THESIS

EFFECTS OF HABITAT COMPLEXITY LOSS ON EASTERN SLOPE

ROCKY MOUNTAIN BROOK TROUT POPULATIONS

Submitted by

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ABSTRACT

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Western U.S. rivers are currently influenced by legacy effects of reduced large wood (LW) loading and retention that has led to reduced in-stream habitat complexity. Historical land use practices such as tie-driving, snag removal, and beaver trapping have all contributed to declines in either input or retention of LW in mountain streams. Effects from these practices have persisted over a century after the activities ceased; suggesting streams have entered an alternative stable state. The alternative state is characterized by loss of multi-thread stream reaches, reduced sediment and nutrient retention, steeper channel gradient, reduced pool volume and altered pool geometry. The cumulative effects of these changes lead to narrower and shallower streams with higher width to depth ratios, and overall decreased stream and valley complexity.

Using a few of the last remaining patches of old-growth forest on the Front Range of Colorado (USA), I compared population densities, individual growth rates, diet compositions, and annual prey consumption demand of Brook Trout *Salvelinus fontinalis* in streams across a gradient of wood volumes. Brook Trout population size was sampled via multi-pass electrofishing and approximately 30 individuals at each site were sacrificed for growth and diet studies. Individual growth was back-calculated from otolith sections, and diet composition was estimated from stomach samples collected at each site. Average growth rates and diet

compositions were then combined in a bioenergetics model that provided an estimate of the amount of prey resources needed to support observed growth and population densities.

Trout population density appears to be positively related to the number of pools, and standing stock biomass of aquatic insects. The scale of measurement was an important consideration in predicting trout biomass. At both the local (square-meter) and landscape (valley length) scales, standing stock biomass of aquatic insects was the best predictor of trout biomass. However, at the valley scale, the number of pools was important in predicting trout biomass in combination with of standing stock biomass of aquatic insects.

Annual individual prey consumption demand did not differ between two sites with high and low wood volume and trout biomass. Therefore, total prey demand at a site was determined by population density, and less so by physical habitat. Between the two sites, however, diet compositions were significantly different during the summer season. Fish at the high wood site were consuming more small aquatic insect larvae (e.g., Family Chironomidae and Simullidae) to support growth and fish biomass, whereas diet composition at the low wood site consisted of terrestrial insects (ants) and larger aquatic insect larvae.

Individual growth rates of age-1 Brook Trout were negatively affected by increasing density. However, growth for the largest and smallest individuals at each site was not affected by density. The largest fish at each site are presumably dominant individuals, and can out compete all other individuals for optimum foraging positions regardless of density, and are therefore not affected by density. While the smallest fish, presumably the most subordinate individuals, are outcompeted for resources at all densities, and are likewise not affected by increasing density.

Large wood, in the correct geomorphic context, can drastically alter stream and valley habitat complexity. My results suggest the pool habitat created by LW and available prey resources can dramatically increase trout populations. However, the negative effects of historical land uses have persisted >100 years and a loss of aquatic animal production in mountain watersheds due to land use changes incurred over a century ago is occurring.

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INTRODUCTION

Factors that influence physical attributes of streams, such as the abundance and

distribution of large wood (LW) and geomorphic features, are important determinants of

salmonid population density and dynamics (Gowan and Fausch 1996*a*; Kellerhals and Miles

1996; White et al. 2011). In geomorphically unconfined stream valleys with intact old growth

forests, LW can be recruited and retained in streams, resulting in multi-thread channel reaches

with increased sediment and nutrient retention, shallower channel gradients, increased numbers

of pools, and greater habitat complexity (Young et al. 1994; Nowakowski and Wohl 2008;

Ruffing et al. 2015). Physical habitat complexity can directly affect stream fish and insect

communities by increasing species richness as well as increasing population sizes (Wallace et al.

1995; Gerhard and Reich 2000; Scealy et al. 2007; Mažeika et al. 2008; Roni et al. 2008).

Richmond and Fausch (1995) demonstrated that stable LW can form nearly 70% of pool habitat

in streams flowing through undisturbed mountain forest systems. Additionally, trout population

density rapidly increased in response to pool habitat created by the addition of LW, and these

increases persist over time (Gowan and Fausch 1996*a*; White et al. 2011). It appears that LW in

the appropriate geomorphic context creates habitats that stream salmonids prefer. Positive

attributes of these habitats include lower velocity areas, under cover, that are directly adjacent to

higher velocity currents that allow salmonids to minimize energy expended on swimming and

predator avoidance and maximize prey encounter rates (Fausch 1984; Fausch 2014).

Land use within watersheds has clear linkages to stream geomorphology and in-stream

habitat characteristics (Keeton et al. 2007) and can exert considerable negative effects on these

aquatic ecosystems (Allan 2004). Historical loss of LW from Rocky Mountain streams and

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reduced recruitment from riparian areas can be attributed to direct (e.g., logging and tie-driving) and indirect (e.g., extensive beaver-trapping) land uses (Wohl 2006), which have markedly changed mountain streams (Czarnomski et al. 2008; Mellina and Hinch 2009). Tie-driving, the act of floating cut timber for railroad ties down streams during spring runoff, was extensively practiced in the Southern Rocky Mountains and directly reduced in-stream habitat complexity initially by loggers reducing channel complexity prior to floating logs, and from the logs themselves artificially straightening and scouring the channel (Young et al. 1994) further homogenizing channel form. The reduction in recruitment and retention of LW in western U.S. streams has resulted in the reduction of multithread channel reaches, changes to stream structure and function, and reductions in habitat complexity (Young et al. 1994; Fausch and Young 2004: Nowakowski and Wohl 2008; Ruffing et al. 2015).

Although these detrimental land use practices ceased almost a century ago, it appears that mountain streams are suffering from legacy effects of reduced LW-loading and storage that has led to an alternative state of reduced stream habitat complexity (Allan 2004; Ruffing et al. 2015). This alternative state is typified by the loss of multithread channel reaches, reduced sediment and nutrient retention, steeper channel gradient, reduced pool volume and altered pool geometry. The cumulative effects of these changes lead to narrower and shallower streams with higher width to depth ratios, and overall decreased habitat complexity (Young et al. 1994; Nowakowski and Wohl 2008; Ruffing et al. 2015; Livers and Wohl 2016). In-stream retention of LW has also declined due to decreased roughness elements in streams ("debris roughness"; Wohl and Beckman 2014). These features that foster LW entrapment are lost as wood-loading decreases (Collins et al. 2012). Local factors, such as abrupt changes in stream width or depth and previously deposited pieces of LW can exert first-order control over whether or not a new piece

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of LW will be retained in a stream reach (Abbe and Montgomery 1996; Braudrick and Grant 2001). As stream habitat is homogenized, logs are more likely to be exported downstream, as opposed to being recruited in a local reach, further increasing the resistance of a stream-riparian ecosystem to return to the pre-perturbation state.

Natural loading rates of LW into streams and formation of logjams in mountain streams increase pool frequency and positively affect macroinvertebrate production, abundance, and community diversity (Wallace et al. 1995; Gerhard and Reich 2000; Lemly and Hilderbrand 2000; Scealy et al. 2007). Potential mechanisms that increase macroinvertebrates are increased area for colonization and refugia from predation (Everett and Ruiz 1993; Rolauffs et al. 2001; Schneider and Winemiller 2008). Further, slower velocity areas interrupt longitudinal transport in streams and serve as localized sinks of carbon and nitrogen by increasing storage of organic and inorganic sediment (Ward and Stanford 1983; Arp and Baker 2007), creating biogeochemical hotpots in headwater streams that increase stream metabolism and animal production (Wallace et al. 1995; Schneider and Winemiller 2008; Hoellein et al. 2009). These changes to prey resources benefit drift-feeding predators, such as trout, at higher trophic levels by contributing additional drifting prey resources not found in stream reaches lacking LW (Coe et al. 2009). Therefore, LW may increase prey availability for salmonids as well as increasing preferred physical habitat.

The potential positive effects of LW on trout population density may have detrimental effects on individual growth through density-dependent mechanisms. As population densities increase, competition for both physical space and prey resources increases, leading to a potential decrease in overall net energy intake and reduced growth rates (Lorenzen and Enberg 2002). Thus, density is a strong regulator of fish size in stream-dwelling salmonid populations (Jenkins

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et al. 1999 and references therein); however, documenting reduced growth due to density dependence in observational data can be difficult (Jenkins, et al. 1999). A complicating factor in demonstrating density dependence in salmonids is the occurrence of stable dominance hierarchies (Nakano 1995) that can obscure density dependent effects on body size (Abbott and Dill 1989). Larger, dominant individuals in all populations can successfully occupy and control profitable foraging positions, reducing the effects of competition for these individuals. The result of these inter- and intra-species interactions is that dominant individuals may show similar growth patterns across a wide range of densities. Alternatively, subordinate individuals have access to poorer feeding positions, obtain fewer resources, and may show greater effects of density than dominant individuals (Sloman et al. 2000). If growth is analyzed without considering dominance, the resulting variation in growth rates could obscure intra- and inter-population differences. Therefore, it is important to consider dominance when comparing growth across sites with different LW loading.

Another important factor controlling individual growth and population density in salmonids is stream temperature (Nicola and Almodovar 2004; Warren et al. 2012). Temperature can vary across sites due to the effects of LW on stream morphology and water velocity. Increasing complexity can influence stream temperatures by slowing flow rates, creating pools, creating shade above streams, and increasing hyporheic flow as water is forced under log jams or other habitat (Poole and Berman 2001). Another potential complication is that most sites with naturally occurring old growth forest and high wood loading are also at higher elevations where logging did not occur (Wohl 2001). Sites at higher elevation increase the likelihood that temperatures in these reaches are consistently lower than lower elevation sites (Isaak and Hubert 2001). As with most ectotherms, external temperatures govern physiological processes such as

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intake, digestion, and assimilation of prey (Railsback and Rose 1999). Therefore, temperature could be a confounding factor and growth could be slower at higher elevation sites, due to lower stream temperatures, which is why it is important to also consider temperature differences among sites when comparing growth rates.

My goals were to explain how reduced physical stream habitat complexity caused by historic losses of instream LW affects population densities, individual growth rates, and prey consumption in trout populations in Rocky Mountain streams. I predicted that increased LW storage would increase habitat complexity and positively affect overall trout densities. While high standing stock of LW would be associated with lower individual growth rates due to higher population densities and lower water temperatures associated with these sites. Finally, overall consumption demand would be positively related to LW storage because of higher trout densities at those sites.

METHODS

Study Area

Study sites were located in or near Rocky Mountain National Park in the Big Thompson, Cache la Poudre, and North St. Vrain drainages in northern Colorado. Two other study sites were located in the North Platte River drainage in the Medicine-Bow National Forest in Southern Wyoming. Study sites were chosen based on fish assemblages being dominated by Brook Trout *Salvelinus fontinalis*. All three Colorado drainages flow east of the continental divide and meet the South Platte River at ~1500 m in elevation. The Wyoming drainage first flows west, then north and east before joining the North Platte River in southeastern Wyoming. Study reaches were located between 2713 and 3076 m in elevation, within the subalpine spruce-fir forest ecozone, dominated by Engelmann spruce *Picea engelmanii*, subalpine fir *Abies lasiocarpa*, and lodgepole pine *Pinus contorta*. USGS gaging stations located near the study sites indicate mean annual peak discharges of approximately 12.3 m^3/s (South Brush Creek, Wyoming, ID: 06622900) to 20 m^3/s (North St. Vrain Creek, Colorado, ID: 401226105340100; Wohl and Beckman 2014*b*), and hydrographs at all streams are snowmelt driven. The North St Vrain Creek drainage contains old-growth forest (stand age >350 years), whereas the other drainages contain forest stands much younger in age (~120 yrs).

Two sites, N St Vrain and Glacier Creeks, were intensively sampled in 2013 and 2014 and are hereafter referred to as intensive sites. They were chosen based on habitat complexity with the N St Vrain representing high habitat complexity ('high wood') and Glacier Creek representing reduced habitat complexity ('low wood') and were sampled multiple times during 2013 and 2014 to quantify patterns in trout populations (Figure 1; Table 1). Eleven other sites

("extensive Sites") were sampled to assess patterns in trout abundance across a wider geographic range and to assess if the patterns observed at the intensive sites were generally applicable to mountain streams (Figure 1; Table 1). The majority of sampling at intensive and extensive sites was in unconfined river reaches. We also sampled three confined river reaches on streams already included in the study (N St Vrain, Mill, and Ouzel Creeks) to explore how fish populations respond to these two valley types (Figure 1; Table 1). Reaches were considered laterally unconfined when the floodplain was >2x bankfull width of the stream channel and largely disconnected from hillslope processes (including partly confined stream reaches; Livers and Wohl 2016). We considered sites laterally confined when the valley width <2x the bankfull width of the stream channel and directly connected to hillslope processes by the geology of the valley (Livers and Wohl 2016). Both stream reach types were chosen to represent a range of wood-loading and physical habitat complexity (Table 2).

Sampling Scale and Habitat Surveys

Sampling efforts were standardized over two scales; square meters and meter of valley length. The square meter scale compares population size or density at a standard area and we typically made these comparisons at the hectare scale (e.g., $N*ha^{-1}$). Comparing at a standard area scale allows direct comparison among sites but does not capture the effects of habitat complexity among sites. Therefore, we standardized the total length of stream in a valley to the length of the valley, which standardizes for increased aquatic habitat in stream systems that have multiple channels within a valley. This scale represents a stream network or valley view of the aquatic habitat and how stream channel form can affect available aquatic habitat in an ecosystem (Figure 2).

Physical habitat surveys were conducted at each sampling site to assess differences in the aquatic habitat available to fish populations. Starting at the upper end of the reach, stream width was recorded every 3m downstream ending at and including the bottom of the reach. Stream depth was measured every 9m downstream, with five equally spaced depths taken perpendicular to the stream channel. Pool volumes were calculated from three transects taken perpendicular to the channel, at the top, middle, and bottom of each pool. Five equally spaced depth measurements were taken at each width transect and the pool length was recorded. If total pool length was < 1.5m, only the top and bottom widths and depths were measured. Only pools with a surface area larger than $1m^2$ were measured.

Standing stock biomass of aquatic invertebrates was measured at each of the extensive sites, except Jack and S Fk Michigan Creeks, as a way to represent prey resource availability across the sites (M. Venarsky, *unpublished data*). Aquatic invertebrate production was also estimated for the intensive sites (M. Venarksy, *unpublished data*), and was used when comparing patterns at the intensive sites.

Wood surveys for each experimental reach were conducted following Wohl and Cadol (2011), and Livers and Wohl (2016). Wood volume was estimated by measuring length and end diameters of each piece and each logjam (defined as ≥3 pieces of LW touching). Most wood surveys were adapted from Livers and Wohl (2016), however, Jack Creek, S Fk Michigan Creek, and Hague Creek were measured following the same protocols.

Population Estimation

Fish abundance was estimated using multi-pass removal electrofishing conducted at the intensive sites in summer 2013, summer 2014, and fall 2014. Fish abundance was estimated at

the extensive sites in the summer of 2013 or 2014. Fish captured during electrofishing were

weighed (to nearest 0.5g) and total length measured (to nearest 1mm). The Huggins (1991)

closed population removal estimator was used in ProgramMARK (White and Burnham 1999) to

estimate population densities at each site for fish >49mm in total length to avoid known

deficiencies with capturing smaller individuals (Saunders et al. 2011).

     I used the information-theoretic approach (Burnham and Anderson 2002) to evaluate the

relative validity of candidate models relating 13 physical and biological predictor variables to

trout density at each sampling site (Table 2; including standing stock biomass of aquatic insects).

Prior to constructing the candidate models, the predictor variable set was examined for the

presence of multicollinearity (Burnham and Anderson 2002). Variables were removed if $R^2 >$

0.7. Variables were removed from inclusion based on how many other predictor variables they

were correlated with (e.g., variables correlated with multiple variables were removed first), and

then by informed inference based on previous research on what may directly affect trout

densities.

     Akaike's Information Criterion (AIC; Akaike 1973) was calculated to assess model fit

using the small-sample bias adjustment (AIC$_c$; Hurvich and Tsai 1989), and Akaike weights

were calculated for each candidate model to assess the relative plausibility of each model

(following Burnham and Anderson 2002). Model averaging (Burnham and Anderson 2002) was

not used to incorporate model selection uncertainty into parameter estimates. Instead of model

averaging, I present a set of models to assess model selection uncertainty and relative importance

of each predictor variable. Normal probability plots were created for each predictor variable, and

if found to deviate from expected, the data was natural-log transformed to ensure normality prior

to model selection.

To account for how stream and valley morphology affect available aquatic habitat and to investigate the importance of variables affecting fish density at different scales, model selection was performed on data transformed to the square-meter scale and meter of valley length scale.

Growth Rate Analysis

Approximately 50 individual Brook Trout were collected from each study site during population survey events. Ten individuals were collected from 5 different size classes (0-50mm, 51-100mm, 101-150mm, 151-200mm, and >200mm) to get a representative sample of brook trout from the different populations. Left sagittal otoliths were removed, mounted in quick-set epoxy, sectioned by saw, polished with sand- and lapping paper, and photographed by microscope camera. Otoliths were measured from the nucleus to each successive annuli including the otolith edge. Right sagittal otoliths were used only in cases where the left otolith was lost, damaged, or was structurally unusable. Otoliths are the most dependable aging structure on brook trout, especially older trout >2 years of age (Stolarski and Hartman 2008). Two separate readers completed two independent estimates of age; if consensus was not met the otolith was removed from further study. Individual trout lengths at previous ages were back-calculated using the biological intercept method (Campana 1990), from which, average lengths at ages were obtained.

Average individual growth rates at the intensive sites were estimated by fitting von Bertalanffy growth curves (Allen 1966) to observed average lengths at ages for each site using R-package "FSA" (Ogle 2016), and confidence intervals were predicted for each parameter by bootstrapping ($n = 1000$). The three parameters estimated include L_{inf}, which is the hypothetical size at which growth stops, K, how quickly the growth curve approaches L_{inf}, and t_0, the

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theoretical age-at-length 0. To identify density-dependent effects on growth at extensive sites,

back-calculated lengths at a specific age (e.g. age-1, age-2, and age-3) were regressed across

natural log-transformed site densities using quantile regression (Koenker and Bassett 1978).

Quantile regression allows observation of response patterns across the entire range of the

response variable distribution (Cade and Noon 2003). Salmonids are known to have feeding

dominance hierarchies based on size and competitive abilities (Nakano 1995) and dominant

individuals may be less influenced by density than less dominant individuals. Additionally,

important body size differences among sites may be obscured by variability associated with

dominance. Quantile regression allowed me to explore potential density-dependent effects on

growth across a wide range of individual fish size across all sites, thereby accounting for

dominance effects.

Bioenergetics Modeling

Predictive Stream Temperature Model

Water temperature loggers were deployed in N St Vrain and Glacier Creeks in July 2013

and August 2014, to capture a range of elevations (from 2557m to 3213m on N St Vrain, and

2740m to 3146m on Glacier Creek). Data loggers recorded stream temperatures every 30

minutes, and those deployed in 2013 were left in stream overwinter, retrieved in August 2014,

and returned to the stream. Loggers deployed in August 2014 were retrieved in late fall 2014.

Data was averaged to get daily average stream temperatures, and mean weekly stream

temperatures (MWST). To estimate stream temperatures during the growing season, I used

temperature data beginning on April 15th or until recorded stream temperature was >0° C,

whichever occurred later and ending on October 15th of each year to avoid confounding effects of annual ice occurrence at our sites.

Following Fraser (2015) and Isaak et al. (2010), I developed a predictive stream model using multiple regression to estimate stream temperature as a function of mean weekly air temperature (MWAT), Julian day, and site elevation. Air temperature was obtained from two separate SNOTEL (SNOwpack TELemetry sites; USDA Natural Resources Conservation Service Snow Survey and Water Supply Forecasting Program) sites located near study streams (Table 3). SNOTEL sites record average daily temperatures, which were downloaded from the NRCS website (www.wcc.nrcs.usda.gov), and were averaged to get MWAT. MWAT from 2010-2014 were averaged to obtain MWAT for an "average air temperature year" based on recent historical observations. The four-year period was used because it represents the temperature history that a 0-3+ year old fish would have experienced, which correlates to my aging analyses on age-1, 2, and 3 year old fish. MWST obtained from five thermal loggers in N St Vrain Creek and eight loggers in Glacier Creek were used as the dependent variable, while MWATs from two SNOTEL sites (Bear Lake, station ID: 322; and Wild Basin, station ID: 1042), Julian day, and elevation were used as the independent or predictor variables. Several possible models were created and the best models were selected based on delta AICc values (Burnham and Anderson 2002). Model-averaging (Multimodel Inference; Burnham and Anderson 2004) was used to combine the top models (delta <1.05), into one global predictive model.

The global model was used to predict MWST at all of our study sites using local air temperature (MWAT from nearest SNOTEL site; Table 3), Julian Day, and sample site elevation. Due to the annual occurrence of ice at our study sites and the breakdown of the linear

air/stream temperature relationship at extreme temperatures (Erickson and Heinz 2000), predictions were restricted from April 15th to October 15th in each year, and any predicted stream temperature less than 0° C was set equal to 0° C. Two separate data loggers deployed in 2013, one in N St Vrain Creek and one in Glacier Creek, were not included in the data used to build the model, but were used to test the predictive capabilities of the final model. Predicted stream temperatures from the model were plotted against observed stream temperatures at these sites, and regressed to compare agreement. Estimated MWST predictions were then used to parameterize the water temperature requirements in separate bioenergetics models.

Fish Diet Analysis

Fish sacrificed for aging were also used to determine diet composition at each study site. Gastrointestinal tracts (esophagus to anus) were removed from fish during sampling events and stored in individually labeled Whirl-Paks in 180-proof ethanol. Stomach contents were later removed from the anterior portion of the stomach excluding the esophagus and intestine. Stomach contents were viewed under a microscope and individual insect taxa were identified to family level and life stage (e.g. adult, larvae, or pupae), and body length recorded. Insect biomass was calculated using previously published length-weight regressions (Rogers et al. 1976; Rogers et al. 1977; Benke et al. 1999; Sabo et al. 2002), and multiplying predicted weights by the number of each taxa present.

Diet composition at the intensive sites were analyzed and compared using analysis of similarity (ANOSIM; Clarke 1993) and similarity percentages (SIMPER; Clarke 1993), two multivariate procedures, and plotted using non-metric multi-dimensional scaling plots (MDS). Diet composition for the intensive sites was compared for samples collected in summer and fall

2014. Following Winkelman and Van Den Avyle (2002), the total number of taxa included in diet composition analysis was reduced to include only taxa found at all sites in the analysis. Reduced diet compositions from each site and each sampling date were then converted to proportions by dividing the mass of individual taxa by the total mass in the stomach. Bray-Curtis similarity matrices were computed on these proportions. One-way ANOSIMs were computed based on these Bray-Curtis similarity matrices and taxa contributing to differences in diet communities were identified using SIMPER analysis.

ANOSIM analyses compare the differences between predefined groups (e.g. study sites) using the test statistic Clarke's R. Values of R near 0 indicate no differences, while values near 1 indicate complete separation between groups. Following Zuellig and Schmidt (2012) when interpreting the ANOSIM results, I interpreted significant Clarke's R-values >0.70 as strong differences between sites, $0.70 > R > 0.40$ as moderate differences between sites, and R <0.40 representing weak differences between sites. Analyses with R-values <0.40 were interpreted as not having enough separation between groups to be significantly different on an ecological scale, and were treated as non-significant. This is due to the sensitivity of Clarke's R to large numbers of permutations that can give significantly different results yet with very low real difference between groups being compared. SIMPER analyses were only completed on ANOSIM comparisons that were significantly different and had a Clarke's $R \geq 0.4$. All Clarke's R-values presented in the Results section are statistically significant, unless otherwise stated. All multivariate community analyses were performed in the Plymouth Routines in Marine Environmental Research (PRIMER-E, v 6.0) program (M.R. Carr and K. R. Clarke, Marine Biological Laboratory, Plymouth, UK).

Invertebrates were grouped by order and life-stage to differentiate between benthic and drifting insects (e.g. larvae vs adult Ephemeroptera) then further grouped into aquatic/benthic vs. terrestrial/adult insects that have an aquatic larval stage to get estimates of terrestrial and aquatic proportions for bioenergetics analyses.

Consumption Demand

Annual fish consumption was estimated at the intensive sites from bioenergetics simulations using the Wisconsin bioenergetics model of Hanson et al. (1997), populated with parameters from the Brook Trout model tested by Hartman and Cox (2008). Simulations were run using Fish Bioenergetics 3.0 Software®.

Brook Trout energy densities were estimated from percent dry mass using the Lake Trout *Salvelinus namaycush* equation found in Hartman and Brandt (1995). Four to twelve fish were randomly selected from length categories from both intensive sites, based on availability of individuals when sampling occurred. Fish were weighed to the nearest 0.01g, oven-dried at 80C to a constant weight, and then weighed again to the nearest 0.01g. Energy densities were then averaged to get a site-specific energy density for both summer and fall seasons.

Fish at each site were divided into age classes based on otolith aging techniques and by constructing an age-length key to age the remaining fish captured at each sampling site (using R-package "FSA"; Ogle 2016). Weight at age was then estimated by combining the predicted lengths at ages with a separate length-weight regression for each site. Average weight, along with 5th and 95th percentile weights were calculated for each age, to estimate the range of consumption when calculating total consumption at each site (Table 4), except for age-0 fish which were assumed to be 0.01g at the start of the growing season at all sites.

Invertebrate prey was divided into terrestrial and aquatic sources based on diet sampling and energy densities were estimated using the terrestrial and aquatic arthropod mean equations in Cummins and Wuycheck (1971). The proportions of diet from terrestrial and aquatic sources was then used in the model, only changing during winter when it was assumed that all prey were coming from aquatic sources (proportion of terrestrial prey in diet = 0). Dietary loss due to indigestible material was estimated at 10% (Sweka and Hartman 2001), and included by multiplying the estimated prey energy densities by 0.9 before entering them into the bioenergetics model. Maintenance temperature in the model (lowest temperature fish growth can occur) was set at 4° C to take into account reduced consumption levels found in field scenarios, as opposed to *ad libitum* feeding in laboratory settings (Hartman and Sweka 2003).

To approximate the sensitivity of the bioenergetics model to diet composition, I ran simulations using the average growth of an individual fish from age 1 to 2 at the N St Vrain Intensive site and varied the proportion of aquatic insects from 0 to 100%, at 10% intervals.

RESULTS

Population Density and Model Selection

Intensive

      Brook Trout population density was approximately 7.5 times higher at N St Vrain (high wood) than Glacier Creek (low wood) in summer 2013, and approximately 7 times higher in summer 2014 (Figure 3). Average Brook Trout biomass was approximately 4 times higher at the high wood site than the low wood site on a per square meter basis (Figure 4a) and approximately 9 times higher when estimated at a meter of valley length (Figure 4a). While fish density was 7 times higher at the high wood site on the square meter scale (Figure 4c), and approximately 14 times higher when estimated at the meter of valley length scale (Figure 4d). Summer density estimates for both sites were similar between years, indicating that fish density is relatively constant within each site when estimated during similar seasons (Figure 3). Fish communities at both sites were dominated by Brook Trout. However, the low wood site fish assemblage also consisted of Brown Trout *Salmo Trutta* (approximately 1% in 2013 and 20% in 2014), and Rainbow Trout *Oncorhynchus mykiss* (approximately 14% in 2013 and 20% in 2014).

Extensive

      Number of Brook Trout per hectare (95% confidence intervals) at all intensive and extensive unconfined sites ranged from 409.53 (343.48, 937.15) to 7441.998 (7342.27, 7752.19), during summer sampling events (Table 5). While trout biomass per square meter was 1.04g (0.98, 1.48) at the lowest site and 16.54g (16.51, 17.25) at the highest site (Table 5). At the

valley scale, trout biomass per meter of valley length showed a much larger range, from 8.81g

(8.29, 8.81) to 128.43g (127.28, 134.78; Table 5) per meter of valley length.

I measured 12 physical habitat predictor variables and two were retained for inclusion in

the model selection analysis, in addition to standing stock biomass of aquatic insects (Table 2).

Eight variables were removed because they were correlated with other variables included in the

analyses. Average pool length, depth, width, surface area, volume, and number of pools per 100

meters of stream were correlated and I retained the number of pools per 100 meters of stream

length as a measure of available trout habitat. My decision was based on previous research that

indicates the creation of pools creates optimal foraging positions for trout, and could predict trout

abundance in a local area (Gowan and Fausch 1996*a*; Torgersen et al. 1999; White et al. 2011).

Streams not historically tie-driven, that currently contain high amounts of LW, are only found at

high elevations in Colorado, therefore, elevation was correlated to LW abundance and was

removed from the model selection analyses. Accumulation of LW was correlated with gradient,

therefore, gradient was removed from the variable set. To further reduce the chance of over-

parameterizing the model, average stream width and average stream depth were combined into a

width to depth ratio, a common stream metric, for each sampling site. Finally, LW was positively

related to the predicted number of pools at the square meter scale (y = 0.92x + 7.09, R^2 = 0.25;

Figure 5a) and had a stronger positive relationship at the meter of valley scale (y = 0.24x + 1.70,

R^2 = 0.59; Figure 5b). I chose to retain the number of pools per 100m of stream length over LW

abundance in the analysis because I felt that trout densities responded directly to pool habitat

created by LW, as opposed to responding directly to LW. I also retained the number of pools per

100m of stream and number of pools per 100m valley because I felt they represented stream

channel complexity and previous research within the study streams indicated differences in LW

abundance were the strongest indicators of channel complexity and were strongly correlated to pool formation (Livers and Wohl 2016).

Model selection was performed based on three predictor variables: 1) standing stock biomass of aquatic insects, 2) number of pools, and 3) width to depth ratio at both the square meter and valley length scale. The model set included all combinations of the three predictor variables, excluding interaction terms. Second-order interactions were originally tested; however, none were significant in explaining trout densities at our sample sites. Due to this, and concerns of over-parameterizing the model selection, interactions were not included.

Insect biomass was the most important factor in predicting trout biomass at the square meter scale (Table 6). Insect biomass was also highly correlated with fish biomass at the square meter scale (Figure 6a). The top four models included standing stock insect biomass with beta estimates and 95% confidence intervals that did not include 0 and accounted for 94.15% of the model weight (Table 6). The number of pools per 100m of stream and width/depth ratio were also in the top four models but had beta estimates and 95% confidence intervals that contained 0, and were not highly correlated with fish biomass (Table 6; Figures 7a and 8). Insect biomass was also highly correlated with fish biomass at the valley scale (Figure 6b), and the top four models included standing stock insect biomass (Table 7). Three of those models had beta estimates for insect with 95% confidence intervals that did not overlap 0. The number of pools was also an important predictor of fish biomass at the valley scale (Figure 7b). Two of the top four models contained the number of pools per 100 meters and had beta estimates with confidence intervals that did not contain 0 (Table 7). At the valley scale, width to depth ratio was contained in the lowest four models and all beta estimates and confidence intervals contain 0 (Table 7).

Process Domains

      Unconfined and confined sites were located adjacent to one another on N St Vrain and

Mill Creeks and approximately 1.5-2 miles apart on Ouzel Creek. The confined sites supported

fewer fish than unconfined sites on streams where they were adjacent to one another (Figure 9).

The Mill Creek unconfined site supported approximately 2.5x more fish than the Mill Creek

confined site (Figure 9). Similarly, the N St Vrain Creek unconfined site supported

approximately 2x more fish than the N St Vrain confined site (Figure 9). The Ouzel Creek

confined site supported similar numbers of fish as the Ouzel Creek unconfined site (Figure 9).

All three confined sites were similar to their paired unconfined reaches in width to depth ratio,

and all three confined reaches had lower standing stock biomass of aquatic invertebrates

compared to their paired unconfined reaches (Table 2; M. Venarsky *unpublished data*). The

largest difference between the confined sites was in number of pools per 100 meters (Table 2).

The N St Vrain confined site had similar numbers of pools to the unconfined site, the Mill Creek

confined site had lower number of pools compared to the unconfined site, and the Ouzel Creek

confined site had more pools compared to the Ouzel Creek unconfined site (Table 2).

Growth Rate Analysis

Intensive

      Despite the large differences in population densities between Glacier Creek and N. St.

Vrain, there were no observable differences in growth rates between the two sites. Von

Bertalanffy growth curve parameters K and t_0 were similar between the sites; however, Glacier

Creek fish appear to have a larger L_{inf} than fish from N. St. Vrain Creek (205 vs 183; Figure 10;

Table 8). Individual fish condition did not differ between sites (F = 0.329, p-value = 0.567);

however, Glacier Creek had a significantly higher intercept (F = 5.0495, p-value = 0.0252) by approximately 1.25 grams wet weight.

Extensive

Average lengths at age-1 were similar across extensive sites and annual growth rates showed high variability within sites (Figure 11). Quantile regression showed that fish in the highest 5 quantiles (presumably dominant individuals) and fish in the lowest 10 quantiles (presumably subordinate individuals) at each site did not appear to be affected by density because the estimated confidence intervals of the regression slopes contained zero (Figure 12a). The majority of fish exhibited a negative response to increasing density with slopes for regression lines for the 10th through the 95th quantiles significantly less than 0 (Figure 12a). Size of age-2 and 3 fish did not show any negative relationship to fish density (Figures 12b and 12c).

Predictive Stream Temperature Model

The predictive stream temperature model included 6 predictor variables: air temperature, site elevation, Julian day, quadratic-transformed Julian day, air temperature and elevation interaction, and air temperature and Julian day interaction (Table 9). The inclusion of the quadratic Julian day term was in response to the nonlinear relationship between Julian day and stream temperature. To check the predictive capabilities of the model, I estimated stream temperatures at both Glacier Creek and N St Vrain Creek and compared them to independently recorded stream temperatures. Model water temperature estimates were highly correlated with the measured temperatures at Glacier Creek ($R^2 = 0.9102$) and N St Vrain Creek ($R^2 = 0.9273$; Figure 13). Predicted mean weekly stream temperatures for an average year did not vary greatly

between the two sites, however, N St Vrain Creek was approximately 1° C cooler than Glacier Creek during the summer season (Figure 14).

Fish Diet Analysis

Insect biomass in stomachs differed among sites (F = 5.318, p < 0.0001), yet there were no clear patterns or predictors of differences between the sites (Figure 15). The streams with the lowest observed average biomass in stomachs were Glacier Creek (fall 2014), Rock Creek and Ouzel Creek, with N St Vrain Creek (summer 2014) having the highest observed average prey biomass in stomachs (Figure 15). Average biomass in stomachs did not appear to be correlated with diet source, whether aquatic or terrestrial, as Order Hymenoptera made up the largest percentage of diets at all four of these sites (Table 10).

Intensive

Of the 81 total taxa identified in the summer diet samples, only 21 taxa were common between the two sites. Of the 60 removed, 58 were only identified at N St Vrain while two were solely consumed at Glacier Creek, representing 41.5% and 0.01% of the average prey biomass in stomachs, respectively. During fall sampling, 61 total taxa were identified, with 34 taxa being represented in diet samples at both sites; 25 taxa were only found at Glacier Creek, while two were removed from the N St Vrain Creek samples. The 25 taxa removed from the Glacier Creek diet samples represented 34.6% of average prey biomass, while the two taxa removed from the N St Vrain samples represented 56.6% of average prey biomass (this number is skewed by one taxa, Family Cantharidae, representing 51.2% of average prey biomass in being removed from the analyses).

Diet composition differed significantly between the sites sampled in summer 2014 (Clarke's $R = 0.434$; Figure 16). Brook Trout consumed a high proportion of ants (Formicidae) at both sites, although fish at the low wood site consumed more ants than did fish at the high wood site, and ants accounted for 21.67% of the dissimilarity in fish diets (Table 11). Brook Trout at the high wood site consumed more Chironomidae larvae than those at the low wood site and this difference accounted for an additional 20.62% in the dissimilarity in diets (Table 11). Brook Trout at the low wood site consumed more stone fly nymphs (Family Perlidae), water mites (Order Acari), and assorted wasps (Order Hymenoptera) than those at the high wood site (Table 11). The differences in these four taxa accounted for over 70% of the dissimilarity in diets (Table 11). Diet composition during the fall sampling period was not different between the two sites ($R = 0.056$; Figure 17), as Clarke's R-value is close to zero, suggesting no real differences between the sites.

Because of the large number of taxa removed prior to ANOSIM analyses, the diet samples were re-analyzed with all taxa to check for any differences in results when comparing the summer and fall diet samples across the two sites. The summer diet samples were still significantly different (Clarke's $R = 0.495$), and the fall samples were still not significantly different (Clarke's $R = 0.068$).

Comparing diet composition at the two intensive across seasons led to seasonal changes in prey at the high wood site but not the low wood site. The low wood site was not statistically different from summer 2014 to fall 2014 (Clarke's $R = -0.167$), however, the high wood site was weakly statistically different between this same time frame (Clarke's $R = 0.319$), showing a potential change in diets across seasons.

Average insect biomass in stomachs were not different between sites during the summer sampling period in 2014, stomachs at the low wood site contained an average of 1.39 (SD = 1.29) mg insect biomass per gram of fish, while stomachs at the high wood site contained an average of 2.42g (SD = 2.18) mg insect biomass per gram of fish (t-value = -0.30147, p-value = 0.764). Average biomass in stomachs was significantly higher during fall at the high wood site 1.78 (SD = 3.46) mg insect biomass per gram of fish compared to the low wood site, 0.35 (SD = 0.65) mg insect biomass per gram of fish (t-value = -2.4447, p-value = 0.0174).

Extensive

Benthic/aquatic invertebrate sources contributed approximately 11% to 97% of biomass to diet composition among the sites, and do not appear to be related to LW volume or fish biomass (R^2 = 0.00356 and 0.03124, respectively). The top three contributing taxa to diet composition at each site were dominated by Order Hymenoptera (terrestrial). Hymenoptera was the number one represented taxa at ten sites, and the number two taxa at three sites (Table 11). Only 3 sampling sites/dates (of 17) did not have terrestrial hymenoptera in the top three taxa consumed.

Consumption Demand

Intensive

Seasonal differences in Brook Trout energy densities were observed at both the low and high wood sites, with fall energy densities being approximately 7% and 13% lower than summer, respectively (Table 12). Most likely, these losses are due to spawning activity, reduced energy

intake as reduced stream temperatures reduce gastric evacuation rates (Cunjak et al. 1987), and/or reduced prey availability.

Biomass of invertebrates consumed per individual Brook Trout per year did not differ between sites when comparing consumption of individual Brook Trout at specific ages (Figure 18). However, overall consumption demand (milligrams wet mass of invertebrate biomass consumed/square meter/per day) was approximately 7 times higher due to higher population densities at the high wood site on the square meter scale (43.80 mg/square meter/day vs 6.75 mg/square meter/day; Figure 19). On the valley scale, consumption demand of invertebrates rose to approximately 13 times higher at the high wood site (614.33 mg/valley meter/day vs 47.42 mg/valley meter/day; Figure 19). When comparing only consumption of aquatic invertebrates, demand was approximately 10 times higher at the high wood site on the square meter scale (31.58 mg/sq meter/day vs 2.96 mg/sq meter/day; Figure 19), and approximately 21 times higher at the high wood site on the valley scale (443.00 mg/valley meter/day vs 20.78 mg/valley meter/day; Figure 19).

The bioenergetics model is sensitive to diet composition, especially when only two diet sources are input that differ in energy content. As the percentage of aquatic prey in diets increased, the amount of insect biomass consumed per year and proportion of estimated maximum consumption (Bioenergetics p-value) also increased to maintain observed growth rates (Figure 20). These response variables increased slightly exponentially, suggesting the bioenergetics model is sensitive to the energy content of different prey types.

DISCUSSION

My study indicates that prey resources and habitat availability control Brook Trout densities in high elevation Rocky Mountain streams. Specifically, Brook Trout densities were positively influenced by the standing stock biomass of aquatic macroinvertebrates at both the local and landscape scale. Brook Trout density was also positively related to number of pools in a valley (i.e. habitat availability). In turn, Brook Trout density had important influences on total prey consumption and subtle effects on growth. Prey consumption demand of individual trout did not appear to differ among sites and Brook Trout density determines the total prey consumption demand at a given site. Increased Brook Trout density resulted in negative density-dependent effects on individual growth for those age-1 individuals that were not dominant or extremely subordinate. Diet composition can be substantially different when comparing fish from streams across a gradient of LW. Lastly, geomorphology can drive population density in trout.

Across the intensive and extensive sites, prey resources were important in predicting trout biomass. At the intensive sites, estimated trout biomass was four times higher on the square meter scale and nine times higher on the valley meter scale at the high wood site; aquatic macroinvertebrate biomass and production is likely a factor in maintaining this difference. Standing stock biomass of aquatic insects was approximately the same between the two sites at the local scale, yet three times higher at the high wood site on the valley scale. Aquatic insect production was approximately two times higher on the local scale, at the high wood site, while almost five times higher on the valley scale. Increased standing stock insect biomass and aquatic insect production indicate prey resources respond positively to increased physical habitat

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complexity suggesting increased prey availability to fish in physically complex stream reaches. Higher abundance and community richness of aquatic insects due to physical habitat complexity have been previously noted (Schneider and Winemiller 2008), along with higher rates of macroinvertebrate drift related to LW (Coe et al. 2009). Further, Ensign et al. (1990) and Shannon et al. (1996) found a positive relationship between prey abundance and trout in lotic environments.

The importance of prey resources at the extensive sites was similar to my inferences made from comparing the intensive sites and strengthens the argument that Brook Trout are responding to prey resources across both the local and landscape scale. For instance, N Mullen and Rock Creeks had the highest fish biomass per square meter, yet very different amounts of LW (235.6 vs. 7.8 cubic meters per ha, respectively). Most likely, trout populations were responding to availability of prey resources at these sites, as they had two of the highest amounts of standing stock biomass of aquatic insects sampled during this study. Conversely, Hague Creek had very low trout biomass per square meter, lower number of individual pools compared to the other unconfined sites, and the lowest measured amount of standing stock biomass of aquatic invertebrates. High standing stock biomass of aquatic insects at Rock Creek may be due to an open riparian canopy at the study reach with minimal overhanging cover. Reduced riparian canopies can increase local primary productivity in streams through increased insolation and stream temperatures (Kiffney et al. 2004); which can lead to increased invertebrate production (Murphy 1998).

The large difference in trout density between the intensive sites was also driven in part by differences in the pool habitat present at each site. Estimated valley scale trout densities at the intensive sites were nine times higher at the high wood site. The high wood site had

approximately 54 to 60 times the volume of LW stored in the stream channel and floodplain, which created a multi-thread stream reach with almost two times the amount of stream length when compared to the low wood site. Due to larger average pool sizes, the low wood site had approximately four times more pool volume at the local scale; yet, the high wood site had approximately twice the number of individual pools at the same scale. Increased pool formation at the high wood site is likely driven by LW and trout populations responded to increased pool habitat (Gowan and Fausch 1996*a*; Korsu et al. 2010) and physical habitat complexity (Smokorowski and Pratt 2007; Kozarek et al. 2010). Trout populations are likely responding to an increased number of favorable holding positions created by these numerous smaller pools (Fausch 1984; Fausch and Northcote 1992; Richmond and Fausch 1995; Fausch 2014).

Across the extensive sites, Brook Trout densities ranged over an order of magnitude from the lowest to highest density sites and number of pools became more important in predicting density at the landscape scale. Previous research confirms my results that trout abundance in mountain streams is positively related to pool habitat (Gowan and Fausch 1996*a*; White et al. 2011) and highlights the importance of this variable in governing trout densities. However, scale is clearly important in evaluating trout abundance.

Annual prey consumption demand was similar for individual Brook Trout at each age at both intensive sites. The similarity in consumption could indicate that differences in physical habitat complexity and density do not affect individuals enough to significantly change prey demand. Most likely, the similarity in estimated stream temperatures at both intensive sites was responsible for the similarity in individual consumption demand as bioenergetics models have been shown to be sensitive to temperature inputs (Railsback and Rose 1999). Average lengths at age from each site were similar and were used to calculate average weight at age as an input to

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the bioenergetics model. Similar average weight at age along with similar temperatures at each site were likely responsible for the similarities in annual individual prey consumption demand.

Despite similarities in individual consumption demand, total prey consumption demand was quite different between the sites. In 2014, the overall annual prey demand was seven times higher at the high wood site and demand for aquatic prey was approximately 10 times higher. The higher total consumption demand is due to much higher trout population densities at the high wood site. The higher demand for aquatic prey could be related to a higher availability of aquatic prey due to increased production at the high wood site.

My data suggest that a large portion of the aquatic invertebrate production at the high wood site is being consumed by fish. At the valley scale, aquatic invertebrate production was five times higher at the high wood site; yet the standing stock of aquatic insect biomass was only two times higher at the same scale. Combining estimated prey demand per day and total stream area per valley at both sites leads to estimates of total insects consumed by fish for the entire valley per day. At the high wood site, approximately 500g of invertebrates are consumed by fish per day, while at the low wood site, fish consume 30g of insects in the same time frame. This represents approximately 25% and 28%, respectively, of the aquatic invertebrate production of the entire valley per day at both sites. Major differences in diet composition between the two sites point to fish at the high wood site consuming more small aquatic invertebrates such as chironomid and black fly larvae, as well as small mayfly larvae during the summer months. In the fall at the high wood site, diet composition shifts to primarily terrestrial Coleoptera that represents 65% of the average diet.

The importance of pool habitat at the valley scale is intuitive because pool habitat could easily be missed when measuring at smaller scales. Taking a local view (e.g., square meter

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scale) can easily overlook important patterns and characteristics in physical habitat (Fausch et al. 2002) leading to improper conclusions regarding population drivers. Research on stream-dwelling Brook Trout has shown that individuals can be highly mobile (Gowan et al. 1994; Gowan and Fausch 1996*b*), with fish-habitat relationships at multiple scales (Deschênes and Rodríguez 2007). Inoue et al. (1997) showed how patterns and drivers of Masu Salmon *Oncorhynchus masou* abundance at local scales could change when measured at larger scales (e.g., salmon density related to cover). While Baxter and Hauer (2000) found large-scale environmental factors (e.g., bounded alluvial valley segments/stream geomorphology) influence Bull Trout *Salvelinus confluentus* spawning redd construction location; easily missed at local scale sampling.

Average annual prey demand for individual fish from age-1 to age-2 fish at both intensive sites (48.97and 76.08 grams/year for high and low wood sites, respectively) was up to two times greater than consumption estimates by Sweka and Hartman (2008) for Appalachian Brook Trout. The differences in prey demand could be explained by the low percentages of maximum consumption by the Appalachian Brook Trout (4.3-8.0%), which are much lower than the estimated percentage of maximum consumption fish in my study (25.3 – 31.8% and 25.8 – 27.2% at the high and low wood sites, respectively). Also, the average size of fish at my study sites was smaller than those used by Sweka and Hartman (2008) and that may affect estimated consumption estimates. For instance, age-1 fish at my low wood site were approximately 31-39% and fish at my high wood site were approximately 21-26% the size of age-1 Brook Trout used by Sweka and Hartman (2008). Other studies have also estimated lower annual prey consumption rates of Brook Trout (e.g., Elwood and Waters 1969, Utz and Hartman 2005). However, these studies occur in Appalachian streams and results may not translate directly to

brook trout in Rocky Mountain streams. Previously mentioned differences in size at age as well as differences in life histories (e.g., population dynamics and oldest age attained; Kennedy et al. 2003) could affect model outputs. To my knowledge, this is the first application of the Brook Trout bioenergetics model (Hartman and Cox 2008) to brook trout in Rocky Mountain streams.

Stream salmonids can experience high variability in overall net energy intake that increases the variability in average individual growth rates. This could be due to periodic resource scarcity (Utz and Hartman 2009), competition for resources (Metcalfe 1986), natural disasters (Elwood and Waters 1969), or environmental conditions (Magoulick and Wilzbach 1998; Sweka and Hartman 2001) that reduce foraging success. To account for variability in my overall estimate of annual prey consumption, I ran bioenergetics models using the mean, 5th, and 95th percentile of weight at age at each site. Estimating consumption at the 5th and 95th percentiles of fish growth may give an inflated estimate of error on total prey consumption; however, it does help capture the high variability in prey consumption. This is especially important in natural stream systems where trout are consistently feeding below maintenance rations (Ensign et al. 1990; Utz 2005). However, by fitting the bioenergetics model to observed growth rates, a technique much less sensitive to error than estimating growth from consumption rates (Railsback and Rose 1999), I can be confident of my annual consumption estimates.

Growth rates of most size classes of age-one fish were negatively affected by density and this is likely due to competition for resources. Utz and Hartman (2009) demonstrated negative density-dependent growth in Brook Trout populations due to increased competition for prey resources during periods of prey resource scarcity. Negative density-dependent effects on individual growth are common in lotic salmonids. Elliot (1994) examined these traits in juvenile

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Brown Trout as young of year trout competed for both food and space, and as a result, growth and survival was reduced.

Despite the evidence for density effects on individual growth rates, negative effects can be difficult to detect. Stable dominance hierarchies can obscure trends in individual growth as larger individuals are less affected by increasing densities leading to similar average growth rates across sites with varying densities (Nakano 1995; Jenkins et al. 1999). Across my sites, the largest and presumably dominant individuals, and the smallest, and presumably most subordinate individuals, were not affected by density. Dominant individuals are likely able to compete for and retain optimal foraging positions at any density and will therefore grow well at any density. The smallest subordinate fish are likely outcompeted for resources at any density and will grow slowly regardless of density. The lack of negative density dependent effects in older year classes of Brook Trout could suggest they are able to outcompete younger individuals for optimal foraging positions and are released from competition for resources. Conversely, this pattern could also suggest Brook Trout in Rocky Mountain streams experience size-selective mortality as individual trout are recruited to older age classes (Xu et al. 2010), leading to similar growth rates across densities in older age classes.

Across the intensive and extensive summer diet composition samples, terrestrial insects were heavily represented. Terrestrial insects were the top invertebrate taxa consumed at 11 of 17 sampling dates/sites, which supports previous research on the importance of terrestrial subsidies to trout populations (Baxter et al. 2005; Utz and Hartman 2007; Sweka and Hartman 2008). My research shows that ants and chalcid wasps (Family Formicidae and Superfamily Chalcidoidea) are important components of brook trout diets during the summer season. Previous research has shown other terrestrial taxa, such as terrestrial beetles (Order Coleoptera), are important

components of Brook Trout diets (Allan 1981; Utz and Hartman 2007), such as those found at the high wood site during fall sampling. Preference for terrestrial prey has been found numerous times in stream salmonids (Hilderbrand and Kershner 2004), with trout actively selecting terrestrial prey over aquatic prey, especially in summer seasons (Nakano et al. 1999). While availability and selectivity of prey organisms was not assessed in the current study, the dominance of Hymenoptera in diets at almost all sites suggests that trout will readily consume them when available, and a lack of Hymenoptera in diets at certain sites could indicate a lack of availability.

Bioenergetics modeling can allow investigators to see how consumption of varying proportions of aquatic and terrestrial invertebrates in diets can alter total predatory consumption demand (e.g., Sweka and Hartman 2008). The results from my research show that brook Trout populations in Rocky Mountain streams are likely supported by a seasonal flux of terrestrial insects entering the stream from the riparian area. The sensitivity analysis of the bioenergetics model suggests that elevated consumption of aquatic prey would elevate percent of maximum consumption rates (Bioenergetics 3.0, P-value) higher than what is thought reasonable for a stream-dwelling brook trout (Hartman and Cox 2008). Sites such as Hague Creek (96.5% aquatic prey, from diet sample) and N St Vrain Highest (86.9% aquatic prey) most likely experience a seasonal shift to terrestrial prey (similar to the terrestrial Coleoptera consumed at the high wood intensive site in the fall season) to support population densities. These results are supported by Kawaguchi and Nakano (2001) and Baxter et al. (2005 *and references therein*) who experimentally showed stream trout populations are supported by terrestrial prey fluxes. Without the prey subsidy, local trout populations would likely decrease (Kawaguchi et al. 2003).

Finally, population estimates from the paired confined and unconfined reaches suggest geomorphic context can play a role in trout population regulation. At the Mill and N St Vrain Creek sites, population densities were 2.5 and 2 times less, respectively, in the confined reaches compared to the unconfined reaches. However, population estimates from Ouzel Creek showed similar numbers of fish at both types of reaches. The similar numbers of fish in Ouzel Creek at both sites could be due to slight differences in physical habitat between the two stream reach types. The Ouzel Creek confined reach had more pools per 100 meters than the unconfined site (26.49 vs 19.29, respectively), and was located just upstream of a waterfall that was impassable to upstream movement from downstream reaches. The combination of these two factors could be limiting downstream fish movement out of the reach (waterfall; Northcote 1981), while providing pool habitat for adult trout to use. The Mill and N St Vrain streams follow a pattern previously found by Bellmore and Baxter (2014) that confined reaches can have large inputs of allocthonous energy, yet that energy and organic material is processed in the unconfined reaches leading to higher aquatic animal production. The Ouzel Creek sites suggest other geomorphic controls (e.g., reduced longitudinal connectivity due to the waterfall and number of pools) outside of stream confinement can exert larger effects on local fish populations than what would be expected.

Large wood in the correct geomorphic context can alter physical habitat and prey resources in stream ecosystems. Elevated rates of wood loading and retention create additional aquatic habitat by forcing multiple parallel channels that increase aquatic animal production. Further, increased LW forces the creation of pool habitat with complex overhead cover that allows adult trout to maximize net energy intake while minimizing risk of predation (Fausch 1984; Fausch 2014). Loss of these low gradient, multi-thread stream reaches, due to historic

land management practices, has dramatically reduced aquatic animal production by creating an alternative stable state of reduced and homogenized stream habitat. This reduced habitat complexity has persisted over 100 years after the cessation of detrimental land use practices (Ruffing et al. 2015), suggesting a resilience of these reaches to return to pre-disturbance conditions. Due to this, large amounts of annual fish production are lost in mountain watersheds due to reduced habitat complexity.

TABLE 1−List of sites sampled in summer 2013 and summer and fall 2014. Table indicates whether the sites were included in the intensive (Int) or extensive (Ext) data sets. What season and year each site was sampled. Valley confinement (unconfined, party confined, or confined; following Livers and Wohl in press), elevation, and UTMs are also presented. Superscript numbers on site list separate the Glacier Creek and N St Vrain Creek intensive site samples.

Site	Data set	Season	Year	Valley type	Elev (m)	UTM
Glacier[1]	Int	Summer	2013	Unc	2713	13T 446245E 4462944N
Glacier[2]	Int	Summer	2014	Unc	2713	13T 446245E 4462944N
Glacier[3]	Int	Fall	2014	Unc	2713	13T 446245E 4462944N
Glacier Up	Ext	Summer	2014	Unc	2983	13T 445297E 4460885N
Hague	Ext	Summer	2014	Unc	2952	13T 438047E 4485482N
Jack	Ext	Summer	2013	Unc	2911	13T 415312E 4475670N
Mill	Ext	Summer	2014	Unc	2800	13T 446223E 4464910N
N Mullen	Ext	Summer	2014	Unc	2749	13T 384105E 4565541N
N St Vrain[1]	Int	Summer	2013	Unc	3024	13T 446715E 4451263N
N St Vrain[2]	Int	Summer	2014	Unc	3024	13T 446715E 4451263N
N St Vrain[3]	Int	Fall	2014	Unc	3024	13T 446715E 4451263N
N St Vrain Down	Ext	Summer	2013	Unc	2903	13T 447918E 4450842N
N St. Vrain Highest	Ext	Summer	2014	Unc	3076	13T 445747E 4451737N
N St Vrain Lowest	Ext	Summer	2014	Unc	2770	13T 449394E 4449881N
Ouzel	Ext	Summer	2014	Unc	3045	13T 446681E 4450195N
Rock	Ext	Summer	2014	Unc	2911	13T 400696E 4588590N
S Fk Michigan	Ext	Summer	2013	Unc	2814	13T 414663E 4481684N
Mill Confined	Ext	Summer	2014	Conf	2733	13T 446726E 4465105N
N St Vrain Confined	Ext	Summer	2014	Conf	2953	13T 447241E 4451066N
Ouzel Confined	Ext	Summer	2014	Conf	2910	13T 448807E 4450045N

TABLE 2–Physical habitat characteristics of confined and unconfined stream reaches sampled during study. Values are reported in meters, except for average pool surface area (m^2), average pool volume (m^3), and wood volume (m^3/ha). Wood volumes are adapted from Bridget and Livers (2016) and from this study (Jack, Hague, and S Fk Michigan Creeks). Superscript values separate sampling dates at the intensive sites, summer 2013 (1), summer 2014 (2), and fall 2014 (3).

Site	Avg Width	Avg Depth	Wood Volume (m^3/ha)	Avg Pool Depth	Avg Pool Width	Avg Pool Length	Avg Pool Vol (m^3)	Avg Pool Surface Area (m^2)	Grad	# Pools per 100m	# Pools per 100m/ Valley	Width/ Depth Ratio
Glacier[1]	6.71	0.26	26.8	0.61	4.60	6.03	16.90	27.74	0.03	4.92	5.15	26.13
Glacier[2]	8.06	0.31	22.3	0.35	2.89	3.75	3.81	10.83	0.03	11.54	10.06	26.07
Glacier[3]	7.29	0.30	24.7	0.37	2.21	2.78	2.24	6.13	0.03	6.80	----	24.20
Glacier Up	6.12	0.26	351.0	0.34	6.66	8.90	19.92	59.27	0.05	6.61	10.61	23.73
Hague	10.76	0.33	0.0	0.45	2.82	5.58	7.16	15.74	0.02	6.58	7.23	33.09
Jack	6.87	0.21	846.8	0.36	1.69	4.05	2.45	6.86	0.04	12.00	----	27.08
Mill	2.98	0.31	181.3	0.33	2.11	3.60	2.49	7.60	0.01	10.87	12.89	9.50
N Mullen	4.29	0.15	235.6	0.14	1.44	2.30	0.47	3.32	0.03	11.90	28.13	28.13
N St Vrain[1]	4.05	0.21	1610.5	0.46	2.18	3.76	3.77	8.21	0.06	13.89	48.14	19.36
N St Vrain[2]	5.51	0.26	1182.3	0.23	1.71	2.64	1.06	4.53	0.06	17.54	44.65	21.58
N St Vrain[3]	4.59	0.24	1419.3	0.27	1.76	2.22	0.95	3.91	0.06	10.22	----	18.89
N St Vrain Down	4.89	0.18	622.2	0.25	1.44	3.05	1.10	4.39	0.03	10.39	18.89	26.87
N St. Vrain Highest	5.39	0.29	1596.8	0.36	4.40	7.25	11.51	31.90	0.08	10.87	29.03	18.68
N St Vrain Lowest	7.7	0.31	129.7	0.40	2.98	4.03	4.81	12.01	0.07	14.63	17.29	24.63
Ouzel	3.79	0.22	640.1	0.21	1.23	1.80	0.48	2.22	0.05	19.29	58.5	17.33
Rock	6.1	0.17	7.8	0.23	1.97	3.36	1.55	6.62	0.02	12.17	17.69	36.97
S Fk Michigan	5.05	0.33	9.7	0.57	3.92	5.95	13.28	23.30	0.01	2.67	----	15.35
Mill Confined	3.44	0.24	174.5	0.29	2.86	7.4	6.14	21.16	0.11	5.25	----	14.33
N St Vrain Confined	6.43	0.36	82.7	0.32	3.45	4.2	4.64	14.49	0.07	15.56	----	17.86
Ouzel Confined	4.62	0.27	331.5	0.31	2.61	2.75	2.22	7.18	0.07	26.49	----	17.11

TABLE 3–SNOTEL sites (SNOwpack TELemtry; USDA Natural Resources Conservation Service Snow Survey and Water Supply Forecasting Program) used to obtain air temperature data to model stream temperatures for use in bioenergetics models.

SNOTEL Site	Site ID	Site Elevation (m)	Latitude	Longitude	Stream Temperatures Predicted
Wild Basin	1042	2913.9	40 deg; 12 min N	105 deg; 36 min W	N St Vrain
Bear Lake	322	2895.6	40 deg; 19 min N	105 deg; 39 min W	Glacier

TABLE 4–Estimated mean, 5th, and 95th percentile weights (wet weight, grams) at ages used as beginning and end growth points in the bioenergetic analyses at the intensive sites, Glacier and N St Vrain (NSV) Creeks. Older age classes were combined if <3 individuals were in the next older age class, or negative growth would have occurred by not combining the age classes. Age classes are considered age+ (e.g., age 1 = age 1+) for these analyses.

Site	Age 1 5%	Age 1 Avg	Age 1 95%	Age 2 5%	Age 2 Avg	Age 2 95%	Age 3 5%	Age 3 Avg	Age 3 95%	Age 4 5%	Age 4 Avg	Age 4 95%	Final Group Ages	Final Group 5%	Final Group Avg	Final Group 95%
Glacier	1.8	5.2	9.3	7.4	21.7	39.4	17.2	42.3	70.1	----	----	----	4-6	29.2	54.7	83.8
NSV	0.7	3.5	6.6	5.5	13.3	22.2	12.4	25.3	39.6	16.6	32.7	50.9	5-11	22.6	48.7	73.7

TABLE 5−Estimated number of fish per hectare, fish biomass per square meter and fish biomass per meter of valley length. Biomass per valley meter was estimated from density estimates transformed by wetted area in the valley. Superscript values separate sampling dates at the intensive sites, summer 2013 (1), summer 2014 (2), and fall 2014 (3).

Site	N per ha	Fish Biomass ($g/meter^2$)	Fish Biomass (g/valley meter)
Glacier[1]	421 (404, 501)	1.55 (1.49, 1.84)	12.32 (11.83, 14.68)
Glacier[2]	410 (343, 937)	2.35 (1.97, 5.38)	18.72 (15.70, 42.84)
Glacier[3]	1990 (1876, 2273)	8.24 (7.77, 9.41)	65.57 (61.81, 74.89)
Glacier Up	1653 (1581, 1855)	7.13 (6.82, 8.00)	54.75 (52.34, 61.43)
Hague	878 (810, 1110)	2.26 (2.09, 2.86)	25.17 (23.23, 31.83)
Jack	1203 (1137, 1484)	2.20 (2.08, 2.72)	17.19 (16.25, 21.20)
Mill	7442 (7342, 7752)	9.94 (9.80, 10.35)	39.70 (39.17, 41.36)
N Mullen	5099 (5088, 5317)	16.54 (16.51, 17.25)	86.60 (86.41, 90.30)
N St Vrain[1]	3157 (3022, 3477)	6.33 (6.06, 6.98)	87.41 (83.65, 96.27)
N St Vrain[2]	2864 (2619, 3946)	8.56 (7.83, 11.79)	118.08 (107.98, 162.71)
N St Vrain[3]	1524 (1428, 1953)	3.24 (3.03, 4.15)	44.65 (41.82, 57.20)
N St Vrain Down	2016 (1976, 2211)	5.75 (5.63, 6.30)	53.29 (52.22, 58.43)
N St. Vrain Highest	2890 (2809, 3287)	9.27 (9.01, 10.55)	39.44 (38.32, 44.85)
N St Vrain Lowest	1322 (1273, 1750)	8.31 (8.01, 11.00)	90.09 (86.77, 119.25)
Ouzel	2880 (2811, 3390)	6.28 (6.12, 7.39)	59.71 (58.27, 70.29)
Rock	4476 (4436, 4698)	15.81 (15.67, 16.56)	128.43 (127.28, 134.78)
S Fk Michigan	564 (530, 807)	1.04 (0.98, 1.48)	8.81 (8.29, 8.81)
Mill Confined	2683 (2569, 3165)	4.99 (4.78, 5.89)	24.97 (23.91, 29.45)
N St Vrain Confined	1523 (1346, 2607)	3.74 (3.31, 6.41)	24.91 (22.01, 42.64)
Ouzel Confined	3012 (3010, 3132)	7.88 (7.87, 8.19)	68.51 (68.47, 71.25)

TABLE 6–Candidate models for predicting trout density at the local (square meter) scale. Asterisks indicate 95% confidence intervals that do not include 0. Range of beta estimates is in parentheses below candidate models.

Intercept	Ln Standing Stock Insect Biomass	Number of Pools per 100m	Width/ Depth Ratio	LogL	AICc	delta	weight
-42.729	X*			-33.168	75.002	0.000	0.695
-43.259	X*	X		-32.575	78.151	3.148	0.144
-44.186	X*		X	-33.053	79.106	4.104	0.089
7.698				-37.832	80.864	5.862	0.037
-46.232	X*	X	X	-32.144	82.860	7.858	0.014
3.685		X		-37.177	83.020	8.018	0.013
6.248			X	-37.777	84.220	9.218	0.007
-0.597		X	X	-36.873	86.746	11.744	0.002
	(6.57, 6.95)	(0.23, 0.42)	(0.06, 0.14)				

TABLE 7−Model selection results based on predictor variables measured at the landscape (valley length) scale. Asterisks indicate 95% confidence intervals that do not contain 0. Ranges of beta estimates are located in parentheses below predictor variables.

Intercept	Ln Standing Stock Insect Biomass	Number of Pools per 100m	Width/Depth Ratio	LogL	AICc	delta	weight
-446.579	X*			-60.929	130.524	0.000	0.595
-373.252	X*	X		-59.904	132.809	2.285	0.190
-36.423		X*		-63.043	134.753	4.229	0.072
-445.342	X*		X	-60.925	134.850	4.326	0.068
-119.593		X*	X	-61.394	135.789	5.265	0.043
-354.869	X	X	X	-59.426	137.424	6.900	0.019
70.679				-66.679	138.558	8.034	0.011
62.267			X	-66.657	141.981	11.457	0.002
	(34.31, 54.80)	(17.50, 46.64)	(-0.09, 2.37)				

TABLE 8–Von Bertalanffy growth curve parameter estimates for Glacier and N St Vrain Creeks (intensive Sites) from back-calculated lengths at ages. Averages and 95% confidence intervals (in parentheses) are reported.

	L_{inf} (mm)	K	t_0
Glacier	205 (196, 216)	0.463 (0.373, 0.56)	-0.052 (-0.278, 0.129)
N St Vrain	183 (179, 187)	0.408 (0.349, 0.463)	-0.193 (-0.462, 0.029)

TABLE 9–Summary statistics for candidate multiple regression models used to predict stream temperatures across our study sites. Two years of stream temperature data were used to construct the regressions (2013-2014). Predictor variables air temperature (ATemp), site elevation (Elev), Julian date (JDay), and the quadratic transformation of Julian date ($JDay^2$) were evaluated for inclusion. Interactions are indicated by a colon symbol (":").

No. of Variables	Adj R^2	AICc	delta	Weight	Variables in the Model
6	0.8383	412.780	0	0.349	ATemp* Elev* JDay* $JDay^2$* ATemp:Elev* ATemp:JDay
5	0.8355	413.547	0.767	0.238	ATemp* Elev* JDay* $JDay^2$* ATemp:JDay
7	0.8387	413.819	1.040	0.207	ATemp* Elev* JDay* $JDay^2$* ATemp:Elev* ATemp:Jday* Elev:JDay
6	0.8369	413.824	1.045	0.207	ATemp* Elev* JDay* $JDay^2$* ATemp:JDay* Elev:JDay
4	0.7971	436.461	23.682	0.000	ATemp* Elev* JDay* ATemp:JDay

TABLE 10—Diet compositions collected from Brook Trout *Salvelinus fontinalis* during summer 2013 and summer and fall 2014. Average prey biomass (mg dry mass of insects/g wet weight of fish) in stomachs, with standard deviations in parentheses. Average contributions of aquatic and terrestrial sources and top three taxa represented (percent contribution in parentheses) in diets. Insect taxa are represented by numbers: 4 = Coleoptera (terrestrial), 18 = Diptera, non-Chiro (Adult), 21 = Hymenoptera, 23 = Diptera, Chiro (Larvae), 35 = Ephemeroptera (Larvae), 36 = Ephemeroptera (Adult), 46 = Hemiptera, 57 = Lepidoptera, 60 = Oligochaeta, 63 = Plecoptera (Larvae), 67 = Plecoptera (Adult), 73 = Trichoptera (Larvae). Superscript values separate sampling dates at the intensive sites, summer 2013 (1), summer 2014 (2), and fall 2014 (3).

Site	Year	Biomass	Percent Aquatic	Percent Terrestrial	1st	2nd	3rd
Glacier[1]	2013	1.61 (2.02)	84.9	15.1	60 (73)	4 (7)	63 (6)
Glacier[2]	2014	1.39 (1.29)	39.2	60.8	21 (58)	63 (29)	35 (7)
Glacier[3]	2014	0.35 (0.65)	20.5	79.5	21 (45)	18 (17)	63 (10)
Glacier Up	2014	1.18 (0.98)	10.8	89.2	21 (70)	4 (9)	67 (6)
Hague	2014	0.40 (0.61)	96.5	3.5	60 (43)	35 (27)	23 (14)
Jack	2013	0.54 (0.72)	53.5	46.5	35 (30)	21 (26)	73 (10)
Mill	2014	1.48 (1.31)	14.2	85.8	21 (58)	4 (8)	57 (7)
N Mullen	2014	0.81 (0.64)	29.9	70.1	21 (39)	67 (13)	35 (10)
N St Vrain[1]	2013	1.04 (1.00)	49.0	51.0	21 (42)	23 (13)	35 (12)
N St Vrain[2]	2014	2.42 (2.18)	37.5	62.5	21 (34)	23 (17)	18 (10)
N St Vrain[3]	2014	1.78 (3.46)	20.4	79.6	4 (65)	21 (13)	73 (8)
NSV Down	2013	0.62 (0.93)	63.5	36.5	63 (34)	21 (32)	73 (16)
NSV Highest	2014	1.65 (1.98)	86.9	13.1	73 (25)	60 (21)	35 (17)
NSV Lowest	2014	1.56 (0.73)	41.1	58.9	35 (31)	36 (25)	21 (20)
Ouzel	2014	0.30 (0.34)	42.8	57.2	21 (19)	67 (19)	35 (16)
Rock	2014	0.37 (0.31)	64.5	35.5	21 (21)	23 (20)	35 (19)
S Fk Michigan	2013	0.92 (0.73)	30.5	69.5	21 (51)	73 (13)	46 (8)

TABLE 11−Results from similarity percentages (SIMPER) procedure comparing the Glacier (GC) and N St Vrain (NSV) Creeks diet compositions during summer 2014 (dissimilarity = 81.09). Average abundances at each site for each taxa is indicated (GC and NSV Abundance) and contributions to overall dissimilarity by each taxa (Contrib %) and cumulative percentage (Cumulative %) are also given.

Taxa	Common Name	GC Abundance	NSV Abundance	Contrib %	Cumulative %
Formicidae	Ants	38.16	22.4	21.67	21.67
Chironimidae	Midge Larvae	0.35	33.77	20.62	42.29
Perlidae	Stonefly Nymph	19.18	5.89	12.74	55.03
Acari	Water Mites	14.29	0	8.81	63.84
Hymenoptera	Wasps and Bees	10.09	2.6	7.35	71.19
Heptageniidae	Mayfly Nymph	4.86	5.28	5.2	76.39
Chalcidoidea	Chalcid Wasps	0.5	7.33	4.58	80.96
Ephemerellidae	Mayfly Nymph	0.92	5.91	3.88	84.84
Baetidae	Mayfly Nymph	3.96	4.89	3.6	88.44
Simuliidae	Black Fly Larvae	0.13	4.12	2.55	90.99

TABLE 12–Estimated energy densities (J/g wet weight) for Brook Trout *Salvelinus fontinalis* at both intensive sites. Energy densities were calculated using the lake trout energy density equation in Hartman and Brandt (1995). Seasonal averages, as well as standard deviations (in parentheses) are reported.

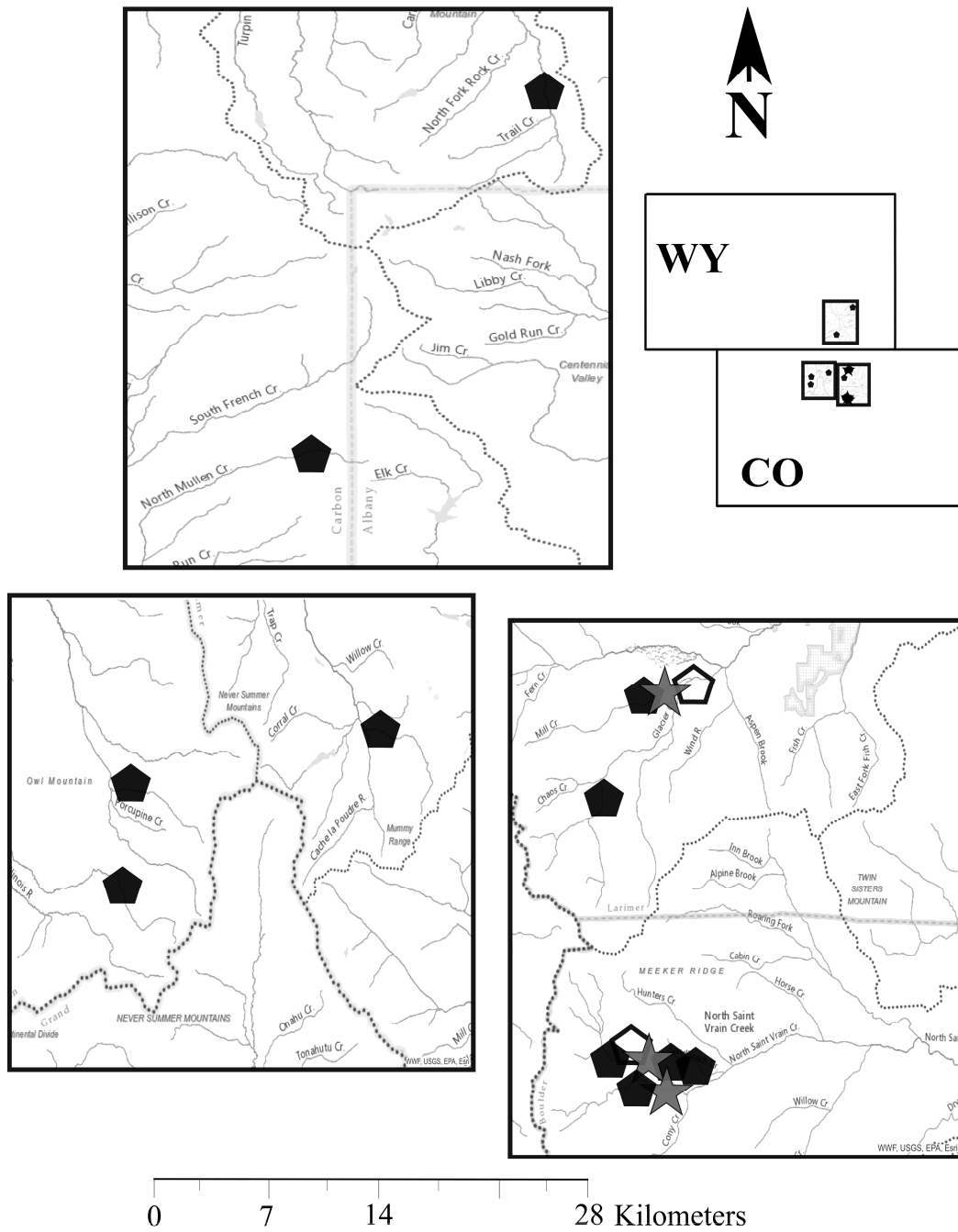| Site	Energy Density	
	Summer	Fall
Glacier	5532.51 (356.72)	5144.46 (534.52)
N St Vrain	5791.69 (511.88)	5053.57 (474.98)

FIGURE 1—Map of study sites in northern Colorado and southern Wyoming. Intensive unconfined reaches are denoted by open pentagrams, extensive unconfined sites are denoted by filled pentagrams, and confined reaches are denoted by gray stars.
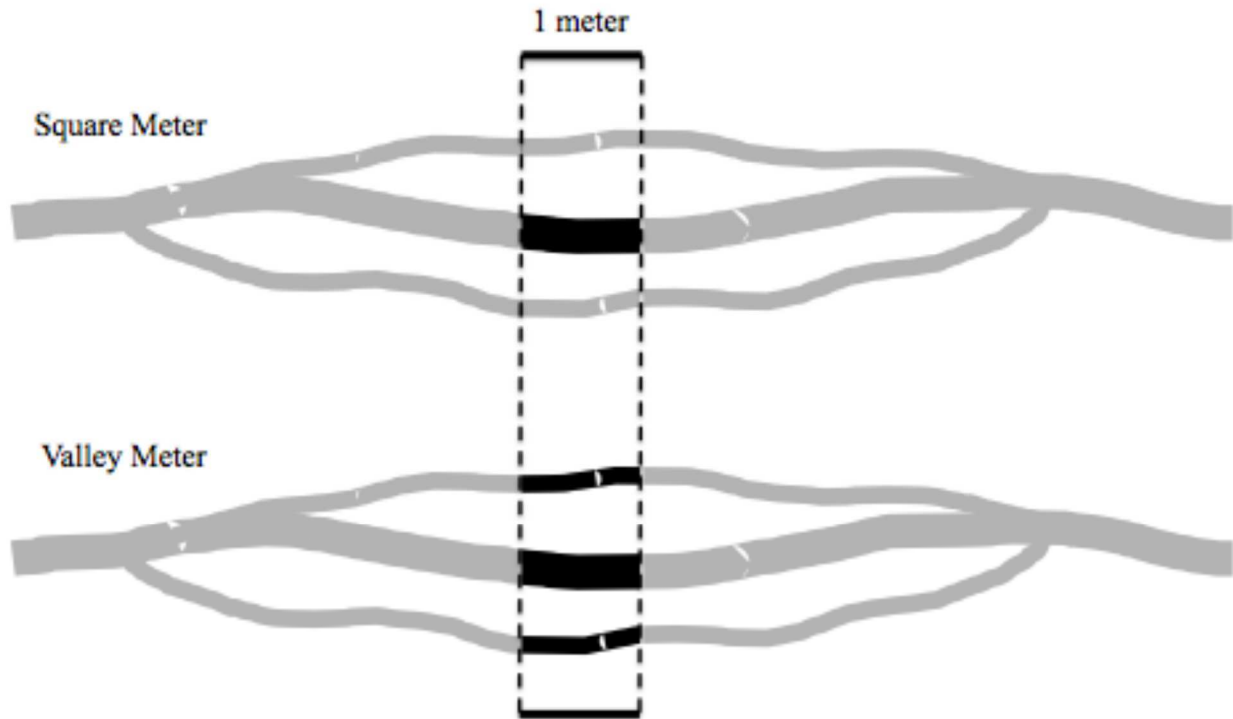
FIGURE 2–Representation of the difference in stream habitat sampled at both sampling scales used at the unconfined sites during this study. The black areas represent the stream habitat included when measuring at both scales. At the square meter scale, stream reaches are treated individually, while at the meter of valley scale, all stream reaches are treated together.
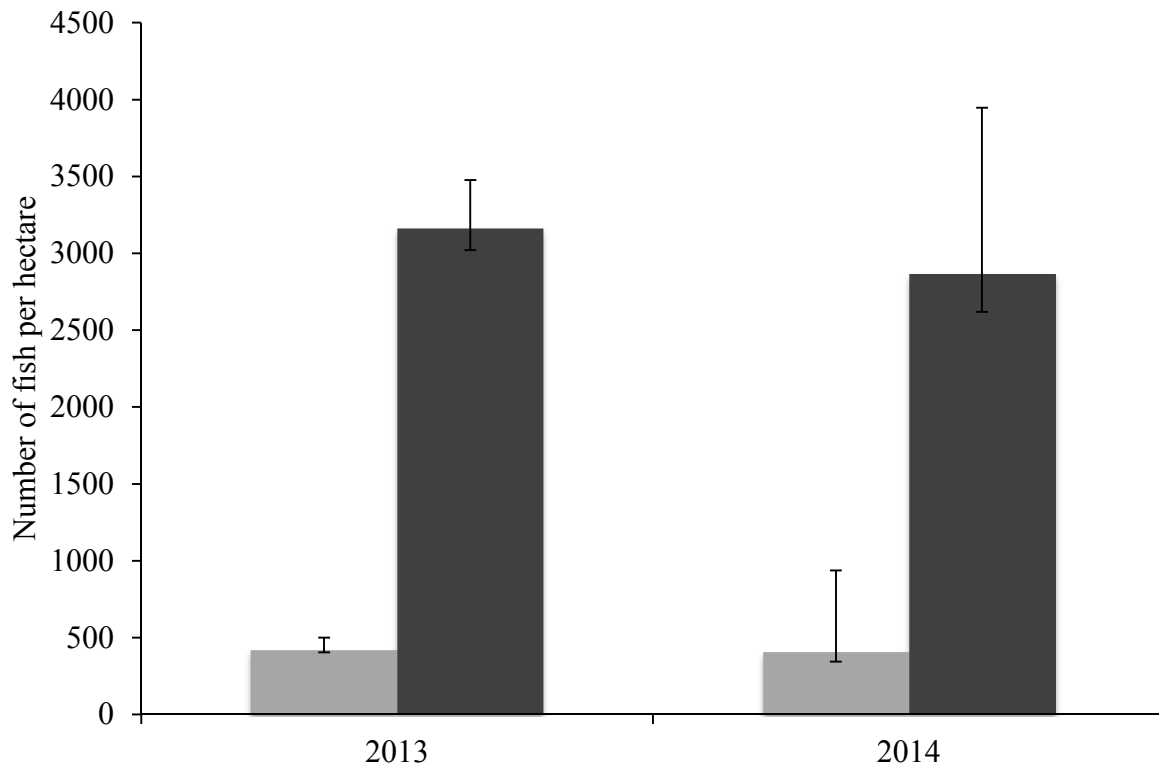
FIGURE 3−Population Densities (N * ha^{-1}) of trout (>49mm) sampled at the "Intensive" sites, N St Vrain (dark gray) and Glacier (light gray) Creeks, in summer 2013 and 2014.

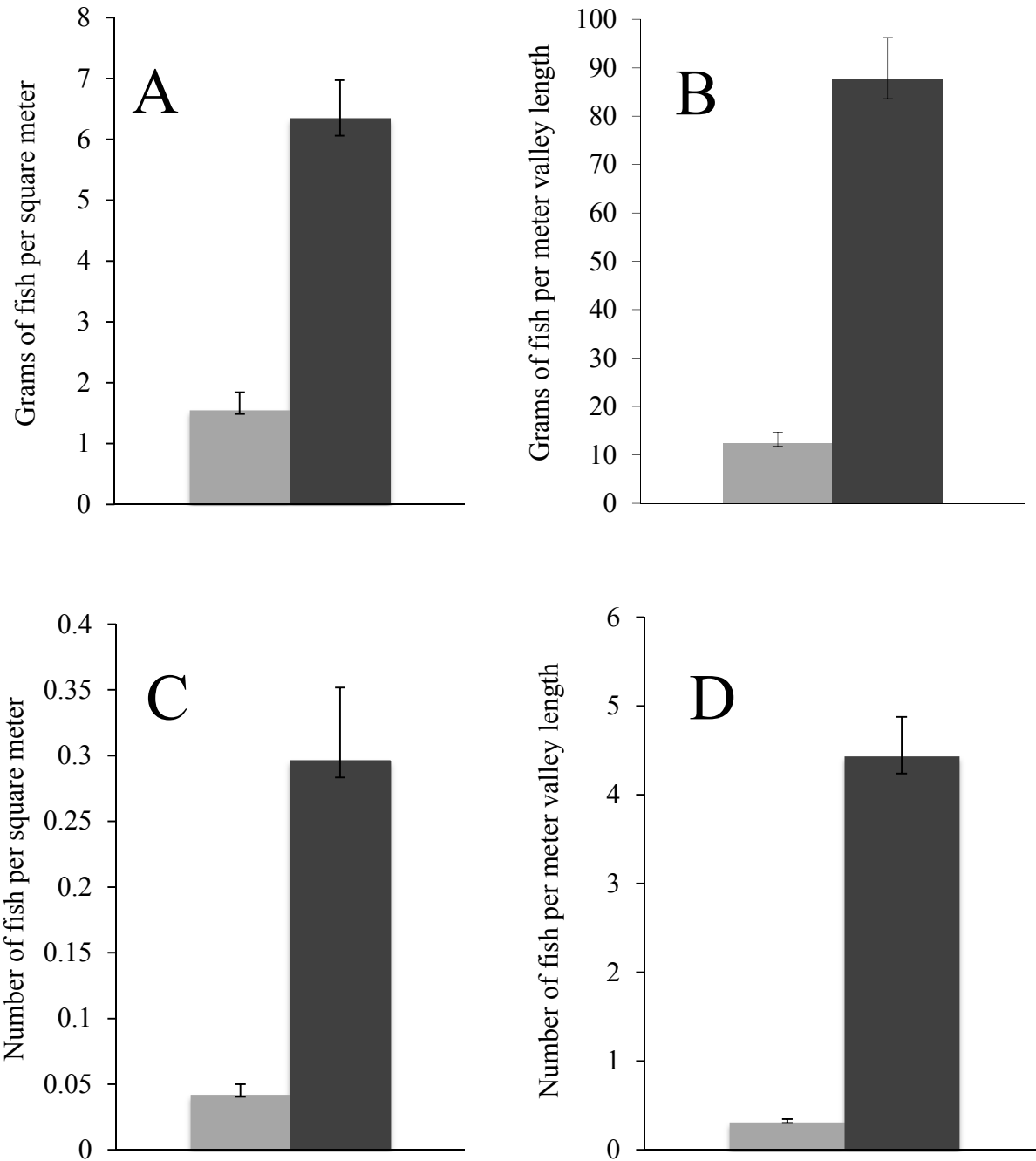FIGURE 4–Estimated trout biomass and density at Glacier (light gray) and N St Vrain (dark gray) Creeks during the summer season. Biomass and density was estimated at the square meter scale (A and C), and at the meter of valley scale (B and D) in summer 2013.
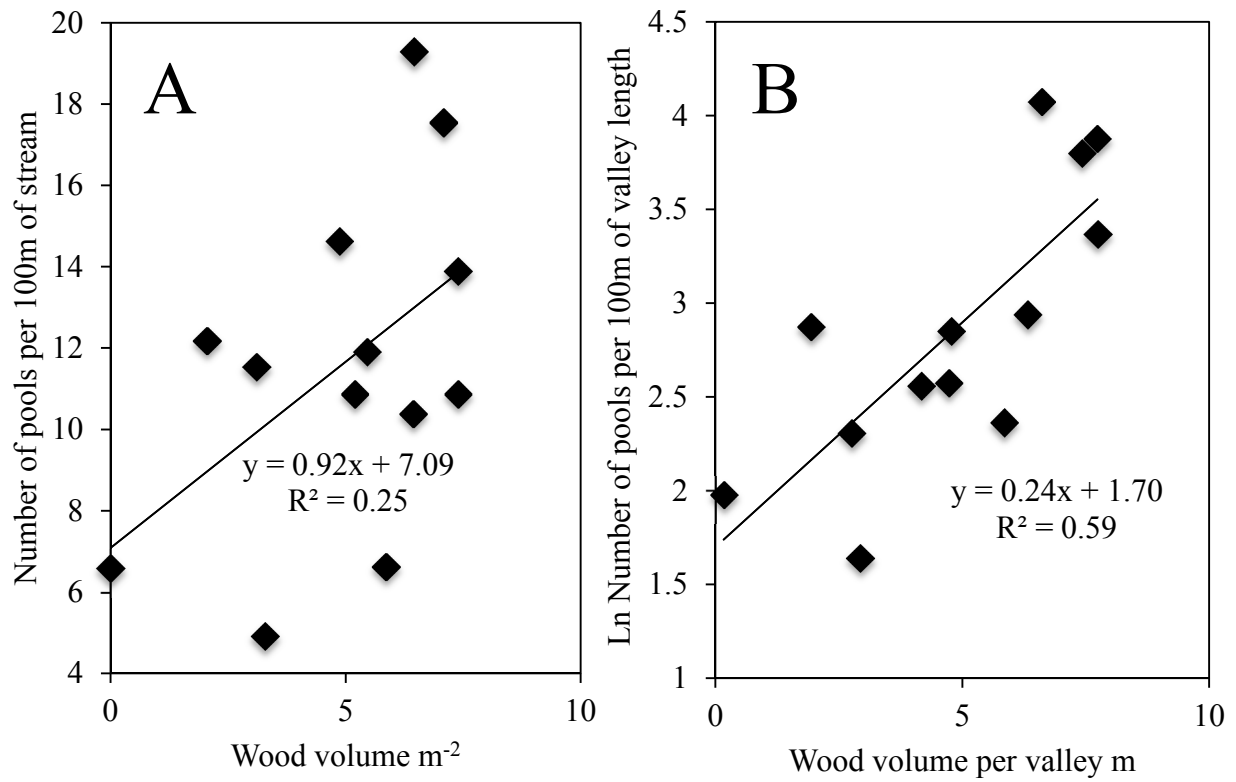
FIGURE 5−Relationship of number of individual pools and volume of large wood at the square meter scale (A) and valley scale (B) across the extensive sites.
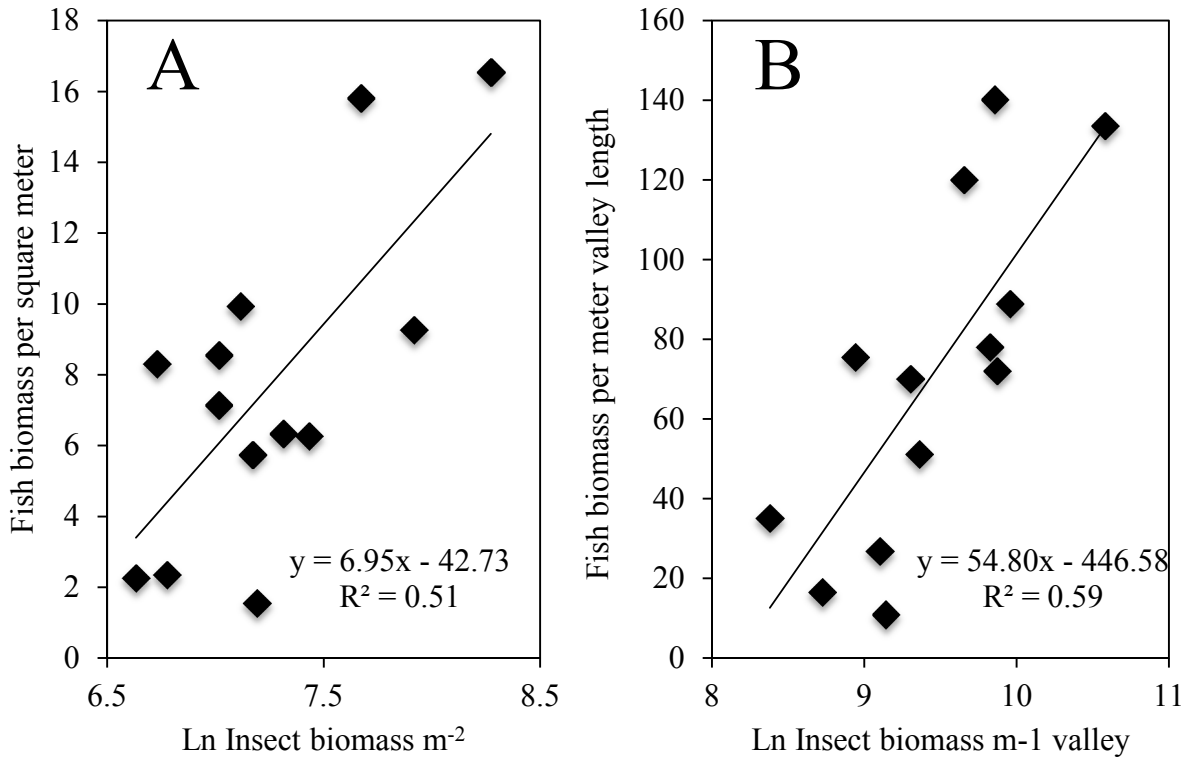
FIGURE 6–Relationship between fish biomass and standing stock biomass of aquatic insects at the square meter (A) and meter of valley length (B) scales.
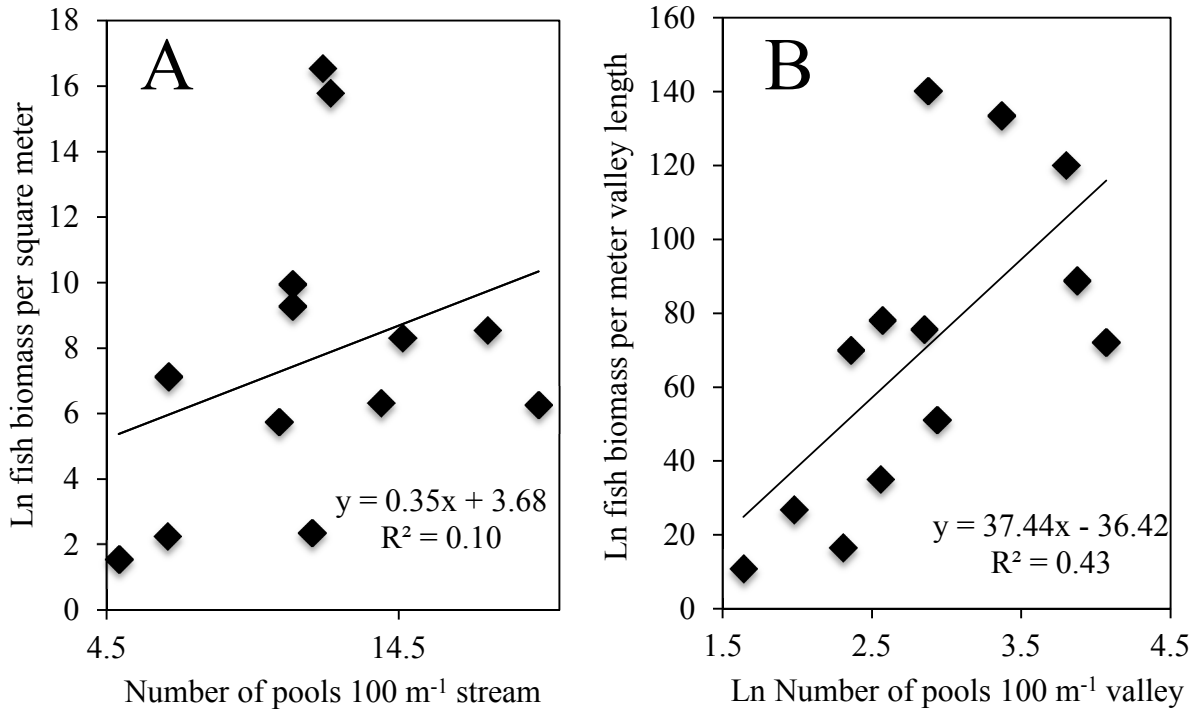
FIGURE 7–Relationship between number of individual pools and fish biomass across extensive sites at the square meter (A) and valley meter (B) scales.
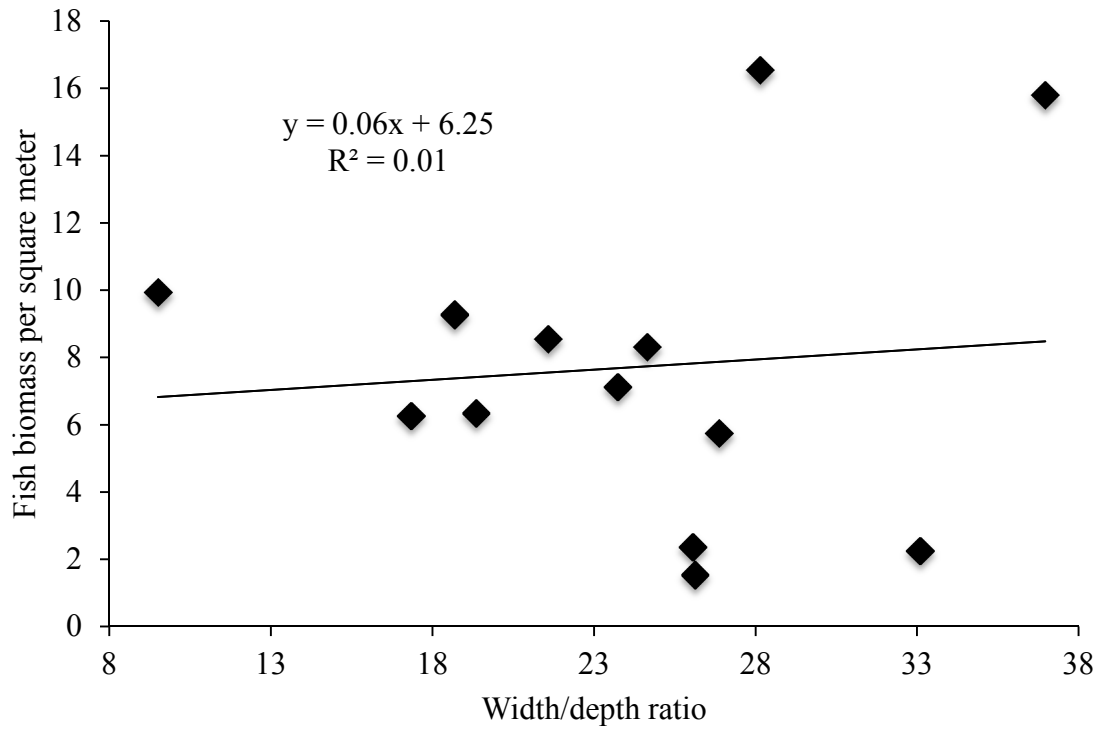
FIGURE 8–Relationship between width/depth ratio and fish biomass across the extensive sites at the square meter scale.
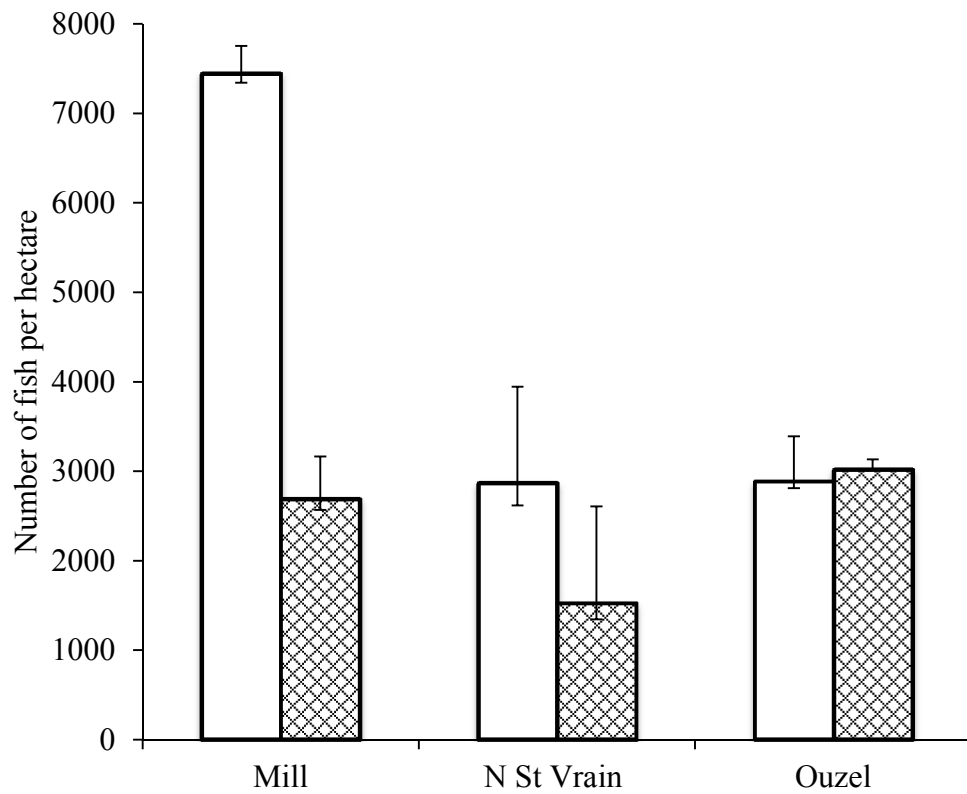
FIGURE 9–Population Densities (N * ha⁻¹) of trout sampled in adjacent unconfined (solid) and confined (hatched) stream reaches on Mill, N. St. Vrain, and Ouzel Creeks in Summer 2014.
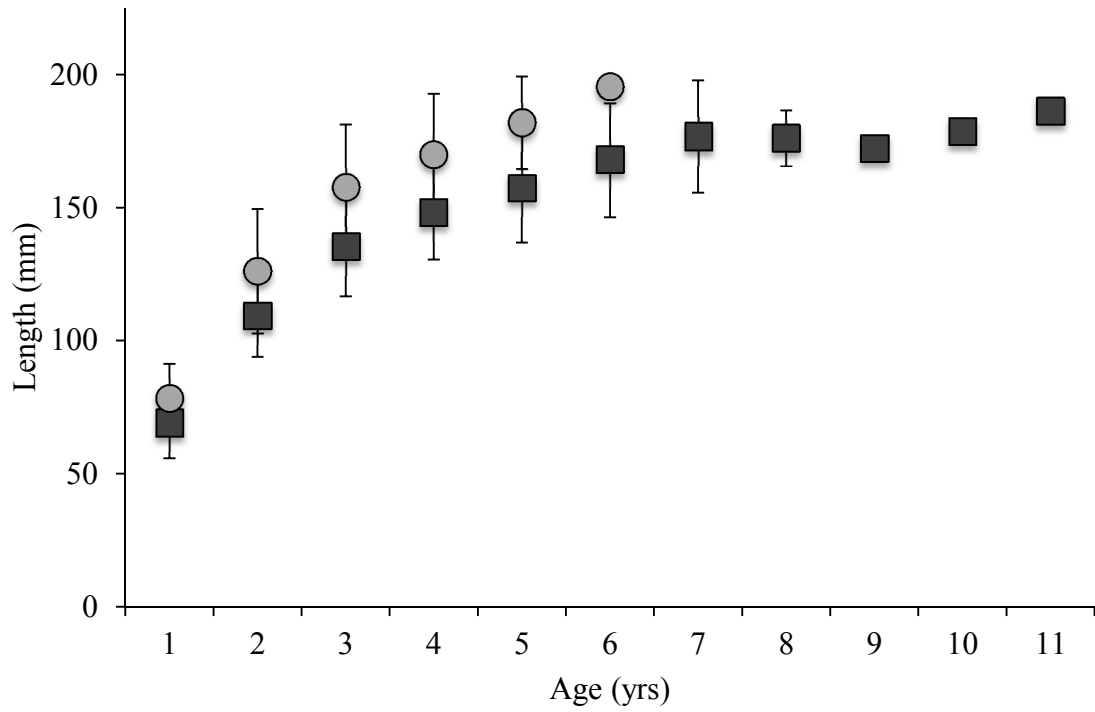
FIGURE 10−Average back-calculated length at age (± SD) for Brook Trout *Salvelinus fontinalis* at Glacier (light gray circles) and N St Vrain (dark gray squares) Creeks from otolith sections.
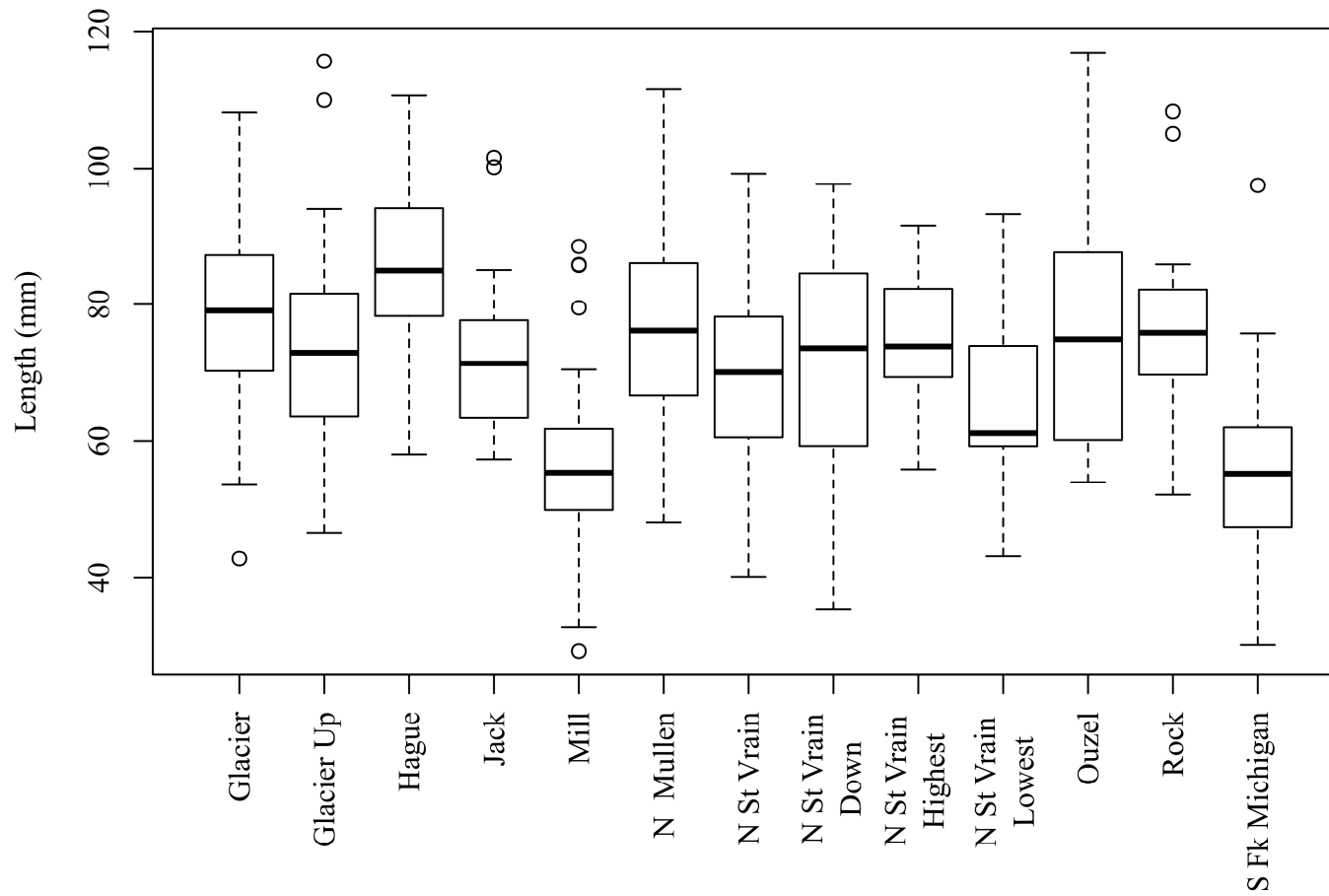
FIGURE 11−Length of age-1 Brook Trout *Salvelinus fontinalis* at intensive (Glacier and N St Vrain) and extensive unconfined sites. Lengths were back-calculated from otolith sections. In each box and whisker plot, the thick, horizontal black line represents the median of that distribution, while the two thinner horizontal lines represent the first and third quartiles of the data. The whiskers represent values within 1.5 times the interquartile range (the distance between the first and third quartiles), while the open circles represent suspected outliers.
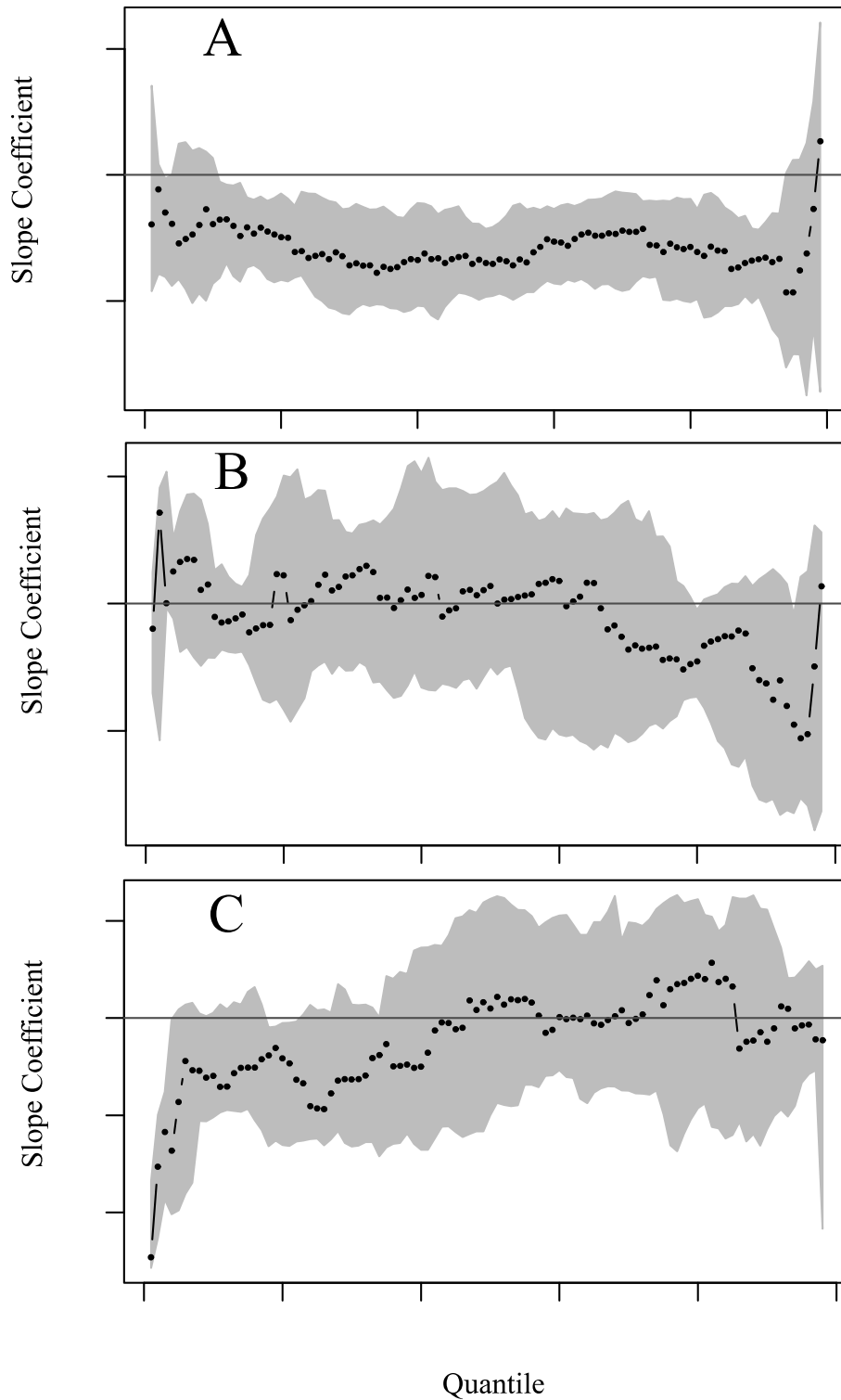
FIGURE 12–Estimated slope coefficients from quantile regression (n=99) for age 1 (A), age 2 (B), and age 3 (C) fish over increasing density at unconfined extensive sites. The black dots represent the estimate at each quantile, while the gray shaded area represents the 95% confidence interval. The 99th percentile is not shown for age-2 and age-3 fish as the 95% confidence interval could not be calculated.
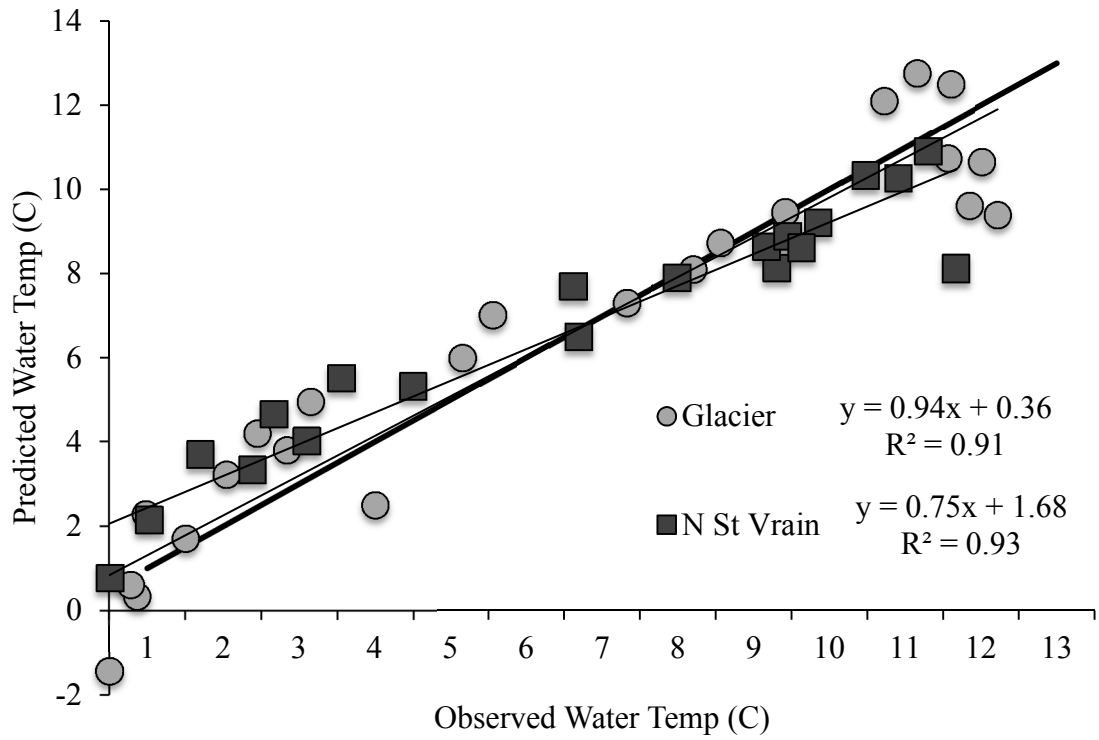
FIGURE 13–Comparison of predicted water temperatures from the stream temperature model developed in this study and observed water temperatures recorded by water temperature loggers placed at both intensive sites. The slope of regressions (thin lines) and a slope of 1 (thick line) are plotted for comparison.
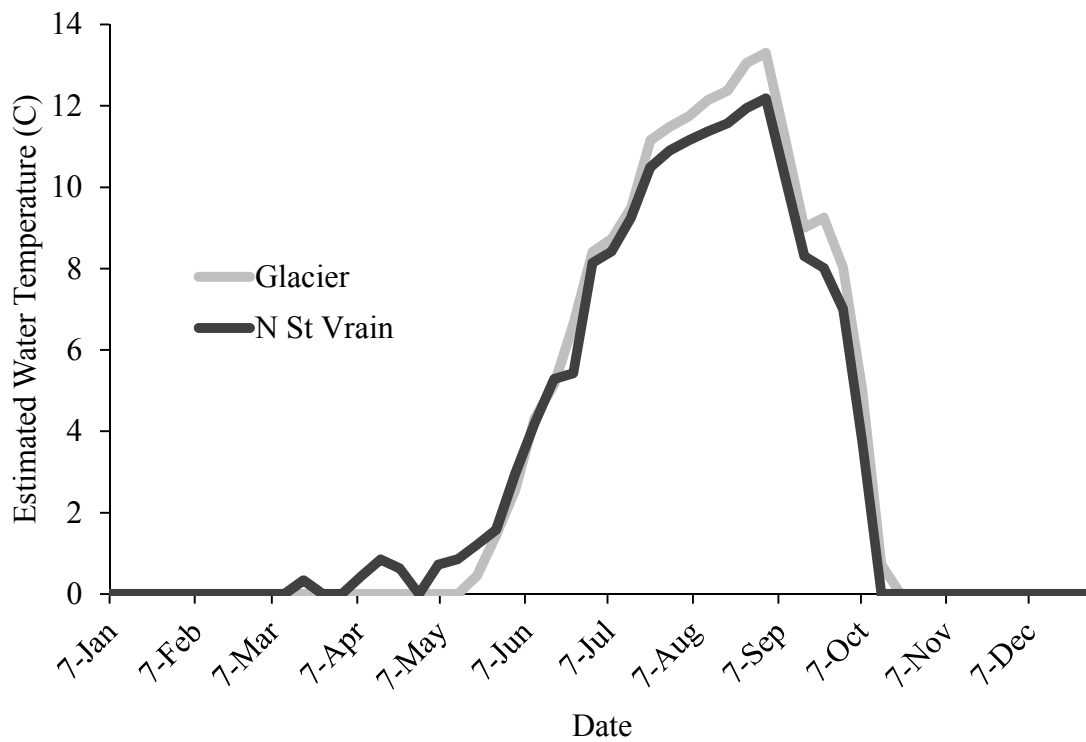
FIGURE 14–Estimated stream temperatures from the stream temperature model developed in this study. Estimated stream temperatures represent the weekly average of four years of temperature data (2011-2014).
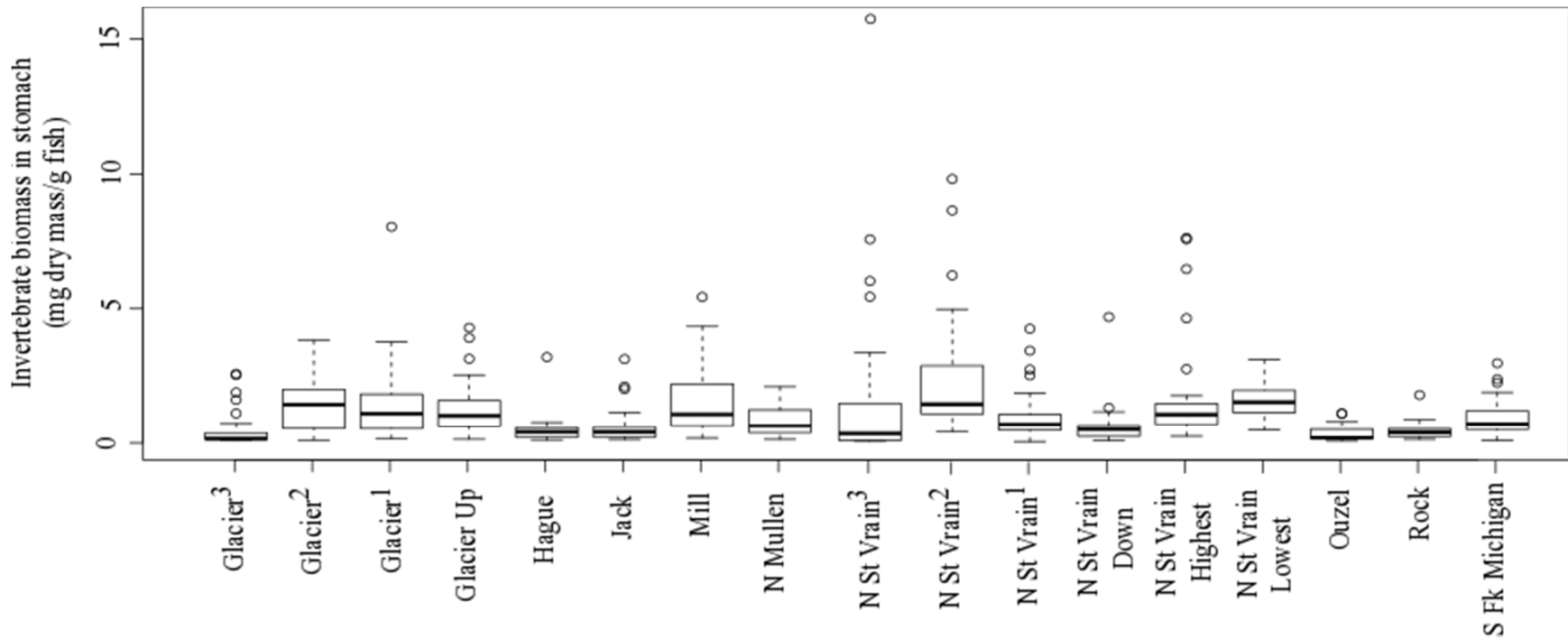
FIGURE 15−Invertebrate biomass (mg dry mass/g wet weight fish) found in stomachs at all sites. Invertebrate biomass was estimated from published length-weight regressions. Superscript values separate sampling dates at the intensive sites, summer 2013 (1), summer 2014 (2), and fall 2014 (3). In each box and whisker plot, the thick, horizontal black line represents the median of that distribution, while the two thinner horizontal lines represent the first and third quartiles of the data. The whiskers represent values within 1.5 times the interquartile range (the distance between the first and third quartiles), while the open circles represent suspected outliers.
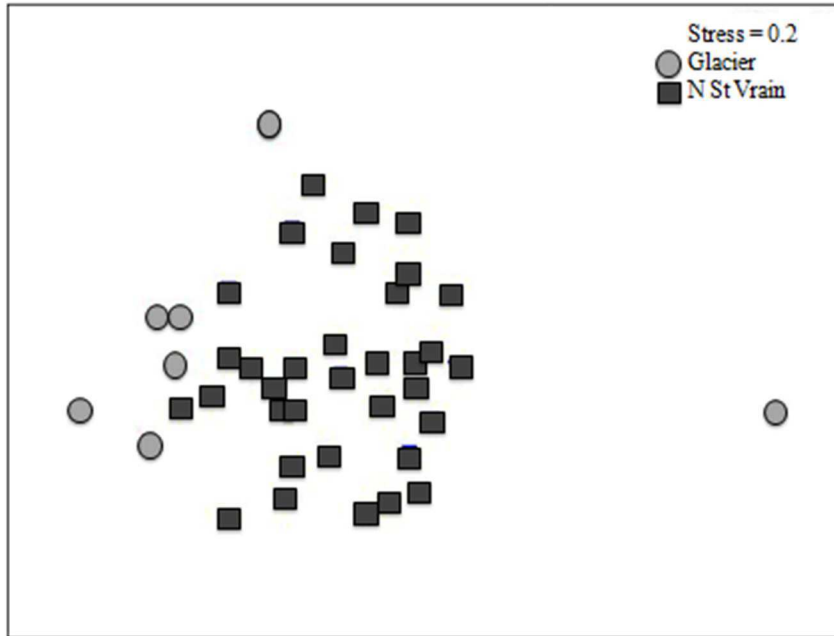
FIGURE 16–Non-metric multidimensional scaling ordination plot of the macroinvertebrate communities found in diet samples from Glacier and N St Vrain Creeks during the summer season. Data points are based on transformed data representing the proportion each taxa contributed to diet composition, and represent the diet community of an individual Brook trout *Salvelinus fontinalis*. ANOSIM analysis indicated diets were significantly different between the two sites (Clarke's $R = 0.495$).
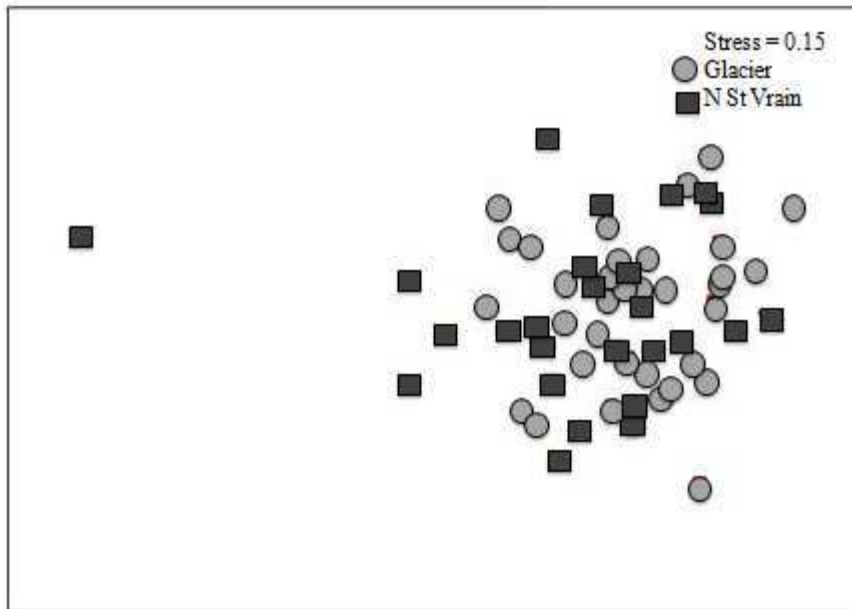
FIGURE 17–Non-metric multidimensional scaling ordination plot of the macroinvertebrate communities found in diet samples from Glacier and N St Vrain Creeks during the fall season. Data points are based on transformed data representing the proportion each taxa contributed to diet composition, and represent the diet community of an individual Brook trout *Salvelinus fontinalis*. Diets were not significantly different during the fall season (Clarke's $R = 0.056$).
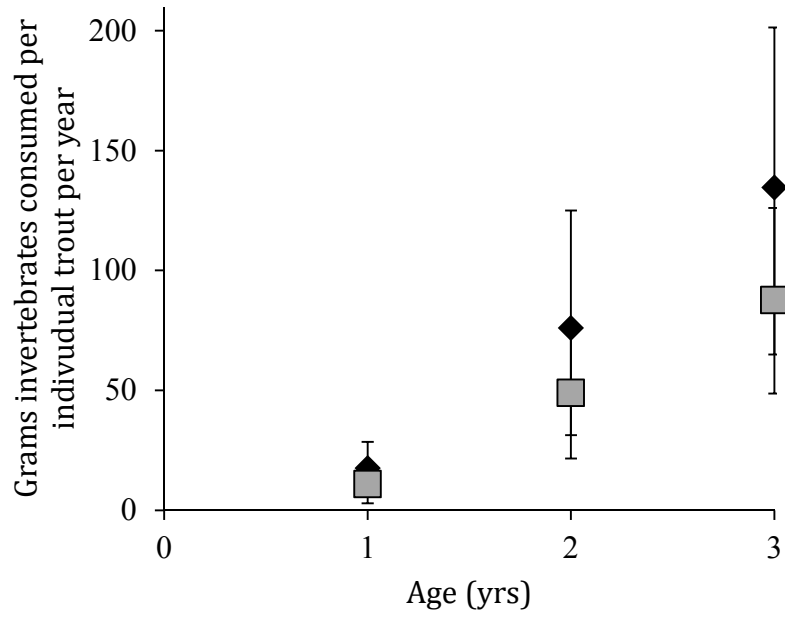
FIGURE 18– Estimated annual consumption of invertebrates by individual Brook Trout *Salvelinus fontinalis* at Glacier (black diamonds) and N St Vrain (grey squares) Creeks. Error bars represent estimated consumption of the observed 5th and 95th percentiles.
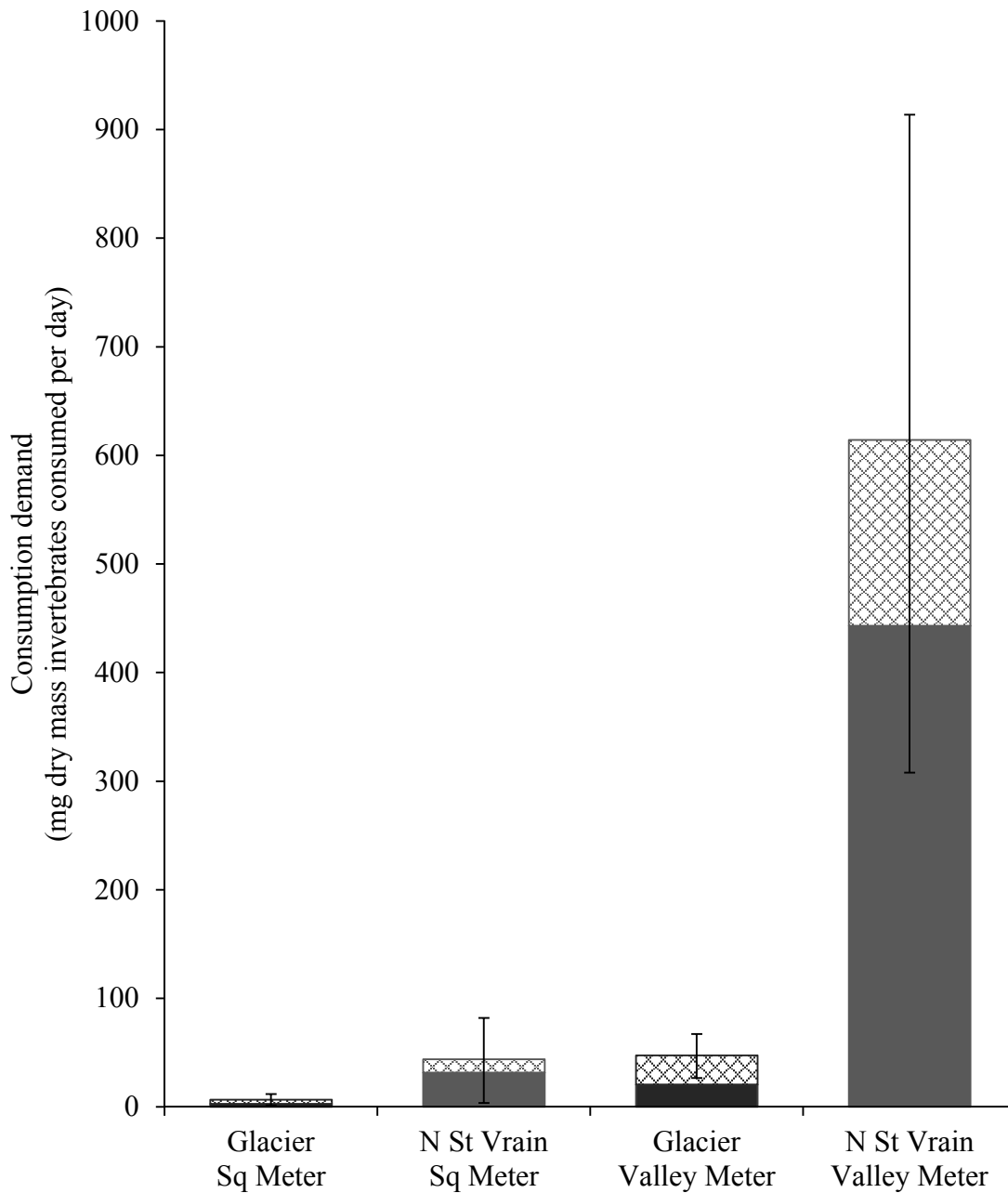
FIGURE 19–Total invertebrate consumption demand at Glacier and N. St. Vrain Creeks. Hatched areas indicate terrestrial invertebrates and solid areas represent aquatic invertebrates. Consumption is expressed as milligrams wet weight of invertebrate prey per square meter or per meter of valley length. Error bars represent estimated consumption at the 5th and 95th percentile.
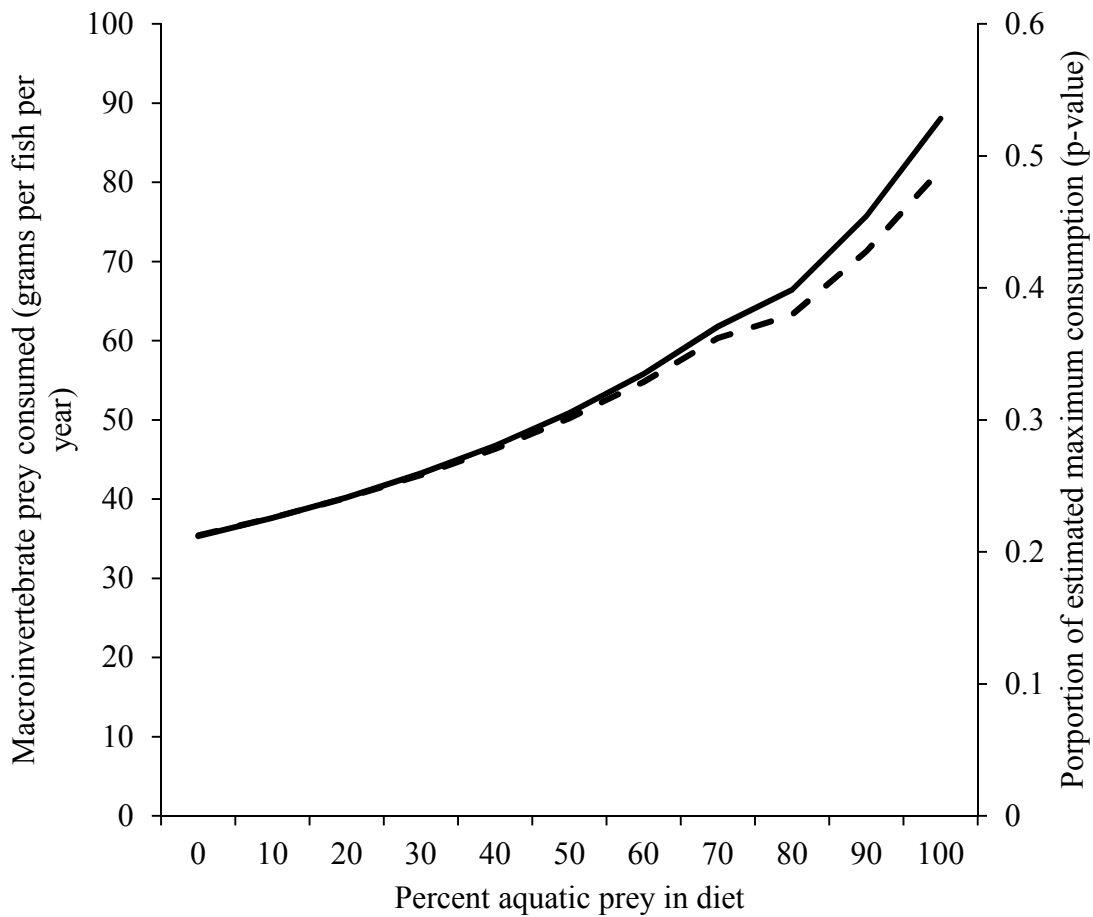
FIGURE 20−Sensitvity analysis of bioenergetics model to diet source using an individual fish (observed growth from age 1 to 2) from N St Vrain Creek. Grams of prey consumed (solid line) and proportion of estimated maximum consumption (dashed line) both increase exponentially as percent of aquatic prey in diets increases.

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