 1) moderate intensity grazing (leaving 10-15 cm stubble height), 2) high intensity grazing (5-7.5 cm stubble height), 3) high intensity grazing plus manual removal of two-thirds of streamside woody vegetation, and 4) a control with no livestock grazing. All treatments were applied with cow/calf pairs with 11 d of grazing pressure or less to limit impacts to aquatic habitat for fish. Overall, short durations of moderate and high intensity cattle grazing that occurred midsummer in a single year, which rapidly reduced both riparian vegetation biomass and vegetative cover by 50 – 80%, had no detectable effect on the biomass of terrestrial invertebrates entering streams. However, high intensity grazing plus removal of streamside woody vegetation caused reductions in terrestrial invertebrate inputs to streams, although these effects were variable. In contrast, all experimental treatments reduced the biomass of terrestrial invertebrates in trout diets in late summer. Although experimental treatments reduced terrestrial prey resources for trout to varying extents, neither trout biomass nor density was reduced during the

experiment. These results indicate that terrestrial invertebrate inputs may be relatively resistant to short, but intensive, bouts of grazing, and that rotational grazing systems that incorporate such short grazing bouts may also support the terrestrial invertebrate subsidies to streams necessary to sustain robust trout populations. Furthermore, grazing practices that maintain streamside woody vegetation, which provides vertical structure and overhead cover, are most likely to support riparian-stream linkages that supply terrestrial prey resources for trout.

Introduction

Habitat degradation is the leading cause of biodiversity loss worldwide (Vitousek et al. 1997; Dirzo and Raven 2003; Fahrig 2003), affecting plant and animal populations directly through habitat loss, but also indirectly by decoupling important linkages among habitats and communities (Foley et al. 2005; Hooper et al. 2005). Globally, livestock grazing is one of the dominant land uses, occurring on more than half of all agricultural land (22% of the land surface, Ramankutty et al. 2008), including >850 million acres in the U.S. (GAO 1988; NRCS 2002), primarily in the West. Although riparian zones make up <1% of rangelands, cattle congregate in these sensitive areas to find forage, shade, and water (Armour et al. 1991), and can have both direct and indirect impacts on fish populations. Cattle grazing of riparian zones can affect fish populations directly by trampling spawning gravels causing increasing mortality of sensitive early life stages (Gregory and Gamett 2009; Peterson et al. 2010). Furthermore, poorly managed riparian grazing can affect fish populations indirectly by trampling stream banks and

overgrazing streamside vegetation. This leads to bank erosion, increased turbidity, siltation of streambed gravel, infilling of pools, and reduced habitat complexity (Platts 1981; Kauffman and Krueger 1984; Belsky et al. 1999). In turn, this can reduce aquatic invertebrate production, growth and reproduction of trout, and ultimately, trout abundance and production.

Current grazing management is primarily designed to protect stream bank stability and instream habitat by maintaining sufficient aboveground plant biomass to sustain roots that bind banks, and to prevent cattle from over-browsing riparian shrubs (Clary and Webster 1989; Meehan 1991; Clary and Kruse 2004). The guiding principle has been that maintaining a minimum level of riparian vegetation (e.g., 10 cm of grass stubble, Clary and Leininger 2000) prevents erosion that destroys habitat for aquatic invertebrates and trout (Wyman et al. 2006). The goal to maintain minimum riparian vegetation has been supported by demonstration exclosures which eliminated cattle grazing from riparian zones altogether. These have shown large increases in both streamside vegetation (Rickard and Cushing 1982; Platts and Wagstaff 1984; Kauffman et al. 1997; Dobkin et al. 1998; Holland et al. 2005) and abundance or biomass of trout (Keller and Burnham 1982; Knapp and Matthews 1996; see Platts 1991 for review) within five years after complete rest. However, full recovery of stream habitat, including stream bank stabilization, lateral scour that creates deep pools with overhead cover, cleaning of stream gravel needed for invertebrate production and trout spawning, and input of woody debris that creates habitat complexity, often requires more than these short periods to achieve (Kondolf 1993; Magilligan and McDowell

1997; see Sarr 2002 for review). Therefore, it is likely that other mechanisms in addition to habitat loss from erosion and siltation are important in influencing trout populations in rangeland streams

Streams have small area but long boundaries with the adjacent riparian areas, and so are strongly influenced by fluxes from the terrestrial habitats they drain (Wallace et al. 1997; Nakano and Murakami 2001; see reviews by Baxter et al. 2005; Fausch et al. 2010). Therefore, two additional indirect pathways by which improved grazing practices that increase riparian vegetation may influence trout are increased inputs of terrestrial insects, and of detritus that supports secondary production of aquatic insects. In addition to invertebrates produced within the stream, terrestrial invertebrates that fall, crawl, or blow into streams from riparian vegetation are important for sustaining trout (Baxter et al. 2005). These prey can account for 50 – 85% of trout diets during summer months (e.g., Dineen et al. 2007; Utz and Hartman 2007) and provide about 50% of their annual energy budget (Kawaguchi and Nakano 2001; Nakano and Murakami 2001; Sweka and Hartman 2008). Moreover, experimental reductions of terrestrial prey using mesh greenhouses in a Japanese stream reduced growth of salmonids by 25% compared to a control (Baxter et al. 2007), and caused half the biomass of salmonids to emigrate in response (Kawaguchi et al. 2003; see Fausch et al. 2010 for review). Bioenergetic simulations yielded similar conclusions about the importance of terrestrial prey (Sweka and Hartman 2008).

Although past research highlights the importance of riparian vegetation in supplying terrestrial invertebrates that help sustain stream salmonids, we have yet to

fully evaluate how actual land uses alter these prey subsidies so that managers can apply the results. Several recent studies have reported that terrestrial prey inputs were strongly influenced by cattle grazing. Edwards and Huryn (1996) found that streams traversing New Zealand grasslands used for livestock grazing received less terrestrial invertebrate biomass than ungrazed native tussock grasslands. Moreover, Saunders and Fausch (2007) and Saunders (2010 [Chapter 2]) showed that terrestrial invertebrate inputs to streams in Colorado and Wyoming with riparian zones under two different types of rotational grazing management were more than double that for streams under season-long grazing. Likewise, terrestrial invertebrates made up $\geq 40\%$ of the biomass of summer afternoon trout diets, and also tended to be greater at sites managed for rotational grazing. Furthermore, trout biomass in the streams under intensive grazing management in Wyoming was more than double that in the streams under season-long grazing. However, the extent to which riparian grazing affects trout populations through these indirect food web pathways has not been tested with rigorous experimental manipulation.

To test the short-term effects of riparian cattle grazing and loss of woody riparian vegetation on terrestrial prey inputs to trout streams, I conducted a field experiment during summer 2008. My objectives were to: 1) evaluate the effects of a single grazing event on terrestrial invertebrate inputs to streams and trout populations, 2) to test whether either moderate or high grazing intensity reduces the input of terrestrial invertebrates, and the use of this prey resource by trout, compared to areas with no cattle grazing (wildlife grazing only), and 3) to compare the effects of a single

season of riparian cattle grazing to riparian conditions that might result from a prolonged period of poor grazing management where woody vegetation has also been reduced. I show that short durations of moderate and high intensity cattle grazing that occur once during midsummer, which rapidly reduce riparian vegetation biomass and overhead cover by 50 – 80%, have no detectable effect on the biomass of terrestrial invertebrates entering streams. In contrast, high intensity grazing plus removal of two-thirds of streamside woody vegetation caused reductions in terrestrial invertebrate inputs to streams, although these effects were variable. All experimental treatments reduced the biomass of terrestrial invertebrates in trout diets by the end of the experiment, but neither trout biomass nor density was reduced by any of the treatments.

Methods

Study sites and experimental design.— I selected four streams for study which had been managed under intensive rotational grazing consistently since the late 1980's (e.g., see Saunders and Fausch 2007), and which had robust herbaceous and woody riparian vegetation and little stream bank erosion. I then used cattle to achieve three intensities of herbivory, rather than selecting streams with a long history of continuous grazing and applying "reduced use" or "rest" treatments in hopes of improving riparian conditions. This experimental design allowed for greater control over riparian vegetation conditions, greater treatment effects, and comparisons of woody and herbaceous vegetation removal. As a result, riparian vegetation and invertebrate

communities resulting from the experimental treatments reflect a single season of riparian use, and may not be similar to conditions where riparian areas have been heavily grazed and are provided short-term rest (i.e., 1 – 5 growing season), or where grazing management is changed to allow for long-term improvement in riparian vegetation conditions.

Grazing treatments and controls were applied using a randomized complete block design (with streams as blocks) by constructing riparian pastures on Beaver, Cherry, Pass, and Red Canyon creeks near Lander, Wyoming (Figure 1, see Saunders and Fausch 2007 for additional description of study area). Study reaches were chosen to have similar riparian vegetation and stream characteristics and to be free of current beaver activity. The segments on Pass and Beaver creeks were at higher elevation than those on Red Canyon and Cherry creeks (average elevation = 2,300 m vs. 1,700 m) and tended to have larger stream substrate (cobbles and pebbles vs. pebbles and fines). The lengths of stream reaches enclosed by riparian pastures were designed to support at least 50 adult trout (based on previous estimates of trout densities, see Saunders and Fausch 2007). Each pasture also enclosed a 25-m long buffer at both the upstream and downstream ends of the study reach. At Red Canyon Creek (mean bankfull width $\overline{BF} = 2.0$ m), riparian pastures enclosed 250 m of stream, whereas at Cherry, Beaver, and Pass creeks ($\overline{BF} = 2.7, 3.0,$ and 3.5 m, respectively), riparian pastures enclosed 200 m of stream (i.e., 150-m study reach plus 50 m of buffer). Additionally, riparian pastures were separated by at least 100 m of stream (except for one pasture on Red Canyon Creek where only 75 m was possible) to serve as a treatment buffer and ensure that the

invertebrate drift entering study reaches was similar. Lateral fences connecting upstream and downstream cross fences (i.e., those perpendicular to the flow) were placed at least 25 m from the channel. The experimental pastures were constructed with three-strand electric fences energized with two solar electric fence energizers (Model S17 Solar, Gallagher USA, Kansas City, MO).

Four experimental treatments were designed to evaluate riparian conditions which would result from cattle grazing of riparian vegetation or livestock exclusion. In the Moderate intensity grazing treatment, cattle were removed from pastures after a residual stubble height of 10 – 15 cm (4 – 6 inches) of herbaceous vegetation was achieved. In the High intensity grazing treatment, cattle were removed when residual stubble height reached 5 – 7.5 cm (2 – 3 inches). A third treatment, labeled Woody Removal, combined high intensity grazing plus removal of streamside woody vegetation. Initially, 66% of the woody vegetation was removed from within 10 m of both sides of the channel, after which cattle were stocked to achieve a residual stubble height of 5 – 7.5 cm as in the High intensity treatment. High intensity grazing treatments resulted in greater grazing pressure than is recommended for riparian areas and greater levels of utilization (see below) than typically supported by healthy rangelands. However, treatments were designed this way to test the effects that extreme levels of grazing pressure, of short duration, have on the flux of terrestrial invertebrates to streams. In a fourth treatment, the Control, livestock were excluded from the riparian area throughout the experiment. The Moderate and High intensity treatments were designed to evaluate the effects of midsummer cattle grazing during a single growing

season, whereas the Woody Removal treatment was designed to simulate riparian conditions where streamside woody vegetation is reduced from prolonged poor grazing management such as may occur from prolonged season-long grazing in some riparian communities. The Control simulated riparian conditions resulting from a growing season without livestock use. Each treatment was designed for rapid implementation to minimize the amount of time cattle were present, and so minimize bank damage through trampling. Each treatment was applied after annual high water levels from snowmelt runoff subsided to minimize physical alteration of the riparian and aquatic habitat. Thus, treatments were designed to test the effects of vegetation removal by livestock on invertebrate prey resources for trout, and not the effects of stream bank degradation resulting from cattle grazing. The four treatments were assigned randomly to four pastures on each of the four streams (16 pastures total; Table 1).

Treatments were applied to pastures (i.e., cattle were stocked) sequentially (Red Canyon and Cherry creeks) or to two pastures at a time (Beaver and Pass creeks) during July 2008 (Table 1). The experiment ended during mid-September, 6 – 9 weeks after cattle had been removed from the last pasture on each stream. The three grazing treatments were applied by stocking 12 – 25 cow/calf pairs and 1 bull in each pasture, consisting of a mixture of Black Angus and Black Angus x Herford crosses. In the Woody Removal treatment, two of every three riparian shrubs within 10 m of each stream bank were first cut to ground level and removed from the pasture. The few aspen *Populus tremuloides* Michx. and lodgepole pine *Pinus contorta* Douglas ex louden <7.5 cm (3 in) in diameter within 10 m of the channel were also cut, but all larger trees were left.

Afterwards, cattle were stocked to achieve the 5 – 7.5 cm residual stubble height treatment. Cattle remained in each pasture for 2-4 d, except on Red Canyon Creek where pasture size and production of herbaceous vegetation were greater and cattle remained for 9 – 11 days (Table 1). Owing to the time required to construct experimental pastures and the availability of cattle, experimental treatments were completed later in Red Canyon and Pass creeks. Consequently, the experiment was about 20 d shorter in these streams. However, both the midterm and final samples of invertebrate inputs and trout diets were each conducted during the same two-week period each, with the two lower-elevation streams (Cherry and Red Canyon) being sampled the first week.

To evaluate the effect of riparian grazing on terrestrial invertebrate subsidies to trout, I measured riparian vegetation, input of terrestrial invertebrates and adult aquatic insects to streams, use of invertebrate prey resources by trout, and trout abundance, both before and after the experiment (i.e., using a BACI design; Stewart-Oaten et al. 1986; Manly 2001). Additionally, vegetation height, input of invertebrates to streams, and trout diets were measured three weeks after cattle had been removed from the last pasture (i.e., during a mid-term sampling period). To minimize the disturbance to aquatic habitat and avoid influencing trout behavior, all sampling, especially that which required handling fish, was conducted using the least intrusive means possible. Sampling procedures were similar to earlier studies, and so are briefly summarized here (see Saunders and Fausch 2007; Chapter 2 for complete description of sampling methods).

Streamside vegetation.—Riparian vegetation was sampled both to determine when grazing treatments had been achieved (i.e., stubble height monitoring), and to evaluate the effects of grazing treatments on streamside vegetation attributes that may influence the flux of invertebrates to streams. Aboveground vegetation biomass, vegetation height, and vegetation cover over the channel were quantified both before treatments and at the end of the 6-week experiment. To measure vegetation overhanging the channel before applying grazing treatments, hemispherical photographs were taken toward the zenith in the center of the channel and at both bankfull marks, at 10-m intervals in each study reach. Additionally, overhead cover was measured at the end of the experiment on 15 - 20 transects spaced 10 m apart that extended 4 m beyond the bankfull mark into the riparian zone. Hemispherical photographs were taken every 2 m on transects, and vegetation cover estimated by counting the points of a 100-point sampling grid, superimposed on each photograph, that intersected vegetation, as in previous work (see Chapter 2). At the end of the experiment, utilization of herbaceous vegetation was estimated by clipping vegetation within, and adjacent to, two 1-m² cattle exclosures located at random distances along the study reach, within 3 m of the channel in portions of the riparian zone dominated by herbaceous vegetation.

To describe vegetation use throughout each pasture, and to monitor vegetation regrowth throughout the experiment, three permanent transects were located perpendicular to the stream at random distances from the downstream end (one transect in each 50-m reach, or 67-m reach in Red Canyon Creek). Transects extended

into the riparian pasture for 30 m or to the pasture fence. The maximum height of grasses, forbs, and shrubs was measured at 1.5 m intervals on each transect.

Vegetation height was measured before grazing, 3 weeks after treatment application, and at the end of the experiment.

Invertebrate input and biomass in trout diets.— To measure the biomass of invertebrates entering streams, six pan traps were deployed in each treatment, three each at the bank and mid-channel, and stratified by the proportion of stream channel with high vs. low overhead cover (>35% vs. <35%; see Chapter 2). Two consecutive 3-d samples were collected during three periods: before applying grazing treatments, 3 weeks after cattle were removed, and at the end of the experiment. Three sampling occasions were conducted because previous research on these streams showed that terrestrial invertebrate inputs peak during August and fall to low levels during September, so there was the potential for fish to respond differently to grazing treatments throughout the experiment. The initial and final sampling was conducted before estimating fish abundance to avoid disturbing riparian vegetation and invertebrates. Each pan trap remained in the same place throughout the experiment, except when declining flow exposed the substrate beneath pan traps. These pan traps were moved to the nearest similar location.

During the 6-d sampling period for invertebrate input, 15 trout were captured in each study reach during late afternoon (ca. 1500 – 1900 h) using electrofishing, and stomach samples were collected using gastric lavage. The initial and final samples were collected at least 5 d before conducting fish abundance estimates to avoid influencing

trout feeding behavior, and also to avoid causing fish to emigrate owing to frequent electrofishing. Stomach contents were collected from trout of 120 – 350 mm fork length, which are those that are primarily insectivorous and large enough to sample efficiently for diets. On four occasions, to increase the number of trout collected when sampling Red Canyon Creek, electrofishing began 10 m below the downstream end of the sampling reach and extended 10 m upstream of it (i.e., within the 25-m buffer reaches inside the pastures). On two occasions I was unable to collect 15 individuals, so I resampled the reach once the following day. Fish sampled on the first occasion were given a partial fin clip (lower caudal) to avoid resampling. After diet samples were collected, trout were held in live wells for 2 h before being released near the location where they were originally collected.

In the laboratory, invertebrates were sorted to the taxonomic level necessary to identify their origin as terrestrial versus aquatic (generally Family, see Saunders and Fausch 2007 for details). Biomass (nearest 0.3 mg) of invertebrates found in pan trap and diet samples was measured after drying at 60°C for 48 h. Biomass of prey items in trout diets were estimated and reconstructed using published length-mass regressions based on total invertebrate length or head capsule width (Rogers et al. 1977; Smock 1980; Meyer 1989; Burgher and Meyer 1997; Benke et al. 1999; Johnston and Cunjak 1999; Sabo et al. 2002). Lengths were measured for up to 15 individuals of each taxon in each fish diet. When more were encountered, the mean mass of these 15 individuals was used to estimate biomass for the total number counted.

Fish abundance estimation.— Trout abundance and biomass were estimated before applying grazing treatments during July, and at the end of the experiment during September. Fish abundance was estimated using three-pass removal electrofishing conducted at night (Saunders et al. *in review* [Chapter 1]). During the initial estimate, fish were held for three hours in live wells after processing and released near their original location in the study reaches. However, they were not released within 25 m of the ends of the reach to minimize emigration after electrofishing.

Habitat and temperature measurements.— To evaluate whether experimental grazing treatments altered the amount and quality of habitat for trout, I measured aquatic habitat before and after the experiment. I measured the dimensions of all pools, runs, and undercut banks, and classified bed substrate, using methods described in Saunders et al. (*in review* [Chapter 1]). In each study reach, water temperatures were recorded hourly using Hobo temperature loggers (Onset Computer Corporation, Pocasset, MA) deployed at the downstream pasture fence.

Data analysis

Analysis of variance (ANOVA) was used to test for differences in vegetation measurements, falling invertebrate input, and density and biomass of trout. For these analyses, the stream reach was the experimental unit, and means of subsamples taken at each site during each sampling period (e.g., individual pan trap samples) were used as data. An ANOVA was also used to analyze differences in invertebrate biomass in trout diets, treating each fish as an individual sampling unit and including fixed effects for fish

species and length to account for individual variation in trout diets. Experimental block (i.e., stream) was included as a random effect in all initial models and removed if clearly not significant ($P \geq 0.15$). In each analysis, fixed factors included grazing treatment ($n = 4$) and sampling period ($n = 2$ or 3). Trout species ($n = 3$) and relative length were also included in the analysis of invertebrate biomass in trout diets to account for variability among individual fish. Larger trout within populations become dominants, hold optimal foraging positions in streams (Fausch 1984; Nakano 1995), and are expected to ingest a greater biomass of prey compared to subordinate fish. Relative length was defined as the length of the individual fish divided by the length of the fish at the 90th percentile, determined from the initial and final electrofishing samples. During both the initial and final electrofishing samples, the size structure of trout populations were similar among reaches within each stream, so the length of the fish at the 90th percentile was determined by pooling fish length data from all reaches on a stream. The length of the fish at the 90th percentile during the midterm diet sample was estimated as the average of those determined for the initial and final sampling periods. For all periods, individuals $\geq 90^{\text{th}}$ percentile were assigned a relative length of 1. All invertebrate data were transformed using natural logarithms before analysis to meet normality assumptions of the analyses. However reported treatment means and effect sizes for these data represent back-transformed data in the original scale. Standard errors for back-transformed data were estimated using the Delta Method (DeGroot and Schervish 2002)

If grazing treatments affected riparian vegetation and subsidies of terrestrial invertebrates to trout, there would be a significant interaction between grazing treatments and sampling period. That is, I expected response variables in grazing treatments to be similar initially to control reaches, but to differ after the treatments were applied during either midterm or final sampling occasions. Therefore, to test this hypothesis I evaluated planned comparisons among predicted treatment means (i.e., Least-Squares Means), but only within sampling periods. Owing to naturally high variation in the flux of terrestrial subsidies to streams and their effects on consumers (Baxter et al. 2005; Marczak et al. 2007), statistical significance was determined at $\alpha = 0.1$ to avoid Type II statistical error. That is, if grazing treatments caused important effects, I wanted to avoid the risk of failing to detect them (Type II error), thereby potentially allowing damage to riparian resources, more than the risk of claiming effects when there are none (Type I error). Before testing for effects, I first verified that initial conditions were similar among all treatments (i.e., $P > 0.1$). Then, conditional on initially finding significant fixed effects (either interaction or main effects), I evaluated whether treatment means differed from control reaches during either the midterm or final sampling period using Fisher's protected LSD for pairwise contrasts.

Results

Aquatic habitat

Overall, aquatic habitat was not affected by grazing treatments, although there was less pool volume and surface area of runs at the end of the experiment because

flows had declined. There was no significant treatment-by-period interaction (ANOVA, treatment x period interaction: $F = 0.48$, $P = 0.70$), suggesting that experimental treatments did not reduce the amount of undercut banks relative to the Control. Sites had similar amounts of undercut banks among all treatments (averaging 36 m per site; ANOVA treatment effects: $F = 0.55$, $P = 0.65$), and the total amount of undercut banks did not differ between the initial and final sampling periods (ANOVA, period effects: $F = 0.71$, $P = 0.41$). Furthermore, although there was less total surface area of runs and total pool volume at site during the final sampling period (ANOVA, period effects: $F_{run} = 6.52$, $P = 0.004$, $F_{pool} = 7.52$, $P = 0.0007$), the total amount of habitat was similar among treatments during both the initial and final sampling periods ($P > 0.52$ for treatments).

Riparian vegetation

Overall, the three experimental grazing treatments resulted in significantly greater utilization of herbaceous vegetation than occurred naturally at Control sites, and quickly reduced riparian vegetation height and standing crop to low levels (ANOVA: $F = 19.26$, $P < 0.0001$; least-squares means comparisons of Control to each grazing treatment, $P < 0.0001$; Figure 2). Moreover, High intensity and Woody Removal sites received 1.6 and 1.4 times the utilization as sites that received Moderate grazing (LS means; $P_{M-I} = 0.001$, $P_{M-WR} = 0.07$). These greater levels of utilization at sites receiving grazing treatments resulted in reductions in maximum height of herbaceous vegetation throughout pastures, and of aboveground biomass of herbaceous vegetation along streambanks. Height of herbaceous vegetation was initially similar among all

treatments ($P > 0.40$) and remained consistent throughout the experiment at Control sites, but was reduced by all three grazing treatments (Figure 3; ANOVA treatment X period interaction: $F_{grass} = 1.83$, $P = 0.1$; $F_{forb} = 4.27$, $P = 0.003$). Throughout the experiment, grasses at Control sites averaged 69 cm tall ($SE = 9.6$), whereas by the end of the experiment grass height was reduced by 53% compared to the Control at sites receiving Moderate grazing (least-squares mean comparison: $t = 2.6$, $P = 0.01$) and, on average, by 74% under both high intensity grazing treatments (LS means: $t_{C-I} = 3.53$, $P = 0.001$; $t_{C-WR} = 3.8$, $P < 0.001$). Similarly, forbs averaged 49.0 cm tall ($SE = 9.4$) at Control sites throughout the experiment, but by the end of the experiment were reduced by 45% at Moderate sites (LS means: $t = 2.25$, $P = 0.03$), and by more than 75% under High intensity (LS means: $t = 4.82$, $P < 0.001$) and Woody Removal treatments (LS means: $t = 4.78$, $P < 0.001$). Differences in forb heights between the Moderate treatment and both High intensity and Woody Removal treatments were also significant during the final sampling period (LS means: $t_{M-I} = 2.58$, $P = 0.01$; $t_{M-WR} = 2.53$, $P = 0.02$).

Aboveground biomass of herbaceous vegetation and total overhead vegetation cover were also initially similar among sites, but reduced by experimental treatments (Figure 4). Aboveground biomass of herbaceous vegetation along stream banks was similar during the initial sampling periods ($P > 0.3$), but was reduced to a similar extent as vegetation height by each of the three grazing treatments (ANOVA treatment x period interaction: $F = 2.76$, $P = 0.07$; Figure 4A). There was, on average, $180 \text{ g} \cdot \text{m}^{-2}$ ($SE = 44.1$) herbaceous streamside vegetation at sites during the initial sampling period, but at the end of the experiment Control sites had, on average, 2.2 times the aboveground

vegetation biomass as Moderately grazed sites (LS means: $t = 2.21$, $P = 0.04$), 6.0 times that at Intensively grazing sites (LS means: $t = 3.25$, $P = 0.004$), and 3.0 times that at Woody Removal sites (LS means: $t = 2.63$, $P = 0.02$). The amount of overhead cover, contributed primarily by streamside woody vegetation, was also reduced by the experimental treatments, but differences between treatments and Control were significant only for the Woody Removal treatment (ANOVA: $F = 3.29$, $P = 0.01$; LS means: $t = 2.79$, $P = 0.01$; Figure 4B). Initially, overhead cover at all sites averaged 63% (SE = 7.0, $P > 0.5$), but after treatments were applied Control sites had 1.4 times the overhead cover as either Moderate or High intensity sites ($P \geq 0.1$), and 1.9 times the overhead cover at Woody Removal sites.

Invertebrate input to streams

The initial biomass of terrestrial invertebrates and adult aquatic insects falling into streams was similar for Control and both Moderate and High intensity sites, but tended to be lower at Woody Removal sites (Figure 5). However, the biomass of invertebrates falling into streams was highly variable throughout the experiment and the effects of experimental treatments were inconsistent among the streams sampled. Before application of experimental treatments, all study sites received similar amounts of terrestrial invertebrate biomass (LS means: $P \geq 0.3$). Terrestrial invertebrate input also varied among sampling periods, with sites receiving, on average, 3.4 times the biomass during the midterm sampling period as during the initial sampling period, and 2.0 times that during the final sampling period (ANOVA: $F_{\text{period}} = 28.6$, $P < 0.0001$).

During the midterm sampling period (i.e., mid-August), when terrestrial input to streams was generally high, Control sites received similar amounts of terrestrial invertebrate biomass as both Moderate and High intensity sites (LS means: $P \geq 0.60$). However, Control sites received 1.8 times the biomass as Woody Removal sites (LS means: $t = 1.86$, $P = 0.07$). During the final sampling period, after the peak of terrestrial input, the biomass of terrestrial invertebrates entering streams was similar for all experimental treatments ($P > 0.39$).

The effect of experimental treatments on input of terrestrial invertebrates differed among streams, which accounted for some of the variability within treatments. Sites responded to the Moderate, High intensity, and Woody Removal treatments as hypothesized on Red Canyon and Cherry creeks, the two lower elevation streams, but treatments had little effect on input at Pass Creek and no effect on Beaver Creek (Figure 6). Therefore, I analyzed the data for Red Canyon and Cherry creeks as a separate pair to see if these sites could account for the general trends found when all four sites were analyzed together. In general, the three treatments reduced the biomass of terrestrial invertebrates to a greater extent at these two sites, such that during the midterm sampling period Control sites received 3.9 times the biomass entering Woody Removal sites (LS means: $t = 2.62$, $P = 0.02$). At these streams, the difference between Control and Woody Removal sites was primarily a result of greater biomasses of Orthoptera, Homoptera, and Lepidoptera taxa entering Control sites (Appendix 1).

The biomass of adult aquatic insects entering sites was similar among control and treatment reaches throughout the experiment, but highly variable among sites

(Figure 5). In contrast to terrestrial invertebrates, the greatest biomass of emerging adult aquatic insects returned to fall into streams during the initial sampling period, and the lowest levels were measured during the midterm sampling period (ANOVA: $F_{period} = 3.87$, $P < 0.03$). During the initial sampling period, before treatment application, and also during the midterm sampling period, the biomass of adult aquatic insects was similar among all sites ($P \geq 0.50$). In contrast, during the final sampling period, Control sites received, on average, 2.3 times the adult aquatic biomass as Woody Removal sites (LS means: $t = 1.65$, $P = 0.1$), whereas Moderate and High intensity sites received intermediate levels of adult aquatic insect biomass (Appendix 2).

Invertebrate biomass in trout diets

In general, the biomass of terrestrial invertebrates in trout diets reflected the biomass of these taxa entering streams across periods, but was significantly greater at Control sites during the final sampling period than at sites which received experimental treatments (ANOVA grazing x period interaction: $F = 2.82$, $P = 0.01$; Figure 7). The length of individual fish, relative to the 90th percentile, had a strong positive effect on the biomass of terrestrial invertebrates in trout diets (ANOVA: $F = 77.4$, $P < 0.0001$), so estimates of treatment effects were made while holding the relative length of fish constant. However, trout species was not a significant parameter, and so was removed from the model to conserve degrees of freedom. Trout at all sites had similar amounts of terrestrial invertebrate biomass in their diets both before applying treatments ($P > 0.10$) and during the midterm sampling period ($P \geq 0.34$). However, during the final

sampling period, trout at Control sites had, on average, 4.4 times the terrestrial invertebrate biomass in their diets as trout at Moderate sites (LS means: $t = 4.35$, $P < 0.0001$), 1.8 times that of trout at Intensively grazed sites (LS means: $t = 1.88$, $P = 0.07$), and 2.4 times that of trout at Woody Removal sites (LS means: $t = 2.58$, $P = 0.01$). Averaged across sampling periods, terrestrial invertebrates contributed more to trout diets at Control sites (55%), than at either Moderate (45%; ANOVA: $F_{\text{treatment}} = 3.27$, $P = 0.02$; LS means: $t_{C-M} = 2.87$, $P = 0.004$) or Woody Removal sites (46 %; LS means: $t_{C-WR} = 2.36$, $P = 0.02$). However, the contribution of terrestrial invertebrates to trout diets was similar at Control and High intensity sites (50%; $P = 0.22$). At all sites, terrestrial invertebrate biomass contributed more to trout diets during both midterm and final sampling periods (ca. 51 -71%) than during the initial sampling period (ca. 26 – 32%; ANOVA: $F_{\text{period}} = 80.52$, $P < 0.0001$).

In contrast, aquatic invertebrate biomass in trout diets (both aquatic larvae and emergent adults that returned to the stream) was greatest during the initial sampling period, but after applying treatments tended to be greater at treatment sites than Control sites. Both trout species and relative fish length had significant effects on the biomass of aquatic invertebrates in trout diets, so these factors were held constant when evaluating treatment effects. There was a significant treatment-by-sampling-period interaction in the biomass of aquatic invertebrates in trout diets (ANOVA grazing x period interaction: $F = 3.70$, $P = 0.001$; Figure 6), but in general the biomass of aquatic invertebrates in trout diets at all sites decreased over the duration of the experiment. Before applying experimental treatments, trout at sites slated for the High intensity

grazing treatment had, on average, 1.5 times the biomass of aquatic invertebrates in their diets of fish at other sites ($P = 0.10$), but during the midterm sampling period trout at Woody Removal sites had significantly more (1.8 – 2.9 times) aquatic invertebrate biomass in their diets than trout at all other sites ($P_{WR-C} < 0.0001$, $P_{WR-M} = 0.02$, $P_{WR-I} = 0.0005$). Furthermore, during the midterm period, trout at Moderate sites had, on average, 1.6 times the aquatic invertebrate biomass in their diets as trout at Control sites ($P = 0.05$). During the final sampling period, trout at High intensity and Woody Removal sites had similar amounts of aquatic invertebrates in their diets, and on average, had 2.0 times that of trout at moderately grazed sites ($P < 0.005$) and 1.4 times that of trout at control sites ($P = 0.1$).

Trout populations

Trout populations did not respond to the grazing treatments (Figure 8). There were no detectable differences in fish density (ANOVA: $F = 0.05$, $P = 0.9$) or biomass (ANOVA: $F = 0.08$, $P = 0.9$) resulting from the experimental grazing or removal of woody riparian vegetation.

Discussion

In general, high intensity grazing combined with removal of woody riparian vegetation had the strongest effect on invertebrate inputs to streams, whereas all three grazing treatments reduced terrestrial invertebrates in trout diets in late summer. Overall, application of a single grazing event of either moderate or high grazing intensity

had no detectable effect on the biomass of terrestrial invertebrates or adult aquatic insects entering streams, owing to high variation among sites receiving the same treatment. In contrast, woody removal treatments reduced invertebrate input during periods when terrestrial and aquatic inputs peaked, although this effect was evident only in the two lower-elevation streams. During the midterm sampling, trout diets had similar biomass of terrestrial invertebrates among all treatments, but the three grazing treatments reduced terrestrial biomass in trout diets by late summer. Strong treatment effects on trout diets may have resulted from selective foraging behavior and high mobility of these fish. In contrast, trout at control sites tended to have less aquatic invertebrate biomass in their diets than trout at treatment sites. Despite these differences, fish populations were unaffected by experimental removal of riparian vegetation. The results reported here indicate that a single grazing event of short duration, even of high intensity, had little detectable effect on terrestrial invertebrate subsidies to streams, but the additional removal of woody vegetation caused significant reductions of this resource, especially in mid-elevation streams. However, it remains unclear whether trout populations would be reduced if these effects had been monitored for a longer duration.

Riparian vegetation

Overall, experimental treatments, applied by stocking cattle in small pastures for short durations, were effective at rapidly reducing riparian vegetation to levels that have been found to reduce terrestrial invertebrate inputs to streams. In general,

grazing reduced the height and aboveground biomass of vegetation remaining in riparian pastures, and manual removal of woody vegetation also reduced the total overhead cover along stream banks. Herbaceous vegetation height was reduced by about 45 – 70% by cattle grazing, and total aboveground biomass of herbaceous vegetation was reduced by 55 – 87%. Estimates of herbaceous utilization indicate even greater levels of grazing intensity than residual stubble heights imply, likely owing to having measured maximum vegetation heights. Additionally, Woody Removal treatments reduced total overhead streamside vegetation to about half of that (52%) at Control sites. Overall, the experimental levels of vegetation reduction achieved in the present study exceed those recommended for riparian areas, and also exceed typical utilization targets for a single grazing season used by most commercial livestock operations.

In general, all grazing treatments resulted in vegetation characteristics that were similar to sites managed for season-long grazing that I studied in Colorado and Wyoming. For example, during the final sampling period, the aboveground biomass of herbaceous vegetation in moderately grazed pastures was $82 \text{ g} \cdot \text{m}^{-2}$ and in intensively grazed pastures was $31 \text{ g} \cdot \text{m}^{-2}$, which are lower than previously measured in the same region for season-long sites (ca. $150 \text{ g} \cdot \text{m}^{-2}$, Saunders and Fausch 2007) but similar to amounts of aboveground vegetation at season-long sites in north-central Colorado (ca. $45 - 90 \text{ g} \cdot \text{m}^{-2}$, Chapter 2). Furthermore, sites from which streamside woody vegetation was removed had similar amounts of overhead cover as season-long sites in Colorado and Wyoming (ca. 23 – 35 %, Saunders and Fausch 2007; Chapter 2). In contrast, sites

receiving grazing-only treatments had levels of overhead cover intermediate between sites elsewhere managed for season-long and rotational grazing. Overall, given these comparisons, one might expect experimental treatments to reduce the biomass of terrestrial invertebrates entering streams to levels similar to those measured at sites grazed season long.

Invertebrate input to streams

There was evidence that removal of woody vegetation combined with high intensity grazing reduced the input of terrestrial invertebrates and adult aquatic insects to streams during periods when input was the highest. Thus, Control sites received more terrestrial invertebrate biomass than Woody Removal sites during the midterm sampling period, and more adult aquatic insect biomass during the final sampling period. These differences coincided with periods of high terrestrial inputs during midsummer, and a period of greater inputs of adult aquatic insects in late summer. Kawaguchi and Nakano (2001) also reported that differences between grassland and forested sites in the biomass of terrestrial invertebrates entering streams were significant only during summer when terrestrial invertebrate inputs were greatest. In contrast, differences between Control sites and either Moderate or High intensity sites were smaller and not significant during either sampling period.

The results reported here indicate that streamside woody vegetation plays an important role in the amount of both terrestrial and aquatic invertebrates entering streams, because the treatment that combined high intensity grazing and woody

vegetation removal resulted in less invertebrate biomass input than control sites during periods when input to sites was high, whereas high intensity grazing only did not reduce invertebrate inputs. Woody riparian vegetation, which provided greater vertical structure along streambanks than herbaceous vegetation, may serve to increase invertebrate densities near streams (e.g., Morris 2000; Zurbugg and Frank 2006), while also increasing the potential for invertebrates to fall or be blown into streams. Saunders and Fausch (2007) also report that input of adult aquatic insects to streams managed for high-density short-duration grazing was greater than at streams managed for season-long grazing, suggesting that streamside vegetation may be important for concentrating recently emerged aquatic insects at the stream-riparian ecotone. However, reductions in overhead vegetation cover caused by removing streamside woody vegetation were highly variable among streams, suggesting that cutting down riparian woody vegetation does not replicate the process of destroying it through prolonged season-long grazing. Although inputs of riparian leaf litter are likely to influence the secondary production of aquatic insects in small streams (Vannote et al. 1980; Wallace et al. 1997), the experimental treatments used here were unlikely to affect these inputs of detritus because they occurred before treatments were applied. This suggests that the patterns measured in this experiment likely resulted from effects on adult insects after they emerged from the streams, not from effects on larval insects within the stream environment.

In contrast to earlier work conducted in rangelands, the results presented here suggest that terrestrial invertebrate input to streams draining semi-arid grasslands may

be both greater and more variable than previously thought. For example, estimates of the biomass of terrestrial invertebrates entering Control reaches during the midterm sampling occasion (i.e., August) ranged from 176 - 780 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, and during the final sampling period (early September) the control site on Red Canyon Creek received 995 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ of terrestrial invertebrate biomass (primarily Orthoptera, Hymenoptera, Lepidoptera, and Homoptera). These upper limits measured at control sites are greater inputs of terrestrial invertebrates to streams than have previously been reported for streams that drain deciduous forests (ca. 450 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, Cloe and Garman 1996; see Baxter et al. 2005 for review). Furthermore, on average, terrestrial invertebrate biomass entering these rangeland streams in Wyoming during 2008 was 2.9 – 9.8 times that entering rangeland streams in Colorado during 2007 (ca. 10 – 58 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, Chapter 2) and was 1.5 – 5.6 times levels previously measured at sites, including some of the same streams, in central Wyoming under high-density short-duration grazing management during 2004 – 2005 (Saunders and Fausch 2007). Finally, terrestrial invertebrate inputs to Wyoming streams during 2008 were more than an order of magnitude greater than measured in grazed and ungrazed grassland streams in New Zealand (ca. 1.3 - 5.7 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$; Edwards and Huryn 1995, 1996). Moreover, because the biomass of terrestrial invertebrates entering the control site at Red Canyon Creek during the midterm and final sampling periods was 4.2 and 28.5 times that entering the control sites at Cherry Creek (two adjacent streams, separated by less than 3 km), these results suggest that factors influencing the biomass of terrestrial

invertebrates entering streams are likely to vary over relatively small spatial scales, and may be affected by differences in local plant communities and microclimate conditions.

Invertebrate biomass in trout diets

All three experimental grazing treatments reduced the biomass of terrestrial invertebrates in trout diets at the end of summer, relative to Control sites, but terrestrial biomass in trout diets was similar among treatments and Control sites during midsummer when input of terrestrial insects was highest. Overall, terrestrial invertebrates were an important component of trout diets, as has been reported by numerous authors (e.g., Wipfli 1997; Nakano et al. 1999a; Utz and Hartman 2007). Terrestrial invertebrates contributed, on average, 59% of the biomass to the diets of trout at all sites during the midterm and final sampling periods, but contributed more to fish at control sites during these periods (68%). This represents a greater contribution to trout diets than was measured in rangeland streams in Colorado where terrestrial invertebrates accounted for, on average, 30 – 40% of the biomass in trout diets (Chapter 2). Furthermore, trout at grazed sites in Wyoming tended to have more terrestrial biomass in their diets than trout in Colorado, except in Colorado streams managed for simple rotational grazing (range: 48 – 106 mg•fish⁻¹). In contrast, Edwards and Huryn (1995, 1996) reported that terrestrial invertebrates generally contributed little to trout diets in New Zealand rangelands, and that biomass of terrestrial prey consumed by trout was not influenced by grazing practices.

Trout diets were generally variable ($CV = 0.43$ averaged across treatments), as in Colorado streams (Chapter 2), owing to variation among individual fish and among study streams, which limited the ability to detect differences among treatments. One apparent paradox is that the biomass of terrestrial invertebrates in trout diets was reduced at all treatment sites compared to the Control during the final sampling period but not during the midterm period when there was greater terrestrial biomass entering streams. Furthermore, during the final sampling period, there was no significant difference in the biomass of terrestrial invertebrates entering streams. At higher levels of terrestrial input during the midterm sampling period, terrestrial prey items might not have been limited at treatment sites. Alternatively, trout may be able to take advantages of smaller differences in the availability of terrestrial prey than were detectable using pan traps by selecting for terrestrial prey over aquatic prey when available, owing to their larger size (Furukawa-Tanaka 1985; Ringler 1989; Nakano et al. 1999a), or selecting foraging locations where terrestrial invertebrates were locally abundant and actively searching for terrestrial prey items (Fausch 1984; Gowan and Fausch 2002).

In contrast, the biomass of aquatic invertebrate prey in trout diets (primarily adult and larval aquatic insects) was lower at Control sites than under High intensity and Woody Removal treatments. These results suggest that fish at intensively grazed sites may have been compensating for reduced terrestrial prey (even though I did not observe significant differences in input to pan traps among treatments), by consuming more aquatic prey, as has been observed in other experiments where terrestrial inputs

were reduced (e.g., Nakano et al. 1999b, Baxter et al. 2004). Overall, the biomass of aquatic prey in trout diets was less variable than terrestrial invertebrate prey (average $CV = 0.17$), and differences in the biomass of aquatic invertebrates among treatments were smaller than for terrestrial invertebrate biomass. Two exceptions to this pattern were the biomass of aquatic prey in trout diets at High intensity sites during the initial sampling period and at Woody Removal sites during the midterm sampling period. In both cases, estimates of the aquatic invertebrate biomass in trout diets was strongly influenced by a few fish from a single site (Beaver Cr. [initial] and Pass Cr. [midterm]), that had consumed large numbers of Diptera larvae (mostly Chironomidae; e.g., one fish had consumed >550 chironomid larvae).

Trout populations

Neither grazing nor Woody Removal treatments had detectable effects on either the density or biomass of trout in study reaches during the experiment. These results contrast those reported by Saunders and Fausch (2007) and in Chapter 2 (although results in Colorado were highly variable), where trout biomass at sites managed for season-long grazing was 40 – 56% lower than at sites managed for rotational grazing. Those season-long sites had similar levels of riparian vegetation as the treatment sites measured here, and characteristics of the Control sites here were similar to sites managed for rotational grazing in both previous studies. These results indicate that prolonged season-long grazing, shown to reduce terrestrial inputs throughout summer months (Saunders and Fausch 2007; Chapter 2), reduces trout populations, whereas fish

may be able to compensate for moderate reductions in terrestrial inputs that occur only for a portion of the summer resulting from a high-intensity grazing event of short duration. Additionally, these results suggest that the short-term effects of manual willow removal on trout populations are not equivalent to the effects of prolonged season-long cattle grazing.

The results reported here also contrast those of another experiment by Kawaguchi et al. (2003) where terrestrial prey subsidies were reduced. Those investigators demonstrated that reducing terrestrial invertebrate input by 70% by erecting greenhouse canopies over stream reaches caused larger fish to emigrate from resource-poor treatments. However, although high intensity grazing resulted in >75% reductions of herbaceous vegetation, and the Woody Removal treatment combined this with removing 66% of all streamside shrubs and small trees, it does not appear that these treatments had a consistent effect on the flux of terrestrial invertebrates to streams. As such, treatments may not have resulted in a strong enough stressor to cause trout to emigrate from study reaches. Alternatively, Bayley and Li (2008) reported that grazing exclosures that protected 123 – 436 m of stream, which were similar in length to those used here, were likely too small to support increased populations of adult trout, even though some exclosures had been in place for 45 years. It is possible that the small pasture sizes in the present study may have allowed fish to move easily among treatment and untreated reaches, and thereby access feeding opportunities elsewhere. Furthermore, final population estimates were conducted in mid-September when brook trout had begun to spawn in the higher-elevation streams, and brown trout

were preparing to spawn in the lower-elevation ones, so prey resources may have been less important to trout than sufficient spawning habitat. During the final sampling period adult brook trout in the higher-elevation streams were ripe and exhibiting spawning behavior (e.g., holding positions on nests [redds]; WCS, personal observation).

Comparison with other experiments on invertebrate inputs to streams

The results presented here contrast those of previous experiments in which treatments were designed to largely eliminate the flux of terrestrial invertebrates to streams. In general, experimental grazing treatments caused smaller reductions of terrestrial invertebrates than earlier experiments, and smaller and more variable effects on trout diets and abundance. For example, experiments in which stream reaches were covered with mesh greenhouses to investigate the effects of simulated deforestation showed that strongly reducing terrestrial inputs can cause trout to emigrate from treatment reaches (e.g., 50% reduction in salmonid biomass; Kawaguchi et al. 2003), reduce their growth (Baxter et al. 2007), and cause them to shift to foraging on aquatic invertebrates, thereby restructuring the entire stream food web (e.g., Nakano et al. 1999b; Baxter et al. 2004; see Fausch et al. 2010 for review). These contrasting findings may result from differences in the intensity of treatments as well as the experimental design. For example, the greenhouse canopies created a relatively uniform barrier to insect fluxes from riparian habitats to the stream, and generally reduced inputs by 70-90%. In contrast, the grazing and woody removal treatments used here formed neither a barrier to insect movement nor resulted in uniform conditions along the stream-

riparian ecotone. As such, these treatments are of lower intensity, but provide a better comparison to actual land use practices in riparian areas such as short-duration rotational grazing. Additionally, previous experiments applied multiple replicates of treatments within the same stream (e.g., Kawaguchi et al. 2003; Baxter et al. 2004), whereas in this study only a single replicate of each treatment was applied to each of four different streams. Thus, variation among streams, which is often high, is combined with variation in the effects of grazing treatments on the processes by which invertebrates fall into streams and trout forage on them. Additionally, all of these processes likely interact in complex ways as streams respond differently to treatments. For example, although input of terrestrial invertebrates tended to be greater at Control sites than at Woody Removal sites, this effect was strong only at the two lower-elevation streams. In contrast, at the higher-elevation streams, experimental treatments had no detectable effect on terrestrial input, contradicting the hypothesis that vegetation removal would reduce inputs. Overall, the results reported here indicate that terrestrial invertebrates are important prey subsidies for trout, but that high-intensity short-duration grazing affects them more under certain conditions than others, such as in the mid-elevation streams I studied. Furthermore, trout may be able to compensate for moderate short-term reductions in terrestrial invertebrate inputs (e.g., through increased foraging movements, stronger selection, or reduced growth). This may explain why trout biomass was not reduced in this experiment to levels that have been measured at sites under prolonged season-long grazing, which results in low

levels of riparian vegetation similar to those caused by the experimental treatments applied here.

Management implications

I tested the specific hypothesis that either moderate or high intensity grazing events of short-duration, and additional removal of woody vegetation, would reduce trout populations by reducing the amount of terrestrial prey entering streams. The data reported here indicate that a single midsummer grazing event, even when intensive (e.g., 53-87% utilization), had few effects on the input of terrestrial invertebrates to streams and trout populations, although it apparently can reduce the biomass of terrestrial prey in trout diets by late summer. However, combining high intensity grazing with removal of 66% of woody vegetation within 10 m of either streambank caused reductions in both terrestrial input and the biomass of terrestrial invertebrates in trout diets. This latter treatment was designed to mimic riparian conditions from prolonged poor grazing management resulting in the loss of riparian shrubs.

These results corroborate the findings of two comparative studies which report that terrestrial invertebrates subsidies to streams grazed season-long were substantially less than sites grazed under rotational systems (Saunders and Fausch 2007; Chapter 2). However, I caution managers that pastures in this study were small, so it is unclear how these results would scale up to pasture sizes typical of commercial livestock operations. Moreover, experimental reaches were not monitored after subsequent high-flow events, so I cannot report on the effects experimental treatments had on bank stability

or aquatic habitat in subsequent years. In general, the results reported here suggest that terrestrial invertebrate subsidies to streams can be relatively resistant to short, but high intensity, bouts of grazing, and that rotational grazing systems that combine high-density short-duration grazing with periods of plant recovery may also support the terrestrial invertebrate subsidies to streams necessary to maintain robust trout populations. Furthermore, managers should design grazing practices that will maintain streamside woody vegetation, which provides vertical structure and overhead cover, in order to support riparian-stream linkages that provide terrestrial prey resources for trout.

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System	Probes	Treatment	Time Spaced	Experiment Duration	Duration (d)	Sampling Rate (Hz)	Fluorescence Area (a.u.)
Cherry	1	High Intensity	1000	11 July - 10 Sep (61 d)	1	10	0.05
Cherry	2	Control	1000	6 July - 10 Sep (67 d)	1	10	0.05
Cherry	3	Viscosity Removal	1000	14 July - 10 Sep (58 d)	1	10	0.05
Cherry	4	Medium Intensity	1000	14 July - 10 Sep (58 d)	1.5	10	0.05
Red Canyon	1	Medium Intensity	1000	6 August - 10 Sep (35 d)	10	60	1.20
Red Canyon	2	Wood's Removal	1000	2 August - 10 Sep (40 d)	9	60	1.01

The data presented in this table are the result of a series of experiments conducted at the Red Canyon site. The experiments were designed to test the effect of different treatments on the fluorescence of the Cherry and Red Canyon systems. The treatments included High Intensity, Control, Viscosity Removal, Medium Intensity, and Wood's Removal. The results show that the fluorescence area (a.u.) is significantly higher for the Cherry system compared to the Red Canyon system. The Cherry system shows a fluorescence area of 0.05 a.u., while the Red Canyon system shows a fluorescence area of 1.20 a.u. The Wood's Removal treatment for the Red Canyon system resulted in a fluorescence area of 1.01 a.u. The duration of the experiments was 61 days for the Cherry system and 40 days for the Red Canyon system. The sampling rate was 10 Hz for the Cherry system and 60 Hz for the Red Canyon system. The time spaced for the Cherry system was 1000 and for the Red Canyon system was 1000. The experiment duration for the Cherry system was 11 July - 10 Sep (61 d) and for the Red Canyon system was 6 August - 10 Sep (35 d). The experiment duration for the Wood's Removal treatment for the Red Canyon system was 2 August - 10 Sep (40 d).

Table 1. — Characteristics of experimental pastures in four study streams in central Wyoming. Four experimental grazing treatments were applied to each stream in a randomized complete block design (see text, Position 1 represents the most downstream pasture). Trout species present (BNT: brown trout, BKT: brook trout, RBT: rainbow trout) are listed in order of abundance. Experiment duration is the period from after application of experimental grazing treatments (i.e., after cattle were removed from experimental pastures), until the final pan trap sampling commenced. For control sites, experiment duration represents the period between initial and final sampling. Grazing duration indicates the number of days of cattle grazing that was needed to achieve treatment stubble heights in riparian pastures. Stocking rate indicates the animal unit days of grazing that pastures received.

Table 2—continued

Stream	Position	Treatment	Trout species	Experiment Duration	Grazing Duration (d)	Stocking Rate (AUD)	Pasture Area (ha)
Cherry	1	High intensity	BNT	11 July – 10 Sep (61 d)	2	30	0.65
Cherry	2	Control	BNT	6 July – 10 Sep (67 d)	-	-	0.73
Cherry	3	Woody Removal	BNT	14 July – 10 Sep (58 d)	2	30	0.80
Cherry	4	Moderate intensity	BNT	14 July – 10 Sep (59 d)	1.5	21	0.91
Red Canyon	1	Moderate intensity	BNT	4 August – 10 Sep (38 d)	11	66	1.20
Red Canyon	2	Woody Removal	BNT	2 August – 10 Sep (40 d)	9	90	1.01
Red Canyon	3	Control	BNT	28 July – 10 Sep (45 d)	-	-	1.21
Red Canyon	4	High intensity	BNT	2 August – 10 Sep (40 d)	9	90	0.90

Table 1—continued

Stream	Position	Treatment	Trout species	Experiment Duration	Grazing Duration (d)	Stocking Rate (AUD)	Pasture Area (ha)
Pass	1	Moderate intensity	RBT, BKT	3 August - 17 Sep (45 d)	2	24	1.04
Pass	2	Woody Removal	RBT, BKT	4 August - 17 Sep (45 d)	2.5	40	1.01
Pass	3	High intensity	BKT, RBT	4 August - 17 Sep (45 d)	2.5	40	0.82
Pass	4	Control	BKT, RBT	31 July - 17 Sep (50 d)	-	-	0.56
Beaver	1	High intensity	BKT	17 July - 17 Sep (63 d)	3	45	0.74
Beaver	2	Moderate intensity	BKT	17 July - 17 Sep (63 d)	2	30	0.96
Beaver	3	Control	BKT	14 July - 17 Sep (66 d)	-	-	0.92
Beaver	4	Woody Removal	BKT	23 July - 17 Sep (56 d)	3	45	0.98

Figure 1. — Map showing the study area in west central Wyoming, and the experimental design. Triangles show locations where four experimental pastures were constructed on each of the four streams. Electric fences that enclosed experimental pastures on one stream are shown as dotted lines (base on GPS delineations), and sampling reaches (see text) are shown as solid lines with bold end points.

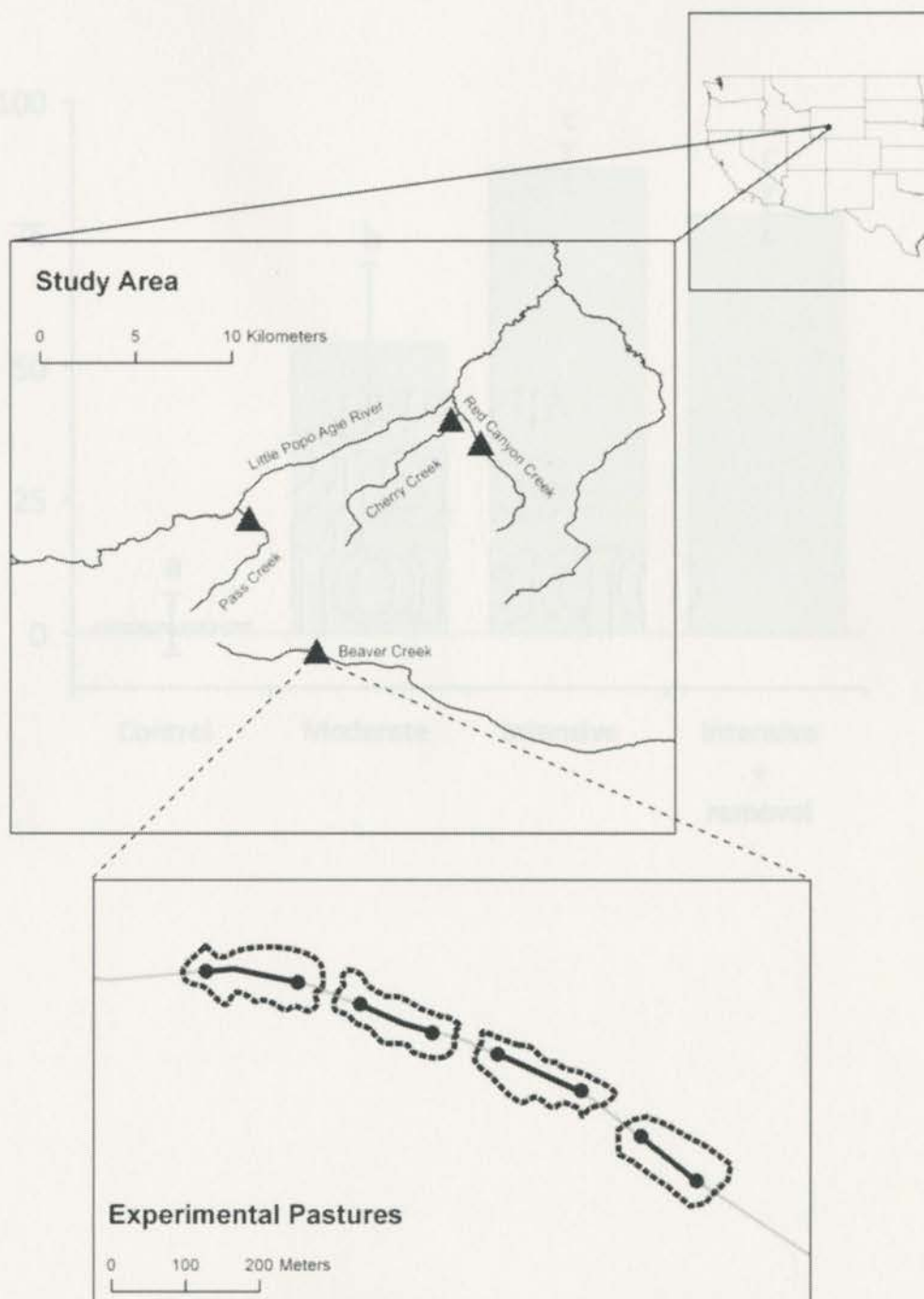


Figure 2. — Average percentage utilization of herbaceous riparian vegetation under four experimental treatments, each applied to four streams in west central Wyoming. Control reaches received no livestock grazing, whereas treatments received either moderate or high intensity grazing, or high intensity grazing combined with removing two-thirds of riparian woody vegetation (see text). Error bars show $\pm$ SE. Different lower case letters above estimates indicate statistically significant differences ($\alpha = 0.05$).

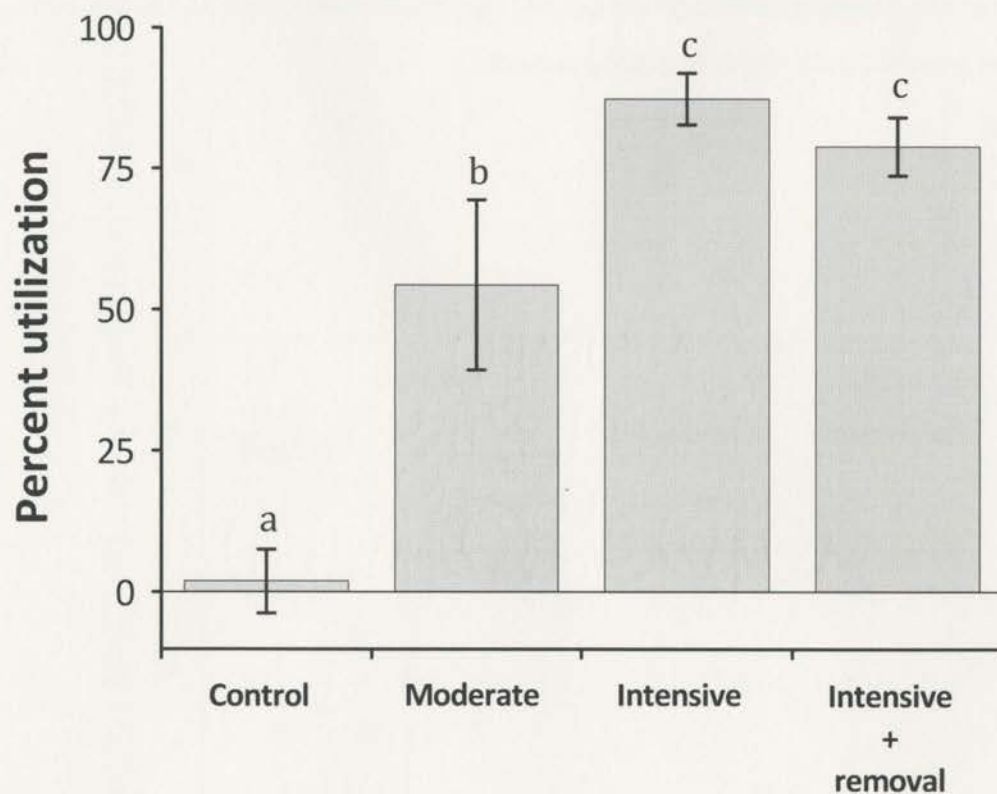


Figure 1. — Average maximum height of grasses and forbs during three sampling periods under three treatment levels: each species was collected in well, control, or high intensity grazing. Control forbs received no herbicide grazing, whereas treatments received either moderate or high intensity grazing or high intensity grazing combined with removing two-thirds of native woody vegetation (see text). Data samples were collected during mid August and early September. Error bars show ± 2 SE. Different letters above estimates indicate statistically significant differences ($P < 0.05$) for comparisons are valid only within a sampling period.



Figure 3. — Average maximum height of grasses and forbs during three sampling periods under four experimental treatments, each applied to four streams in west central Wyoming. Control reaches received no livestock grazing, whereas treatments received either moderate or high intensity grazing, or high intensity grazing combined with removing two-thirds of riparian woody vegetation (see text). Initial samples were collected before treatments were applied (July), and Midterm and Final samples were collected during mid August and early September. Error bars show $\pm$ SE. Different lower case letters above estimates indicate statistically significant differences ($\alpha = 0.05$), but comparisons are valid only within sampling periods.

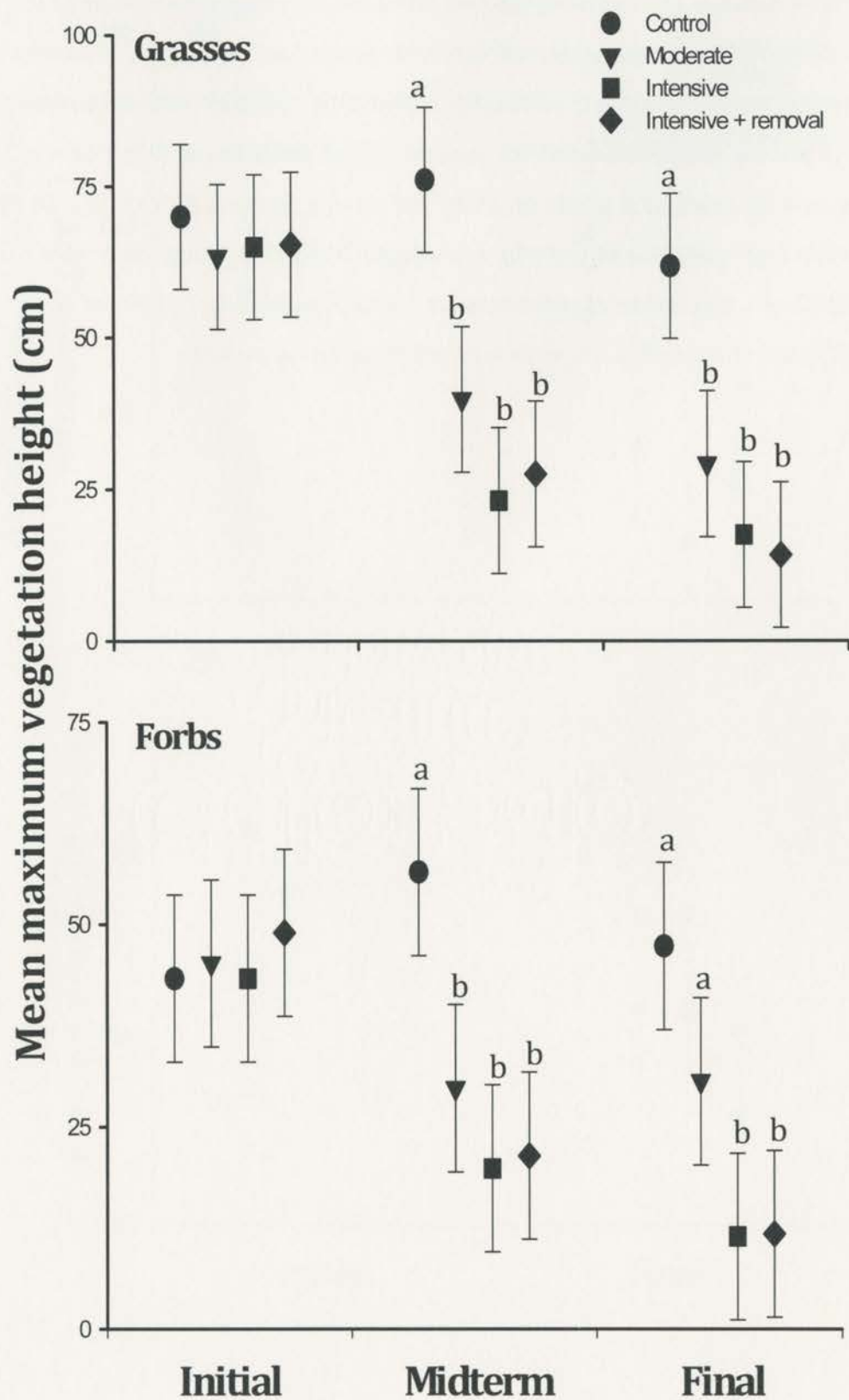


Figure 2 — Average aboveground biomass of herbaceous vegetation (A) and total overhead cover (B) during two sampling periods under four experimental treatments. Each experimental treatment was replicated in six plots in west central Wyoming. Control received no herbicide, while the other three treatments received either herbicide or high intensity grazing or high intensity grazing combined with herbicide. Error bars show 1 SE. Different lower case letters above error bars indicate statistically significant differences ($\alpha = 0.05$), but comparisons are valid only within sampling periods.



Figure 4. — Average aboveground biomass of herbaceous vegetation (A) and total overhead cover (B) during two sampling periods under four experimental treatments, each applied to four streams in west central Wyoming. Control reaches received no livestock grazing, whereas treatments received either moderate or high intensity grazing, or high intensity grazing combined with removing two-thirds of riparian woody vegetation (see text). See Figure 3 for explanation of periods. Error bars show $\pm$ SE. Different lower case letters above estimates indicate statistically significant differences ($\alpha = 0.05$), but comparisons are valid only within sampling periods.

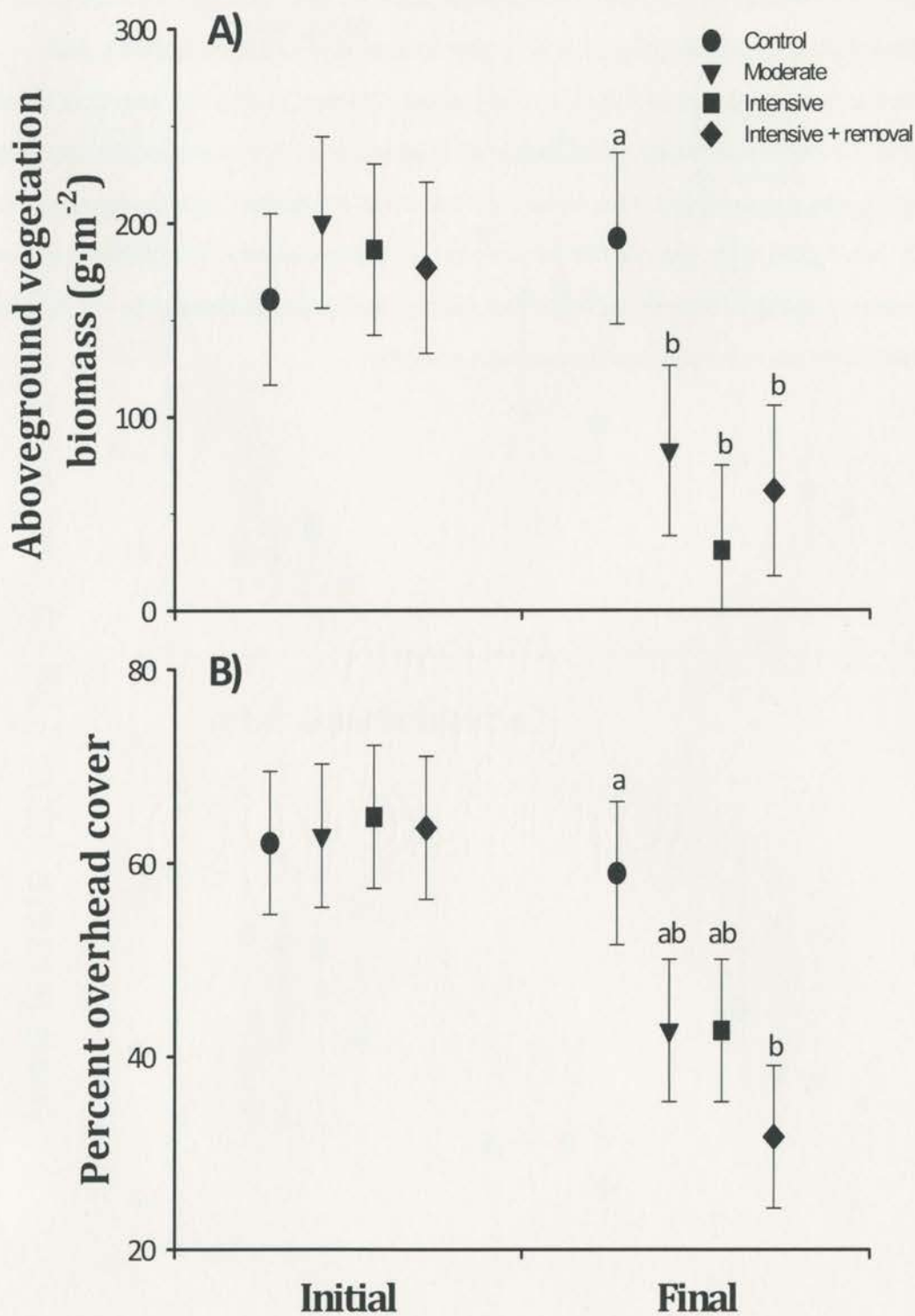


Figure 2 -- Terrestrial invertebrate and adult aquatic insect biomass entering stream reaches during three sampling periods under two experimental treatments, each applied to four stream reaches in each control stream. Control reaches received no livestock grazing while the other reaches received moderate or high intensity grazing or high intensity grazing with added organic matter. Two-thirds of riparian woody vegetation has been removed from the reaches. Error bars show ± 2 SE. Different letters above estimates indicate statistically significant differences ($p < 0.05$) but comparisons are valid only within sampling periods.



Figure 5. — Terrestrial invertebrate and adult aquatic insect biomass entering stream reaches during three sampling periods under four experimental treatments, each applied to four streams in west central Wyoming. Control reaches received no livestock grazing, whereas treatments received either moderate or high intensity grazing, or high intensity grazing combined with removing two-thirds of riparian woody vegetation (see text). See Figure 3 for explanation of periods. Error bars show $\pm$ SE. Different lower case letters above estimates indicate statistically significant differences ($\alpha = 0.05$), but comparisons are valid only within sampling periods.

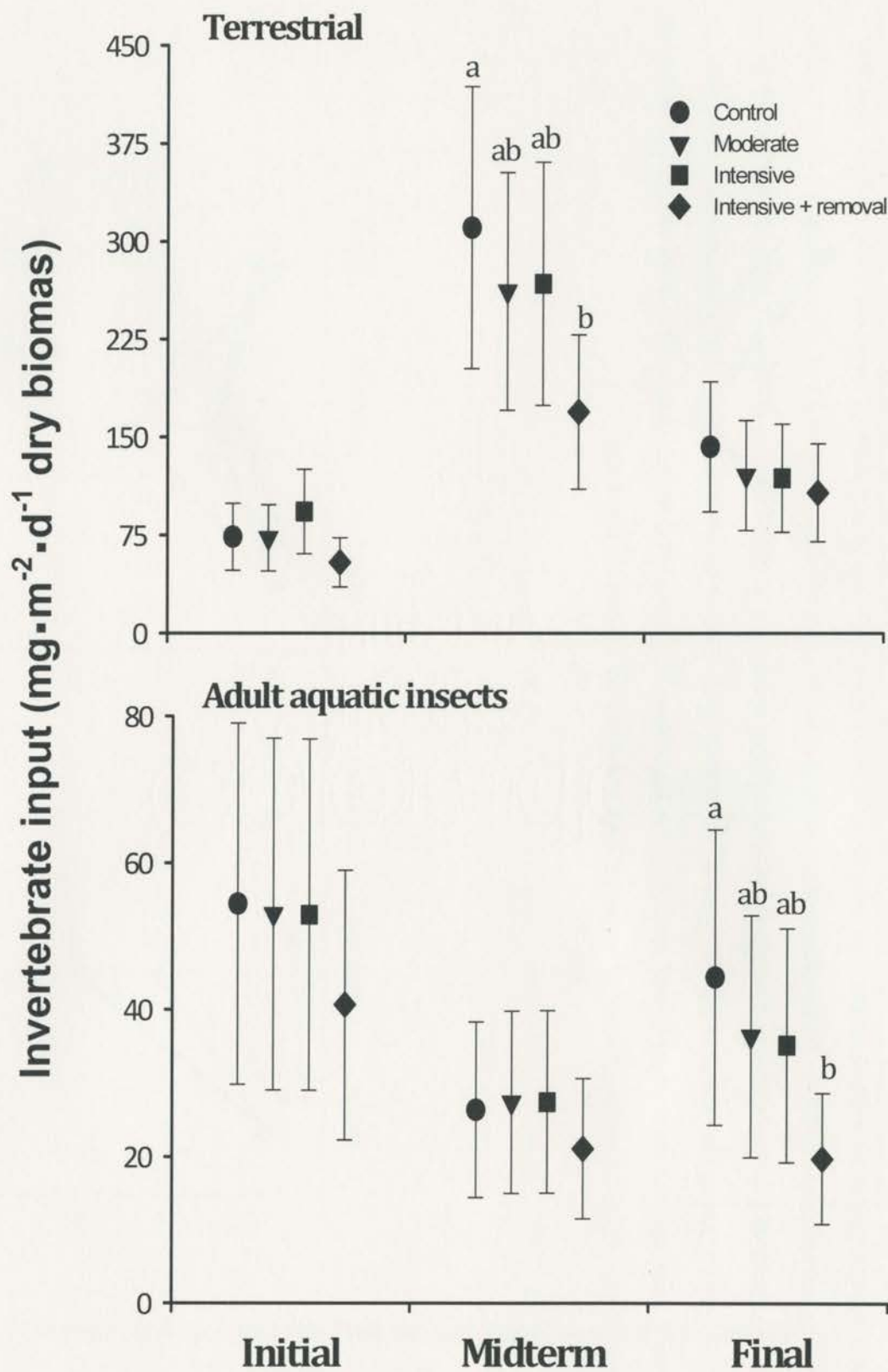




Figure 1. Effect of treatment on plant height and root length. The figure consists of two line graphs. The left graph shows plant height (cm) on the y-axis (0 to 20) and treatment on the x-axis (Control, Fertilizer, Pesticide, Herbicide). The right graph shows root length (cm) on the y-axis (0 to 10) and treatment on the x-axis. Each treatment has three replicates, represented by different symbols (circles, squares, triangles). In both graphs, the Herbicide treatment shows the highest values, followed by Fertilizer, Pesticide, and Control. Error bars are present for each data point.

Figure 1. Effect of treatment on plant height and root length. The figure consists of two line graphs. The left graph shows plant height (cm) on the y-axis (0 to 20) and treatment on the x-axis (Control, Fertilizer, Pesticide, Herbicide). The right graph shows root length (cm) on the y-axis (0 to 10) and treatment on the x-axis. Each treatment has three replicates, represented by different symbols (circles, squares, triangles). In both graphs, the Herbicide treatment shows the highest values, followed by Fertilizer, Pesticide, and Control. Error bars are present for each data point.

Figure 6. — Terrestrial invertebrate biomass entering experimental stream reaches in four west central Wyoming streams. Values represent the average of 12 individual pan trap samples collected from each site during each of three sampling periods, and are therefore an unreplicated estimate of the effect of experimental treatments at each of the four streams studied. Control reaches received no livestock grazing, whereas treatments received either moderate or high intensity grazing, or high intensity grazing combined with removing two-thirds of riparian woody vegetation (see text). X-axis labels refer to sampling periods during the experiment. See Figure 3 for explanation of periods. Error bars show $\pm$ SE calculated from individual pan trap samples collected at sites, and so are estimates of the amount of variation over a 6-d period among six pan traps.

Terrestrial invertebrate input ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ dry biomass)

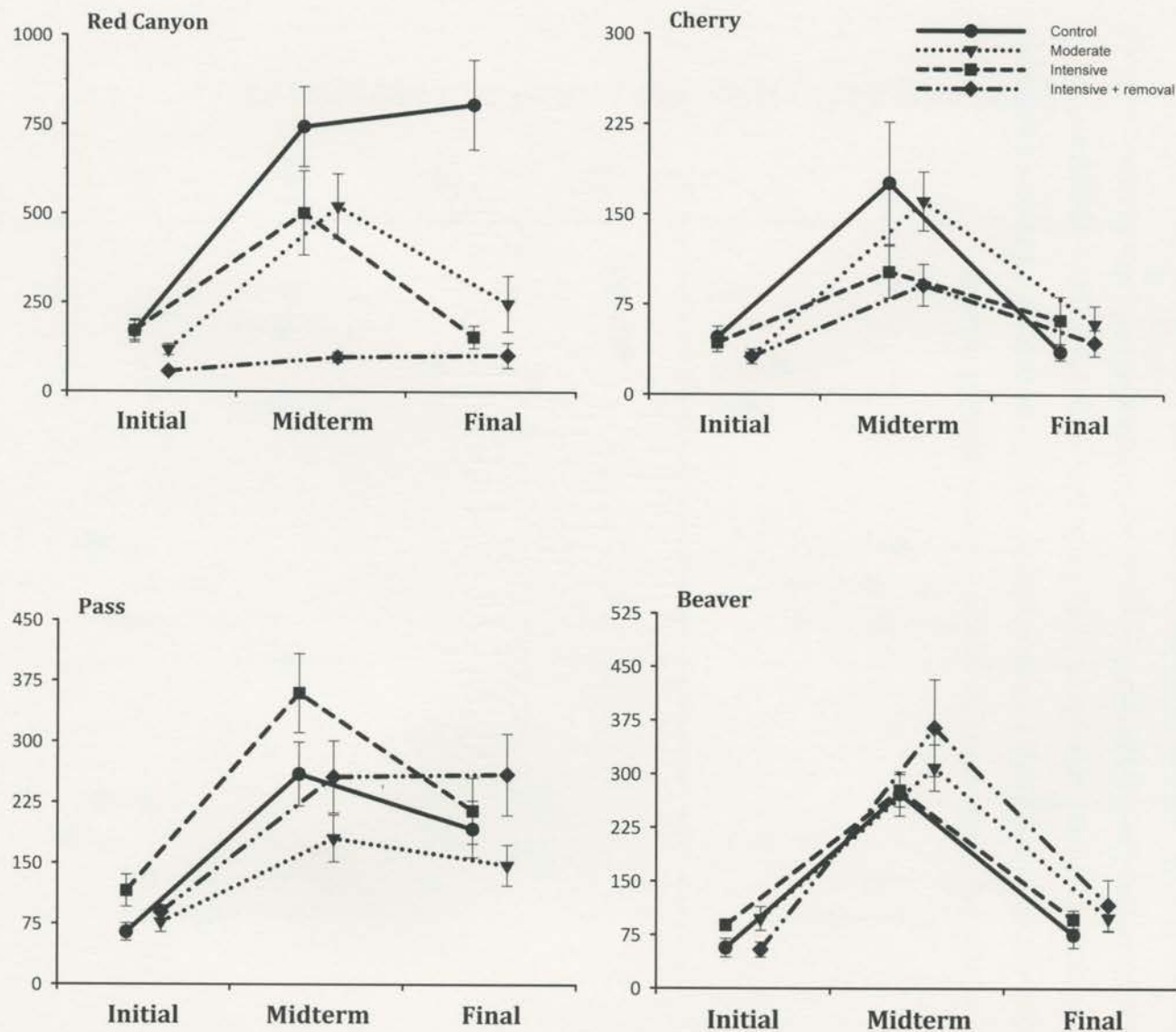


Figure 7. — Terrestrial and aquatic invertebrate biomass in the diet of trout inhabiting stream reaches during three sampling periods under four experimental treatments. Each symbol represents a mean $\pm$ standard error. Letters above symbols indicate significant differences ($p < 0.05$) between treatments. Symbols with different letters indicate significant differences ($p < 0.05$) between sampling periods. Error bars represent standard error.



Figure 7. — Terrestrial and aquatic invertebrate biomass in the diets of trout inhabiting stream reaches during three sampling periods under four experimental treatments, each applied to four streams in west central Wyoming. Control reaches received no livestock grazing, whereas treatments received either moderate or high intensity grazing, or high intensity grazing combined with removing two-thirds of riparian woody vegetation (see text). See Figure 3 for explanation of periods. Error bars show $\pm$ SE. Different lower case letters above estimates indicate statistically significant differences ($\alpha = 0.05$), but comparisons are valid only within sampling periods.

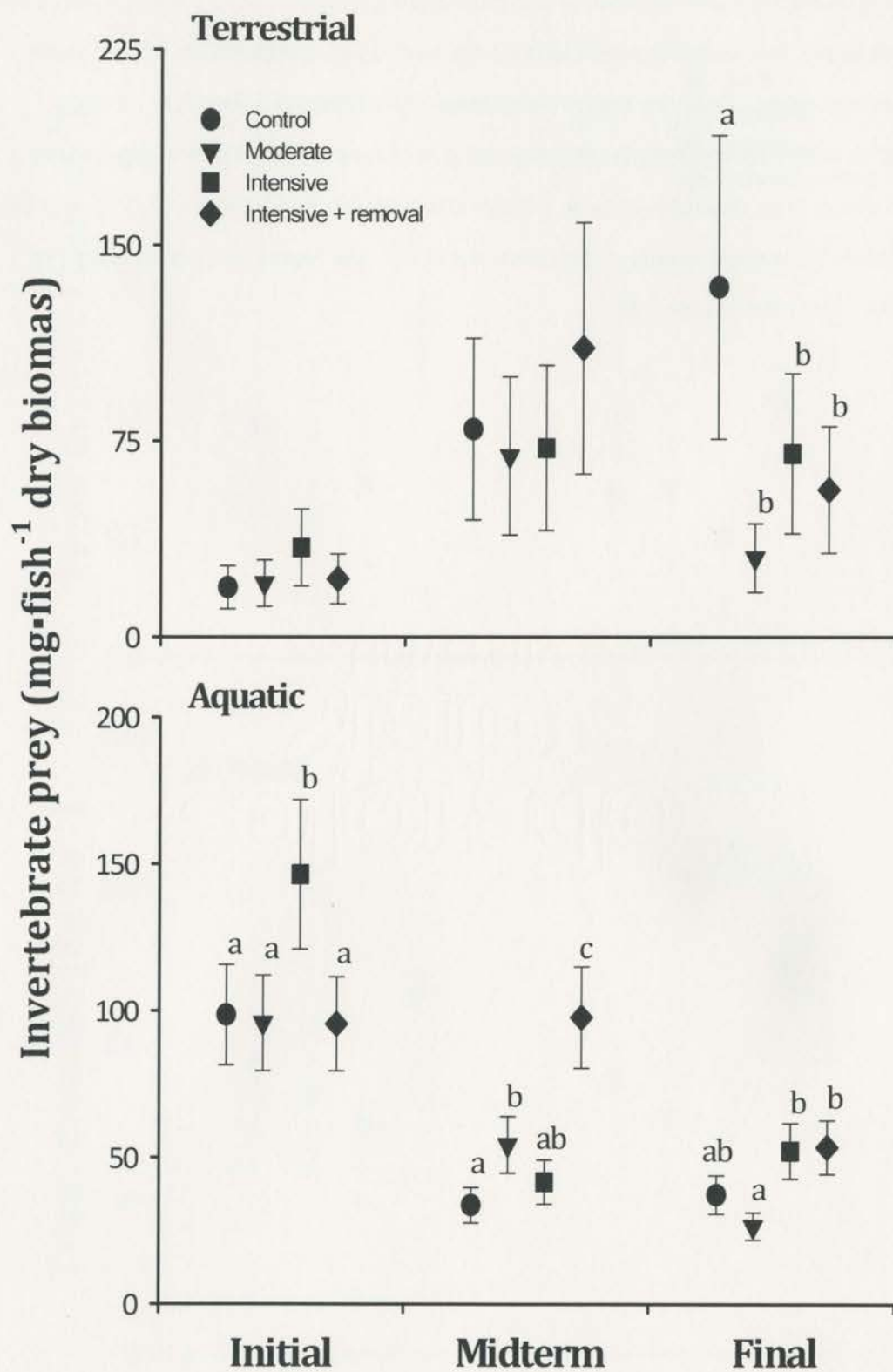
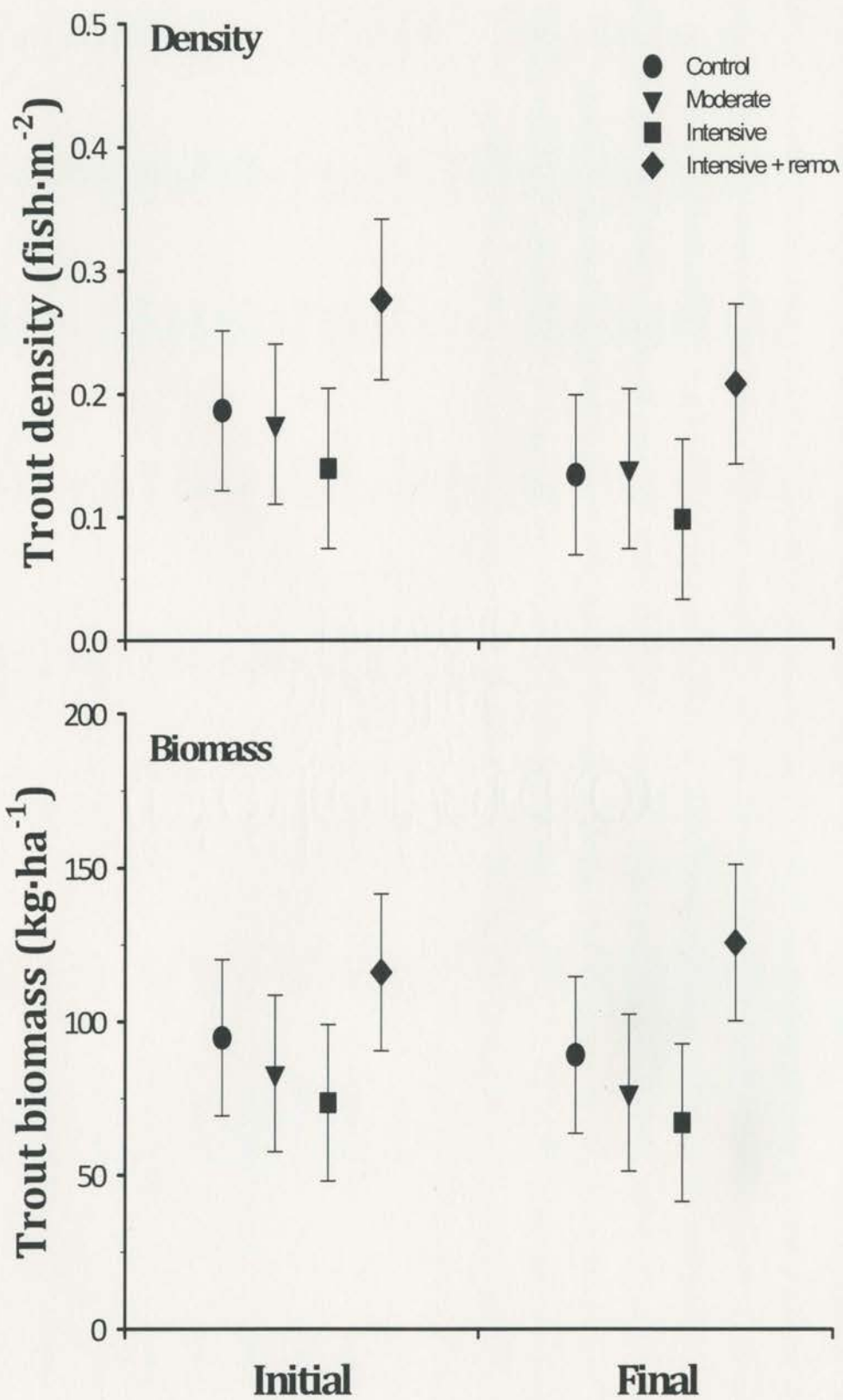


Figure 2. — Density and biomass of trout in riparian stream reaches during two sampling periods under two experimental treatments, each applied to two reaches in each of two reaches. Data are based on two-way analysis of variance conducted at 0.05 level. Control reaches received no stocking during whereas treatment reaches received either moderate or high density stocking or high density stocking combined with stocking two-thirds of riparian woody vegetation (see text). See Figure 3 for explanation of periods. Error bars show ± 1 SE.



Figure 8. — Density and biomass of trout inhabiting stream reaches during two sampling periods under four experimental treatments, each applied to four streams in west central Wyoming. Data are based on removal electrofishing conducted at night. Control reaches received no livestock grazing, whereas treatments received either moderate or high intensity grazing, or high intensity grazing combined with removing two-thirds of riparian woody vegetation (see text). See Figure 3 for explanation of periods. Error bars show $\pm$ SE.



Appendix 1. – Dry biomass ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) of major terrestrial invertebrate taxa entering study sites located within 16 experimental riparian pastures on 4 streams in central Wyoming. Major taxa were identified as those which contributed greater than 1% to the total invertebrate biomass entering streams, averaged across all three sampling periods (see below), or contributed more than 5% to the biomass of terrestrial invertebrates collected at a single site. For each taxon collected at each site, the percentage contribution to the terrestrial invertebrate input is shown in parentheses. Samples were collected using 6 pan traps set for two 3-d sampling periods during July (Initial sampling period), mid-August (Midterm sampling period), and early September (Final sampling period, see text). Four experimental grazing treatments were applied to each stream in a randomized complete block design (see text). Additional rare taxa sampled included Collembola, Dermaptera, Acari, Thysanoptera, Psocoptera, Strepsiptera, Pseudoscorpiones, Dolichopodidae^a (Diptera), Stratiomyidae^a (Diptera), nematodes, snails, earthworms, immature Coleoptera, and immature Neuroptera, immature Hymenoptera, and immature Diptera.

Stream	Treatment	Sampling Period	Total Biomass	Coleoptera	Hemiptera	Homoptera	Hymenoptera	Neuroptera
Beaver	Control	Initial	56.8293	8.4639 (15)	1.03 (2)	5.9561 (10)	1.754 (3)	2.9109 (5)
Beaver	Moderate Intensity	Initial	97.7422	7.3413 (8)	2.1346 (2)	5.6171 (6)	13.9778 (14)	2.2236 (2)
Beaver	High Intensity	Initial	88.6152	6.1713 (7)	0.7526 (1)	7.2318 (8)	10.1533 (11)	1.3752 (2)
Beaver	Woody Removal	Initial	54.1735	13.0542 (24)	1.9978 (4)	5.1177 (9)	6.185 (11)	1.0263 (2)
Cherry	Control	Initial	47.4	4.0846 (9)	1.0673 (2)	5.8497 (12)	4.7551 (10)	0.171 (0)
Cherry	Moderate Intensity	Initial	31.8692	3.3456 (10)	1.3615 (4)	5.9456 (19)	2.8188 (9)	
Cherry	High Intensity	Initial	43.0076	5.3571 (12)	1.731 (4)	7.1429 (17)	8.0528 (19)	0.6295 (1)
Cherry	Woody Removal	Initial	31.5476	5.4255 (17)	0.9442 (3)	6.8624 (22)	2.381 (8)	0.1163 (0)
Pass	Control	Initial	64.6687	2.9214 (5)	1.2247 (2)	4.0777 (6)	2.723 (4)	0.6842 (1)
Pass	Moderate Intensity	Initial	77.0046	3.9477 (5)	2.0662 (3)	5.7471 (7)	5.1519 (7)	
Pass	High Intensity	Initial	115.8319	23.4743 (20)	1.2931 (1)	5.1177 (4)	18.7945 (16)	1.9773 (2)
Pass	Woody Removal	Initial	89.4157	4.8372 (5)	1.3478 (2)	12.2058 (14)	4.3788 (5)	0.2668 (0)
Red Canyon	Control	Initial	169.4581	12.0211 (7)	5.5829 (3)	17.3235 (10)	34.3254 (20)	0.6021 (0)
Red Canyon	Moderate Intensity	Initial	117.4876	18.4934 (16)	2.7983 (2)	9.517 (8)	26.5257 (23)	0.0547 (0)
Red Canyon	High Intensity	Initial	170.4569	30.8771 (18)	1.3684 (1)	13.6905 (8)	26.3342 (15)	0.4721 (0)
Red Canyon	Woody Removal	Initial	56.3517	3.4035 (6)	1.4554 (3)	5.165 (9)	4.0976 (7)	

Appendix 1. -- continued

Stream	Treatment	Sampling Period	Total Biomass	Coleoptera	Hemiptera	Homoptera	Hymenoptera	Neuroptera
Beaver	Control	Midterm	272.1898	1.1867 (0)	1.1942 (0)	16.383 (6)	47.3429 (17)	
Beaver	Moderate Intensity	Midterm	308.8259	7.2181 (2)	2.4357 (1)	8.7575 (3)	47.188 (15)	
Beaver	High Intensity	Midterm	277.0389	1.0673 (0)	1.1289 (0)	14.272 (5)	51.3342 (19)	0.1847 (0)
Beaver	Woody Removal	Midterm	339.3131	1.5189 (0)	1.3478 (0)	4.5772 (1)	40.0999 (12)	
Cherry	Control	Midterm	176.0673	1.3684 (1)	2.511 (1)	12.3974 (7)	10.8443 (6)	0.0411 (0)
Cherry	Moderate Intensity	Midterm	161.1247	3.7083 (2)	5.2135 (3)	8.1281 (5)	24.309 (15)	0.0411 (0)
Cherry	High Intensity	Midterm	102.203	2.0867 (2)	2.5999 (3)	3.5167 (3)	9.2159 (9)	
Cherry	Woody Removal	Midterm	91.3176	3.2362 (4)	1.4915 (2)	4.844 (5)	8.8328 (10)	0.0684 (0)
Pass	Control	Midterm	259.6743	0.9305 (0)	0.3558 (0)	9.127 (4)	49.7674 (19)	0.3284 (0)
Pass	Moderate Intensity	Midterm	180.3571	2.6204 (1)	1.9568 (1)	9.4075 (5)	40.2983 (22)	
Pass	High Intensity	Midterm	359.4006	1.8747 (1)	3.0651 (1)	18.4318 (5)	63.9436 (18)	0.0821 (0)
Pass	Woody Removal	Midterm	256.1371	1.0057	2.5862 (1)	10.2696 (4)	29.5156 (12)	
Red Canyon	Control	Midterm	743.9244	38.8273 (5)	3.243 (0)	60.9674 (8)	59.1954 (8)	29.933 (4)
Red Canyon	Moderate Intensity	Midterm	520.6821	58.0012 (11)	4.4857 (1)	26.907 (5)	36.1173 (7)	0.1941 (0)
Red Canyon	High Intensity	Midterm	501.9779	2.784 (1)	5.9934 (1)	16.9354 (3)	33.1169 (7)	0.0672 (0)
Red Canyon	Woody Removal	Midterm	96.1343	1.7447 (2)	0.6089 (1)	6.014 (6)	13.2457 (14)	

Appendix 1. -- continued

Stream	Treatment	Sampling Period	Total Biomass	Coleoptera	Hemiptera	Homoptera	Hymenoptera	Neuroptera
Beaver	Control	Final	75.2326	0.4447 (1)	1.9568 (3)	3.9203 (5)	10.2833 (14)	
Beaver	Moderate Intensity	Final	98.9463	1.7994 (2)	3.3251 (3)	2.2373 (2)	14.1557 (14)	
Beaver	High Intensity	Final	97.0716	1.8336 (2)	3.6604 (4)	4.7072 (5)	21.3601 (22)	
Beaver	Woody Removal	Final	122.0704	0.7464 (1)	1.4405 (1)	3.2169 (3)	9.2402 (8)	0.0672 (0)
Cherry	Control	Final	35.4748	0.4721 (1)	1.0126 (3)	3.3525 (9)	4.7824 (13)	
Cherry	Moderate Intensity	Final	58.7917	3.9819 (7)	0.5816 (1)	5.3503 (9)	7.3344 (12)	
Cherry	High Intensity	Final	61.8705	0.7116 (1)	0.2258 (0)	3.0104 (5)	6.616 (11)	
Cherry	Woody Removal	Final	42.9666	0.4173 (1)	0.4105 (1)	1.902 (4)	4.1461 (10)	
Pass	Control	Final	192.0498	1.7515 (1)	1.6557 (1)	5.2819 (3)	37.4795 (20)	0.1437 (0)
Pass	Moderate Intensity	Final	147.578	1.1836 (1)	1.7036 (1)	4.7003 (3)	21.2917 (14)	0.0411 (0)
Pass	High Intensity	Final	214.7509	5.3777 (3)	4.5703 (2)	13.5126 (6)	44.7318 (21)	0.0616 (0)
Pass	Woody Removal	Final	259.4485	4.4061 (2)	11.5353 (4)	8.8465 (3)	92.9666 (36)	
Red Canyon	Control	Final	805.9387	7.6902 (1)	4.8919 (1)	46.5654 (6)	380.0424 (47)	0.9442 (0)
Red Canyon	Moderate Intensity	Final	247.2632	3.8998 (2)	1.4505 (1)	12.5411 (5)	75.4379 (31)	0.1026 (0)
Red Canyon	High Intensity	Final	153.5005	0.515 (0)	3.0303 (2)	5.3814 (4)	17.8012 (12)	
Red Canyon	Woody Removal	Final	101.9499	0.5131 (1)	0.0958 (0)	1.5599 (2)	5.0287 (5)	

Appendix 1. -- continued

Stream	Treatment	Sampling Period	Lepidoptera	Immature Lepidoptera	Orthoptera	Spiders	Diptera	Empididae ^a
Beaver	Control	Initial	17.3683 (31)	0.0448 (0)		0.4105 (1)	16.4427 (29)	0.4329 (1)
Beaver	Moderate Intensity	Initial	36.9527 (38)	1.0947 (1)		1.3136 (1)	23.2485 (24)	1.9294 (2)
Beaver	High Intensity	Initial	22.489 (25)	2.6067 (3)		2.3194 (3)	33.0049 (37)	0.821 (1)
Beaver	Woody Removal	Initial	4.2282 (8)	1.3957 (3)	0.5063 (1)	1.5394 (3)	15.2025 (28)	0.5884 (1)
Cherry	Control	Initial	0.4105 (1)	1.4847 (3)	0.431 (1)	3.9409 (8)	20.5597 (43)	0.5679 (1)
Cherry	Moderate Intensity	Initial	0.1368 (0)		0.6363 (2)	1.8473 (6)	13.8342 (43)	
Cherry	High Intensity	Initial	4.3719 (10)	1.9431 (5)	0.6842 (2)	1.4299 (3)	8.9765 (21)	0.2189 (1)
Cherry	Woody Removal	Initial		0.0684 (0)		2.5451 (8)	11.9253 (38)	
Pass	Control	Initial	19.506 (30)			1.3957 (2)	29.543 (46)	1.0194 (2)
Pass	Moderate Intensity	Initial	14.9357 (19)	0.0205 (0)	0.7184 (1)	0.2395 (0)	43.2745 (56)	
Pass	High Intensity	Initial	12.4521 (11)	0.0684 (0)		0.9921 (1)	48.399 (42)	0.7321 (1)
Pass	Woody Removal	Initial	12.7737 (14)	0.691 (1)		1.0947 (1)	50.6774 (57)	
Red Canyon	Control	Initial	12.0484 (7)	0.1368 (0)	29.6388 (17)	6.6639 (4)	45.9565 (27)	1.0605 (1)
Red Canyon	Moderate Intensity	Initial	5.364 (5)	2.251 (2)	6.6845 (6)	5.9319 (5)	35.6801 (30)	0.78 (1)
Red Canyon	High Intensity	Initial	16.1741 (9)		25.5473 (15)	5.0629 (3)	46.538 (27)	0.1026 (0)
Red Canyon	Woody Removal	Initial	13.7856 (24)		0.2762 (0)	0.8135 (1)	0.1493 (41)	0.1493 (0)

Appendix 1. -- continued

Stream	Treatment	Sampling Period	Lepidoptera	Immature Lepidoptera	Orthoptera	Spiders	Diptera	Empididae ^a
Beaver	Control	Midterm	25.78 (9)	0.0597 (0)	0.209 (0)	1.0748 (0)	174.6082 (64)	0.3433 (0)
Beaver	Moderate Intensity	Midterm	20.1492 (7)	0.0821 (0)	16.352 (5)	0.9031 (0)	179.1119 (58)	19.6429 (6)
Beaver	High Intensity	Midterm	19.1639 (7)	0.1505 (0)		0.4721 (0)	184.0175 (66)	1.1015 (0)
Beaver	Woody Removal	Midterm	21.0454 (6)	0.0616 (0)	94.3487 (28)	0.6226 (0)	173.0911 (51)	0.7663 (0)
Cherry	Control	Midterm	8.3812 (5)	0.1095 (0)	122.0717 (69)	2.682 (2)	11.7406 (7)	0.6979 (0)
Cherry	Moderate Intensity	Midterm	10.5296 (7)	4.3924 (3)	46.0386 (29)	2.2988 (1)	51.3889 (32)	0.4173 (0)
Cherry	High Intensity	Midterm	23.0364 (23)	0.6226 (1)	40.2641 (39)	1.1631 (1)	17.7477 (17)	0.3763 (0)
Cherry	Woody Removal	Midterm	7.4439 (8)	0.1026 (0)	44.6908 (49)	3.1951 (3)	15.1273 (17)	0.7115 (1)
Pass	Control	Midterm	47.2838 (18)	0.5131 (0)	14.8468 (6)	0.431 (0)	132.1908 (51)	0.5063 (0)
Pass	Moderate Intensity	Midterm	36.1522 (20)		12.6095 (7)	2.0594 (1)	74.4116 (41)	0.0753 (0)
Pass	High Intensity	Midterm	123.098 (34)	0.3626 (0)	52.8599 (15)	3.1951 (1)	88.6768 (25)	0.7526 (0)
Pass	Woody Removal	Midterm	37.2126 (15)	0.7937 (0)	20.115 (8)	4.7824 (2)	148.7479 (58)	0.0616 (0)
Red Canyon	Control	Midterm	45.6076 (6)	2.0457 (0)	433.306 (58)	3.1472 (0)	61.3232 (8)	0.2258 (0)
Red Canyon	Moderate Intensity	Midterm	13.2706 (3)	0.4702 (0)	319.5552 (61)	4.9037 (1)	53.6349 (10)	0.724 (0)
Red Canyon	High Intensity	Midterm	9.7029 (2)	0.0373 (0)	369.376 (74)	1.9555 (0)	60.0836 (12)	0.1791 (0)
Red Canyon	Woody Removal	Midterm	10.8374 (11)		29.6045 (31)	0.7526 (1)	31.7323 (33)	0.4037 (0)

Appendix 1. -- continued

Stream	Treatment	Sampling Period	Lepidoptera	Immature Lepidoptera	Orthoptera	Spiders	Diptera	Empididae ^a
Beaver	Control	Final	10.5296 (14)		5.5282 (7)	1.5052 (2)	40.2983 (54)	0.1368 (0)
Beaver	Moderate Intensity	Final	2.8872 (3)	0.0137 (0)	4.8303 (5)	0.4516 (0)	67.9666 (69)	0.2258 (0)
Beaver	High Intensity	Final	6.2739 (6)	0.1026 (0)		0.4516 (0)	57.2044 (59)	0.2874 (0)
Beaver	Woody Removal	Final	7.1503 (6)		61.8227 (51)	0.1194 (0)	37.5131 (31)	0.1343 (0)
Cherry	Control	Final	3.0172 (9)	1.9773 (6)	9.5786 (27)	2.5315 (7)	7.8476 (22)	
Cherry	Moderate Intensity	Final	7.1086 (12)		16.5367 (28)	1.5394 (3)	15.9483 (27)	
Cherry	High Intensity	Final	13.28 (21)	0.8005 (1)	24.1174 (39)	0.8347 (1)	11.3506 (18)	0.2532 (0)
Cherry	Woody Removal	Final	3.2841 (8)		8.7917 (20)	1.3684 (3)	21.4012 (50)	
Pass	Control	Final	15.0178 (8)	0.0342 (0)	43.3156 (23)	1.1084 (1)	84.0175 (44)	0.3421 (0)
Pass	Moderate Intensity	Final	27.8873 (19)		41.2972 (28)	1.5531 (1)	46.538 (32)	0.1368 (0)
Pass	High Intensity	Final	23.5906 (11)		45.3407 (21)	0.951 (0)	74.8769 (35)	0.0958 (0)
Pass	Woody Removal	Final	13.6563 (5)	1.3205 (1)	15.8662 (6)	0.2942 (0)	103.5372 (40)	0.4447 (0)
Red Canyon	Control	Final	150.5816 (19)	1.0331 (0)	143.254 (18)	1.7994 (0)	62.5753 (8)	
Red Canyon	Moderate Intensity	Final	51.5394 (21)	2.7162 (1)	73.9532 (30)	0.4721 (0)	23.6111 (10)	0.0821 (0)
Red Canyon	High Intensity	Final	13.3005 (9)		98.5819 (64)	0.2463 (0)	10.2105 (7)	
Red Canyon	Woody Removal	Final	1.471 (1)		72.5848 (71)	0.1574 (0)	19.9371 (20)	

^a Empididae, Dolichopodidae, and Stratiomyidae were classified as terrestrial in origin, but were separated from other terrestrial Diptera owing to potential difficulties identifying aquatic species within these taxa.

Appendix 2. – Dry biomass ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) of major adult aquatic insect taxa entering study sites located within 16 experimental riparian pastures on 4 streams in central Wyoming. Major taxa were identified as those which contributed greater than 1% to the total adult aquatic insect biomass entering streams, averaged across all three sampling periods (see below), or contributed more than 5% to the biomass of adult aquatic insects collected at a single site. For each taxon collected at each site, the percentage contribution to the adult aquatic insect input is shown in parentheses. Samples were collected using 6 pan traps set for two 3-d sampling periods during July (Initial sampling period), mid-August (Midterm sampling period), and early September (Final sampling period, see text). Four experimental grazing treatments were applied to each stream in a randomized complete block design (see text). Additional rare taxa sampled included Culicidae and Blepharoceridae.

Stream	Treatment	Sampling Period	Total Biomass	Chironomidae	Ceratopogonidae	Tipulidae	Psychodidae	Dixidae	Simuliidae	Tabanidae
Beaver	Control	Initial	46.074	3.0975 (7)	1.3733 (3)	4.732 (10)	0.5075 (1)		2.4257 (5)	
Beaver	Moderate Intensity	Initial	57.6833	2.5794 (4)	1.5052 (3)	3.072 (5)	0.8621 (1)		3.072 (5)	
Beaver	High Intensity	Initial	41.9197	3.0857 (7)	0.8005 (2)	5.9866 (14)	1.2589 (3)		2.3194 (6)	1.7378 (4)
Beaver	Woody Removal	Initial	26.4709	3.6741 (14)	0.6294 (2)	3.8246 (14)	0.8142 (3)		1.7583 (7)	
Cherry	Control	Initial	34.038	6.1645 (18)	1.5599 (5)	3.7356 (11)	0.1574 (0)	0.0274 (0)	0.2189 (1)	
Cherry	Moderate Intensity	Initial	26.2999	8.6002 (33)	1.252 (5)	2.5315 (10)	0.8758 (3)		0.1505 (1)	
Cherry	High Intensity	Initial	35.9263	5.754 (16)	1.341 (4)	3.7014 (10)	0.4379 (1)		0.65 (2)	
Cherry	Woody Removal	Initial	36.1727	4.7072 (13)	2.1552 (6)	5.2545 (15)	0.3352 (1)	0.171 (0)	0.0411 (0)	
Pass	Control	Initial	74.0695	3.4825 (5)	0.7321 (1)	4.1872 (6)	1.4778 (2)	0.0753 (0)	0.3489 (0)	
Pass	Moderate Intensity	Initial	91.9403	2.8462 (3)	0.7321 (1)	5.6719 (6)	1.2657 (1)		0.5337 (1)	
Pass	High Intensity	Initial	68.0418	2.3604 (3)	1.1015 (2)	6.1713 (9)	3.4346 (5)	0.0889 (0)	0.5063 (1)	
Pass	Woody Removal	Initial	39.5867	1.7857 (5)	0.39 (1)	3.7151 (9)	1.5668 (4)		0.26 (1)	
Red Canyon	Control	Initial	75.5952	5.4803 (7)	4.4403 (6)	2.2509 (3)	0.5884 (1)	0.2942 (0)	5.0561 (7)	
Red Canyon	Moderate Intensity	Initial	56.6502	5.4666 (10)	5.5008 (10)	3.1814 (6)	0.2463 (0)	0.2395 (0)	3.4962 (6)	0.9647 (2)
Red Canyon	High Intensity	Initial	76.6078	3.6057 (5)	3.5714 (5)	1.382 (2)	0.3968 (1)	0.1437 (0)	4.4882 (6)	4.4677 (6)
Red Canyon	Woody Removal	Initial	71.9883	7.0906 (10)	4.441 (6)	2.2765 (3)	0.3359 (0)	0.112 (0)	1.5972 (2)	2.4556 (3)

Appendix 2. -- continued

Stream	Treatment	Sampling Period	Total Biomass	Chironomidae	Ceratopogonidae	Tipulidae	Psychodidae	Dixidae	Simuliidae	Tabanidae
Beaver	Control	Midterm	13.6587	2.1346 (16)	0.8509 (6)	0.3657 (3)	0.933 (7)		0.5822 (4)	
Beaver	Moderate Intensity	Midterm	15.5514	1.7173 (11)	0.8347 (5)	1.4231 (9)	0.5679 (4)		0.3558 (2)	
Beaver	High Intensity	Midterm	9.948	1.9841 (20)	0.9031 (9)	0.2053 (2)	0.4721 (5)	0.0274 (0)	0.1779 (2)	
Beaver	Woody Removal	Midterm	12.6299	2.7436 (22)	1.1426 (9)	0.4721 (4)	0.9031 (7)	0.0821 (1)	0.5952 (5)	1.8541 (15)
Cherry	Control	Midterm	26.3272	2.2373 (8)	1.8473 (7)	6.2124 (24)	1.1152 (4)		0.2737 (1)	
Cherry	Moderate Intensity	Midterm	57.0265	2.6478 (5)	1.7446 (3)	18.0282 (32)	1.2178 (2)		0.561 (1)	
Cherry	High Intensity	Midterm	23.399	1.9773 (8)	1.4299 (6)	1.7515 (7)	0.4789 (2)		0.1437 (1)	
Cherry	Woody Removal	Midterm	34.9411	3.2294 (9)	1.2383 (4)	11.6927 (33)	0.9715 (3)	0.1232 (0)	0.3284 (1)	
Pass	Control	Midterm	16.1398	1.861 (12)	1.1152 (7)	0.6773 (4)	0.7936 (5)		0.3421 (2)	
Pass	Moderate Intensity	Midterm	17.5424	2.511 (14)	0.4173 (2)	0.6637 (4)	0.4584 (3)	0.0342 (0)	0.6842 (4)	
Pass	High Intensity	Midterm	30.1039	2.1688 (7)	0.6705 (2)	0.5131 (2)	0.8757 (3)	0.1574 (1)	1.3889 (5)	
Pass	Woody Removal	Midterm	15.0245	1.8062 (12)	0.5131 (3)	0.5747 (4)	0.6158 (4)		0.3558 (2)	
Red Canyon	Control	Midterm	83.5385	4.8714 (6)	2.8599 (3)	31.3287 (38)	0.8347 (1)	0.0753 (0)	1.6215 (2)	
Red Canyon	Moderate Intensity	Midterm	36.2068	4.0006 (11)	2.2018 (6)	7.9937 (22)	0.4329 (1)	0.0672 (0)	1.1121 (3)	
Red Canyon	High Intensity	Midterm	80.9448	2.993 (4)	2.4033 (3)	20.4359 (25)	0.6419 (1)	0.0896 (0)	0.8882 (1)	
Red Canyon	Woody Removal	Midterm	28.6398	4.2625 (15)	1.3342 (5)	5.145 (18)	0.6773 (2)	0.0753 (0)	0.2942 (1)	

Appendix 2. -- continued

Stream	Treatment	Sampling Period	Total Biomass	Chironomidae	Ceratopogonidae	Tipulidae	Psychodidae	Dixidae	Simuliidae	Tabanidae
Beaver	Control	Final	16.2219	1.4983 (9)	0.561 (3)	0.0958 (1)	0.0479 (0)	2.4425 (15)	0.1232 (1)	
Beaver	Moderate Intensity	Final	11.85	1.4984 (13)	0.431 (4)	0.1368 (1)	0.0958 (1)	0.1232 (1)	0.1163 (1)	
Beaver	High Intensity	Final	11.6653	1.7173 (15)	0.4173 (4)	0.0616 (1)	0.0205 (0)		0.3079 (3)	
Beaver	Woody Removal	Final	9.673	1.6569 (17)	0.515 (5)	0.3508 (4)	0.1194 (1)	0.1045 (1)	0.3508 (4)	
Cherry	Control	Final	50.561	3.0925 (6)	0.4174 (1)	7.5397 (15)	0.4789 (1)	0.1163 (0)	0.6773 (1)	0.1642 (0)
Cherry	Moderate Intensity	Final	20.9085	3.9067 (19)	0.4037 (2)	1.1289 (5)	0.4447 (2)	0.2942 (1)	0.39 (2)	
Cherry	High Intensity	Final	90.8866	8.2239 (9)	1.5462 (2)	19.8618 (22)	0.5884 (1)	0.2463 (0)	0.4037 (0)	
Cherry	Woody Removal	Final	56.5749	6.4724 (11)	1.2863 (2)	25.4926 (45)	1.2657 (2)	0.6705 (1)	1.252 (2)	
Pass	Control	Final	9.4485	4.2556 (45)	0.4037 (4)	0.1026 (1)	0.171 (2)	0.13 (1)	0.0958 (1)	
Pass	Moderate Intensity	Final	23.7821	5.7882 (24)	0.4652 (2)	0.0342 (0)	0.13 (1)	0.1163 (0)	0.3284 (1)	0.1847 (1)
Pass	High Intensity	Final	14.7509	3.4072 (23)	0.3695 (3)	0.1232 (1)	0.1163 (1)	0.13 (1)	0.3489 (2)	
Pass	Woody Removal	Final	13.7178	4.1188 (30)	1.9431 (14)	0.2668 (2)	0.2942 (2)	0.0684 (0)	0.2121 (2)	
Red Canyon	Control	Final	501.2452	12.2742 (2)	1.5326 (0)	12.9105 (3)	0.5679 (0)	0.7115 (0)	2.7914 (1)	
Red Canyon	Moderate Intensity	Final	296.9075	6.2329 (2)	1.0742 (0)	5.3161 (2)	0.3284 (0)	0.0753 (0)	1.5599 (1)	
Red Canyon	High Intensity	Final	97.4921	2.2839 (2)	0.4702 (0)	0.8957 (1)	0.0448 (0)	0.0821 (0)	0.6941 (1)	
Red Canyon	Woody Removal	Final	20.6486	4.3788 (21)	0.3968 (2)	0.0068	0.1779 (1)		0.4242 (2)	

Appendix 2. -- continued

Stream	Treatment	Sampling Period	Ptychopteridae	Ephemeroptera	Trichoptera	Plecoptera	Odonata	Coleoptera	Hemiptera
Beaver	Control	Initial	4.2842 (9)	3.8215 (8)	20.4359 (44)	4.329 (9)		0.6195 (1)	0.2985 (1)
Beaver	Moderate Intensity	Initial	2.7572 (5)	8.9012 (15)	7.6628 (13)	26.3752 (46)		0.1437 (0)	0.6226 (1)
Beaver	High Intensity	Initial	2.7094 (6)	8.5933 (20)	1.9636 (5)	10.5706 (25)		1.6147 (4)	0.8689 (2)
Beaver	Woody Removal	Initial	3.503 (13)	3.7767 (14)	0.9921 (4)	7.0813 (27)		0.1368 (1)	
Cherry	Control	Initial	1.3684 (4)	4.974 (15)	1.0126 (3)	11.9937 (35)	1.2452 (4)	1.1768 (3)	0.2805 (1)
Cherry	Moderate Intensity	Initial	0.1368 (1)	1.902 (7)	2.3536 (9)	7.136 (27)		0.2874 (1)	0.9579 (4)
Cherry	High Intensity	Initial	2.6957 (8)	3.2977 (9)	6.7187 (19)	10.5364 (29)		0.2463 (1)	0.4994 (1)
Cherry	Woody Removal	Initial	2.4083 (7)	2.9488 (8)	1.0879 (3)	15.3394 (42)		1.4436 (4)	0.2805 (1)
Pass	Control	Initial	1.7994 (2)	5.494 (7)	50.4652 (68)	4.324 (6)		0.6979 (1)	0.4995 (1)
Pass	Moderate Intensity	Initial	1.9225 (2)	8.347 (9)	59.9617 (65)	9.3801 (10)		0.3284 (0)	0.3079 (0)
Pass	High Intensity	Initial	2.162 (3)	5.1314 (8)	40.9551 (60)	5.2887 (8)		0.2053 (0)	0.6363 (1)
Pass	Woody Removal	Initial	0.8484 (2)	6.0824 (15)	22.1607 (56)	2.4836 (6)		0.0547 (0)	0.1779 (0)
Red Canyon	Control	Initial		2.1004 (3)	15.6267 (21)	1.5052 (2)	35.9264 (48)	1.04 (1)	1.2452 (2)
Red Canyon	Moderate Intensity	Initial		1.7926 (3)	10.2217 (18)	0.6226 (1)	22.0854 (39)	1.9636 (3)	0.8689 (2)
Red Canyon	High Intensity	Initial		0.8005 (1)	14.7305 (19)	5.2545 (7)	35.2217 (46)	0.4173 (1)	2.1278 (3)
Red Canyon	Woody Removal	Initial		1.948 (3)	12.2182 (17)	0.5225 (1)	36.6323 (51)	0.6867 (1)	1.5823 (2)

Appendix 2. -- continued

Stream	Treatment	Sampling Period	Ptychopteridae	Ephemeroptera	Trichoptera	Plecoptera	Odonata	Coleoptera	Hemiptera
Beaver	Control	Midterm	0.2836 (2)	2.3362 (17)	5.0008 (37)	0.9927 (7)		0.0373 (0)	0.1045 (1)
Beaver	Moderate Intensity	Midterm		1.902 (12)	6.4381 (41)	0.6294 (4)		0.0547 (0)	1.5394 (10)
Beaver	High Intensity	Midterm		1.3342 (13)	4.0367 (41)	0.2737 (3)		0.2395 (2)	0.2942 (3)
Beaver	Woody Removal	Midterm		2.1483 (17)	2.3125 (18)	0.2121 (2)		0.1642 (1)	
Cherry	Control	Midterm		1.3341 (5)	11.46 (44)	0.0411 (0)		1.0331 (4)	0.5405 (2)
Cherry	Moderate Intensity	Midterm		1.6078 (3)	29.2419 (51)	0.2189 (0)		1.0605 (2)	0.5747 (1)
Cherry	High Intensity	Midterm		1.2452 (5)	14.6483 (63)	0.0479 (0)	0.8073 (3)	0.4652 (2)	0.4037 (2)
Cherry	Woody Removal	Midterm		1.3547 (4)	13.8136 (40)	1.3273 (4)		0.1916 (1)	0.1232 (0)
Pass	Control	Midterm		1.471 (9)	7.5192 (47)	1.6763 (10)		0.2942 (2)	0.39 (2)
Pass	Moderate Intensity	Midterm		1.601 (9)	10.8648 (62)			0.13 (1)	
Pass	High Intensity	Midterm		1.6557 (5)	21.7364 (72)				0.3626 (1)
Pass	Woody Removal	Midterm		0.821 (5)	9.8385 (65)			0.0342 (0)	0.4652 (3)
Red Canyon	Control	Midterm		1.4915 (2)	29.584 (35)	1.2521 (1)	1.2315 (1)	1.3684 (2)	6.835 (8)
Red Canyon	Moderate Intensity	Midterm		0.821 (2)	14.6067 (40)		3.8439 (11)	0.2538 (1)	0.7389 (2)
Red Canyon	High Intensity	Midterm		0.9777 (1)	28.8252 (36)		21.8167 (27)	1.3286 (2)	0.5449 (1)
Red Canyon	Woody Removal	Midterm		3.1541 (11)	8.8054 (31)		2.7025 (9)	0.9647 (3)	1.1768 (4)

Appendix 2. -- continued

Stream	Treatment	Sampling Period	Ptychopteridae	Ephemeroptera	Trichoptera	Plecoptera	Odonata	Coleoptera	Hemiptera
Beaver	Control	Final		2.3604 (15)	7.1839 (44)	1.4436 (9)		0.1368 (1)	0.2805 (2)
Beaver	Moderate Intensity	Final		1.1973 (10)	7.1429 (60)	0.9715 (8)			0.1368 (1)
Beaver	High Intensity	Final		1.382 (12)	5.3093 (46)	0.3284 (3)		0.8415 (7)	1.2452 (11)
Beaver	Woody Removal	Final		2.2839 (24)	2.0675 (21)	0.6643 (7)		1.3062 (14)	0.1866 (2)
Cherry	Control	Final	0.0342 (0)	0.8894 (2)	36.1522 (72)	0.6226 (1)		0.0684 (0)	0.0753 (0)
Cherry	Moderate Intensity	Final		1.382 (7)	12.1305 (58)	0.171 (1)			0.6568 (3)
Cherry	High Intensity	Final		1.4231 (2)	58.0118 (64)	0.3489 (0)			0.1095 (0)
Cherry	Woody Removal	Final		2.2099 (4)	17.0498 (30)	0.3831 (1)			0.2737 (0)
Pass	Control	Final		1.1357 (12)	1.5941 (17)	0.6979 (7)		0.6295 (7)	0.2326 (2)
Pass	Moderate Intensity	Final		0.8826 (4)	14.5183 (61)	0.13 (1)		0.0684 (0)	1.0673 (4)
Pass	High Intensity	Final		1.4436 (10)	7.8339 (53)	0.1984 (1)		0.2668 (2)	0.5131 (3)
Pass	Woody Removal	Final		0.4173 (3)	5.9319 (43)	0.2189 (2)		0.0411 (0)	0.2053 (1)
Red Canyon	Control	Final		1.642 (0)	467.7067 (93)			0.2258 (0)	0.2532 (0)
Red Canyon	Moderate Intensity	Final		0.9031 (0)	280.7814 (95)			0.4652 (0)	0.0684 (0)
Red Canyon	High Intensity	Final		1.2017 (1)	91.5435 (94)			0.2762 (0)	
Red Canyon	Woody Removal	Final		2.7915 (14)	10.2901 (50)		0.9647 (5)	0.2395 (1)	0.9784 (5)