

A BIOENERGETIC ASSESSMENT OF SEASONAL HABITAT SELECTION
AND BEHAVIORAL THERMOREGULATION OF RAINBOW TROUT
Oncorhynchus mykiss IN A SOUTHWESTERN HEADWATER
STREAM

BY

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“A bioenergetic assessment of seasonal habitat selection and behavioral thermoregulation of Rainbow Trout *Oncorhynchus mykiss* in a southwestern headwater stream,” a thesis prepared by Bradley W. Kalb in partial fulfillment of the requirements for the degree, Masters of Science, has been approved and accepted by the following:

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ABSTRACT

A BIOENERGETIC ASSESSMENT OF SEASONAL HABITAT SELECTION AND BEHAVIORAL THERMOREGULATION OF RAINBOW TROUT

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Dr. Colleen A. Caldwell, Chair

Throughout western North America, stream salmonids are experiencing declines due to hydrologic modifications, non-native fish introductions, and habitat degradation. Additionally, climate change is expected to impact salmonids through increases in stream temperatures and alterations to the hydrologic cycle. The goal of this research was to describe the relationship among habitat limitations and margins of energetic profitability for a Rainbow Trout *Oncorhynchus mykiss* population in a high elevation, headwater stream. To reach this goal, the objectives were to 1) describe habitat use and selection of Rainbow Trout of varying size classes across

varying seasons (temperatures), 2) assess the bioenergetics of microhabitat use and availability and habitat suitability across varying climate change scenarios, and 3) characterize summer and winter behavioral thermoregulation of Rainbow Trout in a small headwater stream.

Habitat use and availability was assessed monthly for one year within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Data from microhabitat use and availability was linked to environmental variables of macroinvertebrate drift and temperature using a foraging-based bioenergetic model. Fish displayed a strong selection of stream positions that were close to cover during the winter, likely to minimize metabolic costs and risk of predation. Fish of all size classes selected deeper average depths (34.5 cm) and slower average focal velocities (average $1.0 \text{ cm}\cdot\text{s}^{-1}$) than available. Due to the large capture area from greater depths and minimal swimming costs from slow velocities, bioenergetic model predictions indicate that 81% of all fish met maintenance rations and 40% maximized their growth. Bioenergetic model predictions of winter net energy intake rates (NEI) were generally positive and infers greater chances at survival, while more than 80% of energy was predicted to be acquired for age-1+ fish during the months of May, June, and September indicating the majority of growth occurred during these three months. Additionally, when climate change scenarios were modeled with a 6°C increase for summer and winter months, the amount of available habitat capable of supporting Rainbow Trout was predicted to be reduced by as much as 12% during the summer and 17% during the winter. Mean NEI rates were also predicted to decline by 67-75% over the summer while NEI would increase over the winter.

Fish tagged with radio telemetry devices and archival temperature loggers revealed that fish made frequent, but short (2-4 h) use of coolwater refugia that was as much as 3°C cooler than ambient temperatures during the summer. Mean differences in prolonged coolwater refugia use differed by 0.16°C from ambient stream temperatures during the summer. During the winter, fish also made periodic use of warmwater refugia to escape supercooled waters while mean warmwater refugia use differed by 0.04°C.

Results from this study can be used to guide managers in future restoration and management of small headwater streams, particularly in arid-land systems where discharge and velocities are relatively low throughout the year compared to larger streams in the intermountain west. Stream restoration efforts should focus on creating deep, pool habitat with abundant cover for overwintering fish. This research also demonstrated the importance of protecting areas of thermal refugia as these areas can reduce the metabolic costs associated with rising temperatures and protect fish from supercooled waters.

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Chapter 1: Seasonal Habitat Selection of Young-of-Year, Juvenile, and Adult Rainbow Trout in a Small Headwater Stream

Abstract

Information of habitat selection by salmonids can be used to guide managers in restoration efforts and identification of habitat that is necessary to support critical life stages of the species, particularly as habitats change due to anthropogenic causes. Micro- and mesohabitat use, availability, and selection by young-of-year, juvenile, and adult Rainbow Trout *Oncorhynchus mykiss* was measured monthly for one year. Fish of all three size classes were frequently observed in pool mesohabitats (>98%). Focal velocities of positions selected by fish varied from 0 to 21 $\text{cm}\cdot\text{s}^{-1}$ (mean, 1.0 $\text{cm}\cdot\text{s}^{-1}$) and was less than mean available focal velocity (6.4 $\text{cm}\cdot\text{s}^{-1}$). Fish were observed using deep water habitats ranging from 4 to 74 cm (mean, 34.5 cm) throughout the year that was significantly greater than mean available depth (13.2 cm). Logistic regression models revealed that all age classes displayed a strong tendency to select greater depths. During the winter season, all size classes displayed strong selection of cover and slower water velocities in addition to greater depths while selection of cover and focal velocity were weaker in other seasons. This study demonstrated Rainbow Trout selected deep water habitat throughout the year and preferred slower focal velocities, likely to increase foraging area while minimizing swimming costs. This study also demonstrated fish selected positions close to cover during the winter, and illustrates the need for stream management and restoration programs to ensure such cover is available in salmonid wintering areas. The data

from this study can be used to guide future identification and restoration of suitable Rainbow Trout habitat in arid-land streams, particularly where stream discharge and velocities are extremely low.

Introduction

Throughout western North America, stream salmonids are experiencing declines due to hydrologic modifications, non-native fish introductions, and habitat degradation related to livestock grazing, logging, roads, mining and water diversion (Young 1995; Rieman et al. 2003; Fausch et al. 2006). Reversing and mitigating any one of these factors can be difficult due to high costs as well as political and logistical difficulties (Williams et al. 1997). Moreover, resources for fisheries managers are limited, and because of this, they must have a solid scientific understanding of fish-habitat relationships to ensure that the habitats critical to the life history of the species are protected and restored. Knowledge of these habitat requirements aids in informing managers of the types of habitats that may need protection and restoration necessary to improve fish growth, survival, reproductive success, and abundance. For example, management has attempted to improve fish abundance by adding physical structures (e.g., wing deflectors, overhead bank cover), or large woody debris often without regards to limiting factors or benchmarks necessary to sustain salmonids throughout their life history. Bond and Lake (2003) suggested fish habitat improvement projects experienced a high rate of failure as a result of not knowing sufficient habitat needed to sustain fish populations. When limiting factors might be identified, the effort and cost can be substantial. For instance, Roni et al. (2010)

estimated that a substantial amount of resources would be required to restore 20% of the available in-stream habitat to detect a 25% increase in Coho Salmon *Oncorhynchus kisutch* and Steelhead *O. mykiss* smolt production throughout streams in western Washington and Oregon. Thus, managers must be certain habitat and associated microhabitat will be suitable for targeted species.

The seemingly simple concept of habitat can be complex and our understanding of the relationship between habitat variables and fish populations, for example, is rudimentary at best. Explaining which habitat features limits fish populations and how they limit populations is a difficult task. Effectively managing habitat is even more difficult. To functionally manage habitat requires identifying “limiting” factors which change spatially (juxtaposition to fish location), and temporally (hourly, daily, seasonal changes) as it relates to physiological requirements and life history requisites. As such, studies of fish habitat use are often only conducted during the summer or only during the day (e.g., Pratt 1984; Bozek and Rahel 1991; Adams 1994; Goetz 1994). As habitat use by salmonids vary seasonally and by fish size (Baltz et al. 1991), knowledge of both seasonal variation and changing size class in habitat use is necessary to adequately characterize a species’ habitat requirements. For example, habitat use during summer may not reveal limitations on carrying capacity resulting from insufficient winter habitat. In a small headwater stream in California, Baltz et al. (1991) found that Rainbow Trout *O. mykiss* of all size classes selected different microhabitats according to season, and the most notable influence was related to velocity. The authors cite temperature as the major component in fish selecting lower velocity habitats during winter because

salmonids forage less efficiently in higher velocity water when temperatures are below thermal optima (Smith and Li 1983).

Microhabitat, mesohabitat, and macrohabitat represent three functional scales of fish habitat. The microhabitat scale is the smallest spatial scale where habitat variables (e.g., water velocity, depth, temperature) are measured at the snout of the individual fish, with additional information in the immediate area around the fish corresponding to patches up to square centimeters (Bardonnnet and Bagliniere 2000). Mesohabitats represent the smallest homogenous geomorphological unit of habitat in streams that generally spans the width of the stream, such as individual pools, riffles or runs. Macrohabitat composes the largest homogeneous geomorphological unit corresponding to patches from a few to tens of square meters (Bardonnnet and Bagliniere 2000). Macrohabitat variables most often collected include such items as stream size, gradient, or combined mesohabitat or geomorphological units (e.g., segments or reaches of pools, runs, and riffles). The importance of these larger scales is that they are the scales at which active management occurs. Classifying and measuring mesohabitat or macrohabitat units assumes that a specific suite of microhabitats contained within a particular habitat “type” will be relatively similar among units of a similar type given similar geomorphological considerations, and thus they “index” microhabitat quantity and quality. However, knowledge of microhabitat is crucial to understanding habitat use at larger scales.

Models have attempted to characterize how microhabitat variables such as water velocity and depth affected selection by fish species of various sizes classes. It is important to characterize these microhabitat variables by age class due to varying

metabolic demands of fish of different ages (Clarke and Johnston 1999). Additionally, competition influences habitat choice resulting in habitat partitioning. A dominance hierarchy often occurs in streams where the largest fish occupies the most energetically beneficial location while subordinates tend to occupy less favorable positions (Fausch 1984). Small trout often occupy riffles and larger trout occupy pools (Bohlin 1977; Heggenes 1988, 1996; Maki-Petays et al. 1997). Metabolic demands increase exponentially as fish size increases, requiring shifts in habitat to meet their needs (Elliott 1976). In particular, microhabitat selection by young-of-year salmonids has gained attention due to the importance of habitat protection and enhancement of juvenile microhabitats as a means to increase recruitment (see Moore and Gregory 1988a,b). Elliott (1985) determined that availability of suitable habitat to establish and maintain a feeding territory was a limiting factor to first-year survival and year-class strength of Brown Trout *Salmo trutta*.

The objective of this research was to describe microhabitat use and selection of Rainbow Trout of varying size classes across seasons (temperatures). Specific hypotheses included: 1) Available microhabitat would differ by season, 2) microhabitat use and selection would differ between seasons among young-of-year, juvenile, and adult Rainbow Trout.

Methods

Study Area

The study area was located within a 1.5 km reach between two natural fish barriers of the Middle Fork Rio Ruidoso on the Mescalero Apache Reservation in south-central New Mexico (Figure 1.1). The Middle Fork Rio Ruidoso is a second order stream originating within the Sacramento Mountains with a drainage area of approximately 7.2 km². Precipitation occurs largely as snow with peak runoff occurring in late March through April and additional precipitation in July and August in the form of large monsoonal rain events. Elevations of the study area range from 2,450 m at the lower barrier to 2,627 m at the upper barrier of the study area. The riparian community is dominated by a dense mixed conifer forest. There are no perennial tributaries within the study area. The Middle Fork Rio Ruidoso is characterized by a high gradient (>5%) step-pool complex with short riffles and runs. Stream temperatures within the study area frequently fell below 0°C during the winter and exceeded 20°C during the summer.

Rainbow Trout were the dominant species within the study area (100-200 fish·100 m⁻¹) with few Brook Trout *Salvelinus fontinalis* (<1 fish·100 m⁻¹) that periodically migrated downstream from above the upper barrier (Figure 1.1). Rainbow Trout within this section of the Middle Fork Rio Ruidoso were selected as they were the predominant species present and there was an absence of fishing pressure that could bias fish behavior. Additionally, temperatures within the study area offered an opportunity to observe microhabitat selection at a range of temperatures typically found in many western U.S. streams (i.e., <0 to >20°C).

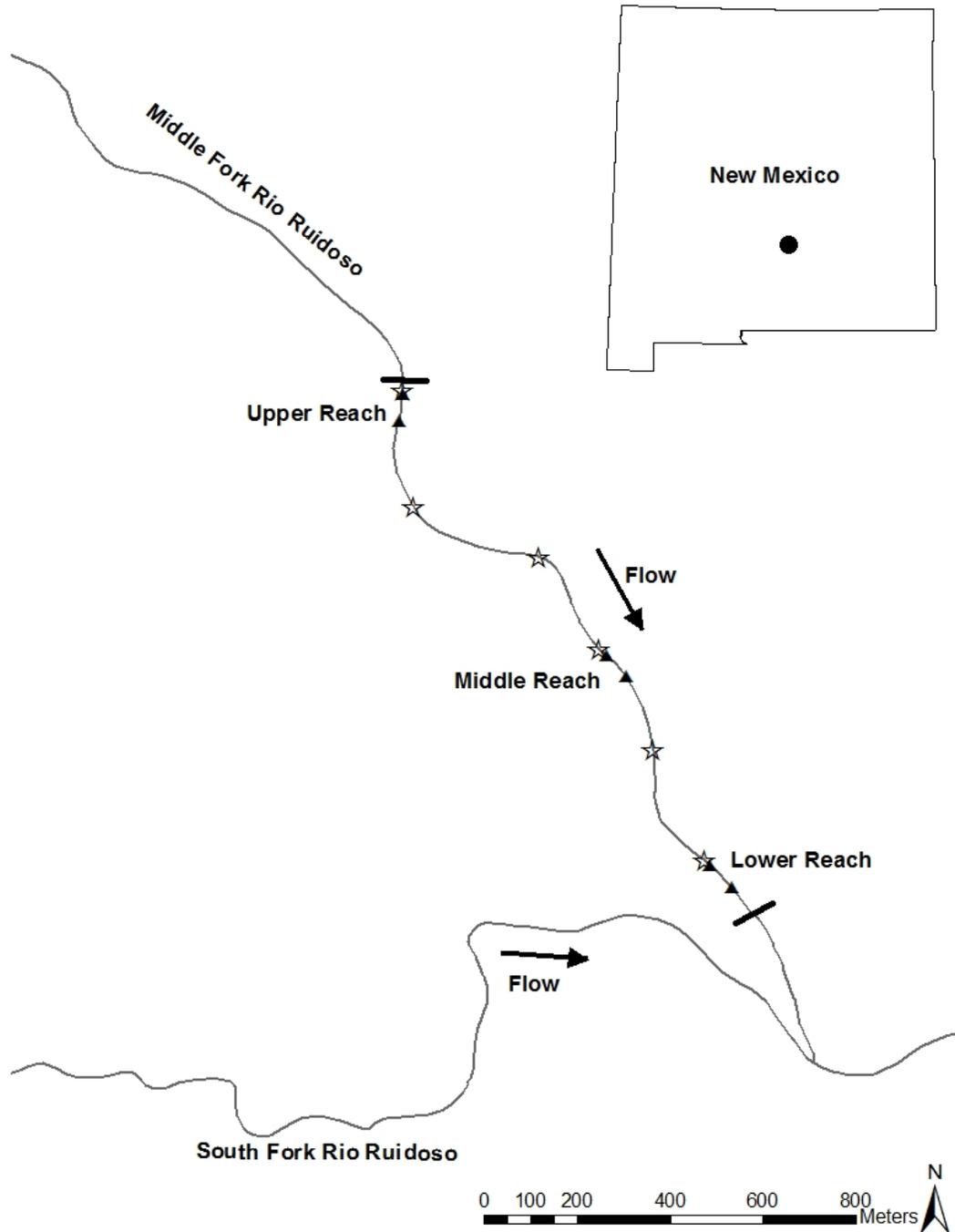


Figure 1.1. Study area illustrating the location of the lower (elevation 2,491 m), middle (2,552 m), and upper reaches (2,620 m; between solid triangles) and locations of six instream data loggers (open stars) within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. The solid lines represent the upper and lower terminus of the study area. Inset map indicates the location of the study area within New Mexico (black dot).

Three 50 m long reaches were randomly placed on the Middle Fork Rio Ruidoso for the monthly assessment of habitat use and availability by Rainbow Trout (Figure 1.1). Reaches were selected based on the location of instream data loggers. The first logger was randomly placed between 0 m and 240 m upstream from the lower barrier and subsequent loggers were systematically placed every 240 m upstream of the previous logger. Reaches were then placed downstream of the first, middle, and last data loggers.

Habitat Use

Habitat use by Rainbow Trout was evaluated monthly at all three reaches of the Middle Fork Rio Ruidoso between December 2011 and November 2012. Fish were presumably repeatedly sampled; however, repeated measures designs could not be used because fish were not individually identifiable. Shallow water precluded the use of underwater observation techniques (Heggenes et al. 1990). Therefore, fish were observed from positions along each stream bank by two observers before measuring habitat variables. Prior to observations, the observers calibrated their visual estimates of fish lengths downstream of the reach using pieces of PVC cut to known lengths and placed on the stream bottom next to fish positions to increase accuracy (Dolloff et al. 1996). Observers cautiously moved upstream to minimize disturbance to fishes. For each mesohabitat unit (i.e., run, riffle, pool, or pocket), observers allowed a minimum of 10 minutes for all fish to adjust their position until all fish within the mesohabitat unit selected a position. The observers then sketched the locations of the fish and estimated the total length (± 1 cm) and focal height

(distance of fish from substrate) of each fish (± 1 cm). Fish were categorized into age classes [young-of-year (age-0), juvenile (age-1), adult (age-2+)] based on back-calculated length at age data from fish scales collected throughout the study period using the Fraser-Lee method as described by DeVries and Frie (1996). Once each mesohabitat unit was surveyed, an observer entered the stream to place colored markers under the position of each fish with the guidance of the second observer from the stream bank.

After the entire reach was surveyed for fish, the stream depth, focal water velocity, mean water velocity, distance to cover, dominant substrate, and mesohabitat type was measured at every marked fish location. Stream depth (± 0.01 m) was recorded with a meter stick, and current velocity was measured with a portable velocity meter (± 0.001 m/s, Hach model FH950, Loveland, Colorado) and wading rod at the focal velocity of the fish and at the mean water velocity. If the stream depth was <0.50 m then the mean water velocity was taken at 60% of the stream depth and if the stream depth was ≥ 0.50 m, then mean water velocity was taken at 20% and 80% of the stream depth and the two were averaged (Gordon et al. 2004). Cover was defined as anything that can provide concealment for a salmonid including woody debris, boulders, undercut banks, overhanging vegetation, and ice. The dominant substrate was estimated visually and classified as silt (<0.06 mm), sand (0.06-2.0 mm), gravel (2.0-15 mm), pebble (16-63 mm), cobble (64-256 mm), or boulder (>256 mm) (Cummins 1962). Mesohabitat types were classified as pool, pocket, riffle, or run as defined by Arend (1999).

Available Habitat

To measure available habitat, transects were systematically placed along the thalweg of each 50 m reach by randomly selecting the location of the first transect between 1 and 150 cm upstream of the lower end of the reach and placing subsequent transects every 1.5 m upstream of the previous transect. From December 2011 through March 2012, transects were spaced every 1.5 m. After assessing the distribution of the data, it was determined that transect intervals could be increased to 3 m with minimal loss of information thereby reducing sampling effort from April 2012 to the conclusion of the study in November 2012. Water depth, focal velocity, mean velocity, distance to cover, dominant substrate, and mesohabitat type were measured at 0.25 m intervals along each transect. Values were averaged along each transect for statistical analyses.

Statistical Analyses

Focal velocity and mean velocity were highly correlated (Spearman rank correlation, $R = 0.71$, $P < 0.0001$) and had a high variance inflation factor (VIF = 9.39) inferring multicollinearity effects. Thus, mean velocity was not included in the analysis. Focal velocity is the most commonly reported microhabitat variable that provides comparability among other studies. Substrate type was reported but was not included in any analysis as it was believed this variable was largely a function of focal velocity (e.g., coarser substrates at higher velocities).

Each reach exhibited similar ranges of available microhabitat within each month, between months, and within a season. Therefore, all data were combined for

each season. Seasons were delineated based on mean monthly temperatures. The coolest three months were classified as winter (December-February), and the warmest three months were classified as summer (June-August). Spring (March-May) and fall (September-November) were classified as the transitional periods between summer and winter.

Focal velocity, depth, and cover distance were tested for normality (Shapiro-Wilk W statistic) and were all determined to be non-normal; thus a nonparametric Kruskal-Wallis analysis was used to identify differences in microhabitat availability and use among seasons. When the Kruskal-Wallis analysis was significant ($\alpha = 0.05$), post-hoc pairwise Mann-Whitney U -tests were conducted with a Bonferroni correction for familywise error rate. Kruskal-Wallis tests were also performed to identify differences in microhabitat use of Rainbow Trout between size classes within each season. Post-hoc pairwise tests were conducted where applicable as previously described. The significance levels (α) for all tests were assessed at 0.05 except where mentioned otherwise (Zar 1999).

Fisher's exact test was used to test if the proportion of mesohabitat type used (observed) differed from available (expected). Observed counts were the total number of fish observed using the mesohabitat type and expected counts were the proportion of available mesohabitat types multiplied by the total number of fish counted. Fisher's exact test was chosen over chi-squared tests as expected values were small (<5). Although row and column totals were not fixed, Fisher's exact test is still considered to be more accurate than chi-squared tests with small numbers (McDonald 2009).

Logistic regression was used to develop microhabitat selection models for each size class of fish and season (LOGISTIC procedure; SAS Institute, Inc. 2011). Logistic regression uses predictor variables to model a binary response variable (e.g., fish presence or absence) (Hosmer and Lemeshow 2000). In this study, fish use (1) and available positions (0) were the binary response variables and the associated microhabitat variables were the predictors. Selection (expressed as the relative probability of use) was described as a ratio between microhabitat use and availability. Selection was normalized to values ranging from 0 to 1 with 1 representing the highest probability of use and 0 representing the least probability of use.

An information-theoretic approach was used to evaluate the logistic regression models. Depth, cover distance, and focal velocity were included in the global model. A set of ecologically meaningful candidate models were created from the global model and the fit and parsimony of each candidate model was assessed using Akaike's Information Criteria (AIC; Akaike 1973) with a small sample bias adjustment (AIC_c; Hurvich and Tsai 1989). Models with uninformative parameters were removed from the model set. This included models within 2 AIC_c ($\Delta\text{AIC}_c \leq 2$) of a higher ranking model but included one additional parameter with poor explanatory power (Burnham and Anderson 2002; Arnold 2010). The best model and any competing model parameter estimates were averaged under the assumption that coefficients of models not containing a predictor variable are equal to zero. This assumption serves to "shrink" the coefficient back toward zero and ameliorates much of the model selection bias (Burnham and Anderson 2002). The best model and competing models were averaged until the sum of the Akaike weights (w_i ; probability

that model i is the actual expected Kullback-Leibler information best model) exceeded 0.90 (Burnham and Anderson 2002). Odds ratios and associated 95% confidence intervals (95% CI) were calculated as described by Hosmer and Lemeshow (2000) using model averaged parameter estimates and unconditional standard errors. A positive or negative association could not be judged for parameters with odds ratio confidence intervals that included 1. The goodness-of-fit of the global model was tested using the Hosmer-Lemeshow goodness-of-fit test at a significance level (α) of 0.05 (Hosmer and Lemeshow 2000). Empirically, candidate models that were more parsimonious also fit the data when the global model fit sufficiently (Burnham and Anderson 2002).

Results

Available Habitat

Habitat surveys could not be conducted during August 2012 due to heavy rain events and high turbidity that prevented visual observations. Therefore, the summer season included only June and July sample collections. Additionally, this event led to increased accumulations of fine substrates (silt and sand) throughout the fall season within the study area (Appendix A).

Discharge and available focal velocity, depth, and cover distance differed substantially by season (Table 1.1). Discharge was significantly higher during the winter and spring than the summer and fall seasons (Table 1.1). The higher discharge observed during winter and spring led to similar trends in available microhabitat where the highest velocities and greatest depths were also observed during the winter

Table 1.1. Mean \pm standard error of discharge and available microhabitat variables along with results of Kruskal-Wallis tests that were used to determine differences between seasons within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Shared superscripts within a row are not significantly different from one another (pairwise Mann-Whitney U -tests with Bonferroni correction, $\alpha = 0.0083$).

Variable	Season				Kruskal-Wallis		
	Winter	Spring	Summer	Fall	d.f.	χ^2	P
Discharge ($\text{m}^3 \cdot \text{s}^{-1}$)	0.006 ± 0.0005^a	0.007 ± 0.0009^a	0.002 ± 0.0004^b	0.002 ± 0.0003^b	3	47.43	< 0.0001
Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	7.1 ± 0.56^a	6.8 ± 0.62^{ab}	4.7 ± 0.81^b	5.2 ± 0.63^b	3	14.02	0.0029
Depth (cm)	14.0 ± 0.53^a	13.7 ± 0.59^a	11.7 ± 0.87^{ab}	11.5 ± 0.71^b	3	17.29	0.0006
Cover distance (cm)	20.7 ± 1.62^a	41.4 ± 3.09^b	77.2 ± 11.00^c	80.9 ± 8.95^c	3	175.84	< 0.0001

and spring (Table 1.1). Cover distance was significantly lower during the winter when ice covered much of the stream (Table 1.1).

Habitat Use

Ontogenetic shifts.—Fish of all size classes used depths ranging from 4 to 74 cm and focal velocities ranging from 0 to 21 cm·s⁻¹. Young-of-year fish selected significantly greater depths than juvenile and adult fish during the winter and summer and significantly shallower depths during the spring (Table 1.2). During the fall, juvenile fish selected depths that were significantly greater than either young-of-year or adult fish (Table 1.2). Post-hoc analysis of focal velocity revealed no significant difference between age classes for spring, summer, or fall while juvenile fish used significantly higher water velocities during the winter than young-of-year fish (Table 1.2).

Rainbow Trout of all size classes used cover distances ranging from 0 to 400 cm with an average of 48.5 ± 1.2 cm (mean \pm standard error) from closest cover. There was no difference in cover distance between size classes during the winter or spring, while young-of-year fish used positions during the summer that were closer to cover than juveniles and adults (Table 1.2). Young-of-year fish also selected stream positions that were closer to cover than juveniles during the fall (Table 1.2).

Seasonal shifts.—Fish of all size classes displayed varying use of focal velocity, depth, and cover distance among seasons; however, trends differed depending on age class (Table 1.3). For instance, juveniles did not use winter focal velocities that were significantly different than the spring, however, young-of-year

Table 1.2. Mean \pm standard error of used microhabitat variables for each season with results of Kruskal-Wallis tests to determine differences in microhabitat variables between age classes [young-of-year (YOY), juvenile, adult] and available habitat within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Shared superscripts within a row are not significantly different from one another (pairwise Mann-Whitney U -tests with Bonferroni correction, $\alpha = 0.0167$).

Season	Variable	Age Class			Kruskal-Wallis		
		YOY	Juvenile	Adult	d.f.	χ^2	P
Winter	Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	0.47 ± 0.13^a	1.14 ± 0.11^b	0.74 ± 0.15^{ab}	2	14.69	0.0006
	Depth (cm)	39.51 ± 1.48^a	34.71 ± 0.71^b	31.62 ± 1.62^b	2	17.51	0.0002
	Cover distance (cm)	1.59 ± 0.85	5.89 ± 1.19	4.11 ± 1.82	2	2.63	0.2681
Spring	Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	1.64 ± 0.26	1.20 ± 0.10	1.66 ± 0.15	2	5.16	0.0757
	Depth (cm)	28.93 ± 1.21^a	34.15 ± 0.80^b	35.05 ± 0.99^b	2	20.58	< 0.0001
	Cover distance (cm)	44.86 ± 3.79	56.35 ± 3.40	50.96 ± 3.29	2	1.92	0.3827
Summer	Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	0.68 ± 0.14	0.62 ± 0.09	0.63 ± 0.14	2	2.38	0.3049
	Depth (cm)	43.64 ± 2.54^a	30.65 ± 0.81^b	32.52 ± 1.08^b	2	22.31	< 0.0001
	Cover distance (cm)	45.70 ± 7.32^a	81.90 ± 2.91^b	64.30 ± 3.83^c	2	40.76	< 0.0001
Fall	Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	0.54 ± 0.12	0.63 ± 0.10	0.97 ± 0.22	2	0.46	0.7951
	Depth (cm)	35.34 ± 1.32^a	41.64 ± 0.92^b	35.77 ± 1.16^a	2	22.77	< 0.0001
	Cover distance (cm)	50.07 ± 4.33^a	72.70 ± 3.92^b	61.97 ± 5.20^{ab}	2	14.43	0.0007

Table 1.3. Mean \pm standard error of used microhabitat variables for each age class [young-of-year (YOY), juvenile, adult] with results of Kruskal-Wallis tests to determine differences in microhabitat variables between seasons within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Shared superscripts within a row are not significantly different from one another (pairwise Mann-Whitney U -tests with Bonferroni correction, $\alpha = 0.0083$).

Age Class	Variable	Season				Kruskal-Wallis		
		Winter	Spring	Summer	Fall	d.f.	χ^2	P
YOY	Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	0.47 ± 0.13^a	1.64 ± 0.26^b	0.68 ± 0.14^{ab}	0.54 ± 0.12^a	3	21.02	0.0001
	Depth (cm)	39.51 ± 1.48^{ab}	28.93 ± 1.21^c	43.64 ± 2.54^a	45.70 ± 7.32^b	3	44.63	< 0.0001
	Cover distance (cm)	1.59 ± 0.85^a	44.86 ± 3.79^b	45.70 ± 7.32^b	50.07 ± 4.33^b	3	88.13	< 0.0001
Juvenile	Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	1.14 ± 0.11^a	1.20 ± 0.10^a	0.62 ± 0.09^b	0.63 ± 0.10^{ab}	3	27.28	< 0.0001
	Depth (cm)	34.71 ± 0.71^a	34.15 ± 0.80^a	30.65 ± 0.81^b	41.64 ± 0.92^c	3	73.01	< 0.0001
	Cover distance (cm)	5.89 ± 1.19^a	56.35 ± 3.40^b	81.90 ± 2.91^c	72.70 ± 3.92^c	3	344.02	< 0.0001
Adult	Focal velocity ($\text{cm} \cdot \text{s}^{-1}$)	0.74 ± 0.15^a	1.66 ± 0.15^b	0.63 ± 0.14^a	0.97 ± 0.22^a	3	31.18	< 0.0001
	Depth (cm)	31.62 ± 1.62^a	35.05 ± 0.99^a	32.52 ± 1.08^a	35.77 ± 1.16^a	3	9.50	0.0233
	Cover distance (cm)	4.11 ± 1.82^a	50.96 ± 3.29^b	64.30 ± 3.83^c	61.97 ± 5.20^{bc}	3	108.70	< 0.0001

and adult age classes used significantly lower velocities during the winter than the spring (Table 1.3). Young-of-year and adult fish used similar velocities during the winter, summer, and fall, while juvenile fish used velocities during the summer that were significantly less than the winter (Table 1.3). Regardless of age class, the highest mean focal velocities were observed during the spring (Table 1.3).

Young-of-year and juvenile fish displayed varying use of depth by season (Table 1.3). Analysis of adult fish also showed varying use of depth by season ($\chi^2 = 9.50$, $df = 3$, $P = 0.0233$), however, post-hoc pairwise analysis revealed no significant differences among seasons (Table 1.3). Young-of-year fish used the shallowest depths during the spring (28.93 ± 1.21 cm) while juvenile fish used the shallowest depths during the summer season (30.65 ± 0.81 ; Table 1.3).

Cover distance was significantly less for all age classes during the winter than any other season (Table 1.3). Juveniles also used positions that were significantly closer to cover during the spring than either summer or fall (Table 1.3). Adults also used positions during the spring that were closer to cover than the summer (Table 1.3).

Habitat Selection

Mesohabitat selection.—Fish of all size classes selected mesohabitat types that were disproportionate to availability (Fisher's exact $P < 0.05$; Table 1.4). Pool mesohabitat was the most abundant available type (70-86%), followed by riffles (7-23%), runs (3-5%), and pockets (1-5%; Table 1.4). More than 98% of all fish used pool mesohabitat throughout the year (Table 1.4).

Table 1.4. Expected and observed mesohabitat use (%) for young-of-year (YOY), juvenile, and adult Rainbow Trout for each season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Fisher's exact test was used to determine whether use differed significantly ($P < 0.05$) from availability.

Season		Mesohabitat type				Fisher's exact P
		Pool	Riffle	Run	Pocket	
Winter	Expected use	70.4	20.3	5.1	4.2	
	Observed use					
	YOY	100.0	0.0	0.0	0.0	< 0.0001
	Juvenile	100.0	0.0	0.0	0.0	< 0.0001
	Adult	100.0	0.0	0.0	0.0	< 0.0001
Spring	Expected use	76.3	13.1	5.0	5.6	
	Observed use					
	YOY	100.0	0.0	0.0	0.0	< 0.0001
	Juvenile	98.8	0.4	0.4	0.4	< 0.0001
	Adult	98.8	0.0	0.6	0.6	< 0.0001
Summer	Expected use	86.3	7.3	4.1	2.3	
	Observed use					
	YOY	100.0	0.0	0.0	0.0	0.0127
	Juvenile	99.5	0.0	0.5	0.0	< 0.0001
	Adult	100.0	0.0	0.0	0.0	< 0.0001
Fall	Expected use	86.2	9.0	3.4	1.4	
	Observed use					
	YOY	98.9	0.0	1.1	0.0	0.0012
	Juvenile	100.0	0.0	0.0	0.0	< 0.0001
	Adult	100.0	0.0	0.0	0.0	< 0.0001

Microhabitat selection.—Logistic regression analysis revealed the global model of all model variables fit the data sufficiently (Hosmer-Lemeshow goodness-of-fit, all $P > 0.05$). The results of all models are displayed in Appendix B. The highest ranking model for each age class of Rainbow Trout during the winter season was the global model containing all predictors. Depth had a strong positive association for all age classes with fish 9-17% more likely to be present for every 1 cm increase in depth (Table 1.5). All age classes also displayed a strong relationship with cover distance and focal velocity indicating fish were selecting positions closer to cover (3-6% higher probability per 1 cm closer to cover) and lower focal velocities (18-34% higher probability per 1 $\text{cm}\cdot\text{s}^{-1}$ lower velocity) (Table 1.5).

Model analysis of young-of-year and juvenile fish during the spring season revealed all parameters improved the explanatory power of the final model while cover distance was not important for adult fish, and thus was not included in the final model (Table 1.6). All age classes of fish were 12-19% more likely to select deeper water (Table 1.6). Juvenile fish displayed a slight negative affinity for cover distance with a 1% increase in probability of fish selecting a position for every 1 cm increase in cover distance (Table 1.6). The probability of juvenile fish selecting focal velocities that were 1 $\text{cm}\cdot\text{s}^{-1}$ lower was 14% (95% CI, 6-22%; Table 1.6). Young-of-year and adult age classes did not reveal an association with cover distance or focal velocity (Table 1.6).

Model analysis during the summer season revealed that cover distance did not improve the explanatory power of any age class, and thus was not included in the final model (Table 1.7). Depth was the only parameter selected by the adult age class

Table 1.5. Model averaged parameter coefficient estimates, unconditional standard errors (SE), importance weights, odds ratios, and 95% odds ratio confidence intervals (CI) for each parameter selected from the best models for young-of-year (YOY), juvenile, and adult Rainbow Trout microhabitat selection during the winter season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Age class	Variable	Coefficient	Unconditional SE	Importance weight	Odds ratio	Odds ratio 95% CI	
						Lower	Upper
YOY	Intercept	-4.234	0.739				
	Total depth	0.135	0.021	1.00	1.14	1.10	1.19
	Cover distance	-0.058	0.024	1.00	0.94	0.90	0.99
	Focal velocity	-0.417	0.212	1.00	0.66	0.43	1.00
Juvenile	Intercept	-3.483	0.415				
	Total depth	0.160	0.015	1.00	1.17	1.14	1.21
	Cover distance	-0.039	0.008	1.00	0.96	0.95	0.98
	Focal velocity	-0.198	0.072	1.00	0.82	0.71	0.94
Adult	Intercept	-2.333	0.464				
	Total depth	0.083	0.015	1.00	1.09	1.05	1.12
	Cover distance	-0.034	0.012	1.00	0.97	0.95	0.99
	Focal velocity	-0.398	0.131	1.00	0.67	0.52	0.87

Table 1.6. Model averaged parameter coefficient estimates, unconditional standard errors (SE), importance weights, odds ratios, and 95% odds ratio confidence intervals (CI) for each parameter selected from the best models for young-of-year (YOY), juvenile, and adult Rainbow Trout microhabitat selection during the spring season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Age class	Variable	Coefficient	Unconditional SE	Importance weight	Odds ratio	Odds ratio 95% CI	
						Lower	Upper
YOY	Intercept	-2.582	0.761				
	Total depth	0.114	0.016	1.00	1.12	1.09	1.16
	Cover distance	0.003	0.004	0.63	1.00	1.00	1.01
	Focal velocity	-0.064	0.039	0.90	0.94	0.87	1.01
Juvenile	Intercept	-3.047	0.372				
	Total depth	0.136	0.013	1.00	1.15	1.12	1.18
	Cover distance	0.009	0.002	1.00	1.01	1.00	1.01
	Focal velocity	-0.156	0.049	1.00	0.86	0.78	0.94
Adult	Intercept	-4.183	0.476				
	Total depth	0.172	0.018	1.00	1.19	1.15	1.23
	Focal velocity	-0.032	0.043	0.54	0.97	0.89	1.05

Table 1.7. Model averaged parameter coefficient estimates, unconditional standard errors (SE), importance weights, odds ratios, and 95% odds ratio confidence intervals (CI) for each parameter selected from the best models for young-of-year (YOY), juvenile, and adult Rainbow Trout microhabitat selection during the summer season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Age class	Variable	Coefficient	Unconditional SE	Importance weight	Odds ratio	Odds ratio 95% CI	
						Lower	Upper
YOY	Intercept	-3.972	0.789				
	Total depth	0.155	0.029	1.00	1.17	1.10	1.24
	Focal velocity	-0.166	0.246	0.53	0.85	0.52	1.37
Juvenile	Intercept	-1.959	0.440				
	Total depth	0.155	0.020	1.00	1.17	1.12	1.22
	Focal velocity	-0.247	0.098	1.00	0.78	0.64	0.95
Adult	Intercept	-4.123	0.607				
	Total depth	0.208	0.028	1.00	1.23	1.17	1.30

(Table 1.7). Total depth was a strong predictor in all age classes with probability of fish selecting deeper water increasing by 17-23% per cm (Table 1.7). Juvenile fish selected lower velocities with the probability increasing by 22% (95% CI, 5-22%) for every 1 cm·s⁻¹ reduction in velocity while young-of-year did not display any association (Table 1.7).

During the fall season, model analysis revealed that focal velocity was not a strong predictor variable for any age class and was not included in the final model (Table 1.8). Total depth was the only variable used for juvenile fish in the final model (Table 1.8). Similar to other seasons, probability of fish selecting depths that were 1 cm deeper ranged from 19-25% (Table 1.8). Neither young-of-year nor adult fish displayed a strong association with cover distance, however, both age classes were skewed towards selecting closer cover distances (Table 1.8).

Discussion

All size classes of Rainbow Trout within the Middle Fork Rio Ruidoso displayed strong selection for deeper water (mean, 34.5 cm). This has been well documented in age-1+ salmonids, however, young-of-year salmonids often select shallower habitats than adults in pool margins and riffle/run habitats (Baltz et al. 1991; Bozek and Rahel 1991; Maki-Petays et al. 1997). Presumably, young-of-year fish are relegated to shallower depths due to intraspecific competition, however, they can persist at these depths due to reduced metabolic demands (Rosenfeld and Boss 2001). Rosenfeld and Boss (2001) demonstrated that young-of-year Cutthroat Trout *O. clarkii* preferred deep pool habitat over shallower riffle habitat but were able

Table 1.8. Model averaged parameter coefficient estimates, unconditional standard errors (SE), importance weights, odds ratios, and 95% odds ratio confidence intervals (CI) for each parameter selected from the best models for young-of-year (YOY), juvenile, and adult Rainbow Trout microhabitat selection during the fall season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Age class	Variable	Coefficient	Unconditional SE	Importance weight	Odds ratio	Odds ratio 95% CI	
						Lower	Upper
YOY	Intercept	-4.639	0.667				
	Total depth	0.208	0.027	1.00	1.23	1.17	1.30
	Cover distance	-0.005	0.006	0.69	0.99	0.98	1.01
Juvenile	Intercept	-6.044	0.801				
	Total depth	0.226	0.029	1.00	1.25	1.19	1.33
Adult	Intercept	-3.869	0.499				
	Total depth	0.172	0.020	1.00	1.19	1.14	1.23
	Cover distance	-0.003	0.004	0.57	1.00	0.99	1.00

to grow in either habitat. In contrast, older individuals could only achieve growth in pool habitat. Young-of-year Rainbow Trout in this study were frequently observed in deepest areas of the pools. However, mean cover distance of young-of-year fish was less than that of older age classes for every season indicating that young-of-year fish were using deep water microhabitats that differed from older individuals. Closer proximity to cover by young-of-year salmonids may be influenced by competition and predation from larger individuals (Schlosser 1987).

Very few fish of any size class were observed using riffles or runs throughout the study reach. While riffle/run habitats can provide large amounts energy to fish when prey drift is high due to the higher drift velocities (Fausch 1984), swimming costs increase exponentially with velocity (Brett and Glass 1973), thereby negating energetic benefits. Increased prey encounter rate from higher velocities can also be mitigated at deeper depths from an increased foraging radius and reduced swimming costs from lower focal velocities (see Chapter 2). Additionally, low discharge within the Middle Fork Rio Ruidoso created shallow riffle/run habitats (<15 cm) where risk of predation can be much higher than deeper pools (Gregory 1993) making use of deep water more beneficial.

The Middle Fork Rio Ruidoso is typical of small headwater streams in the southwest U.S. However, it was atypical from streams typically used in microhabitat studies because discharge was extremely low (<0.007 m³·s⁻¹) throughout the year. A similar study of microhabitat selection of Rainbow Trout by Baltz et al. (1991) in a California stream with a discharge of 0.1 m³·s⁻¹ (>20 times that of this study) reported young-of-year Rainbow Trout using mean focal velocities of 5 cm·s⁻¹ and adult

Rainbow Trout using mean focal velocities of 12-14 $\text{cm}\cdot\text{s}^{-1}$. Focal velocities in this study were generally low ($<1 \text{ cm}\cdot\text{s}^{-1}$) throughout pool habitats resulting in general homogeneity of velocities throughout the pools.

In this study, analysis of microhabitat use among age classes revealed differences but no clear trends. Baltz et al. (1991) demonstrated that young-of-year Rainbow Trout selected shallower depths and slower velocities than older individuals. It is often cited that the reason for this relationship is younger individuals are relegated to marginal habitats (e.g., pool margins) through intraspecific competition. Young fish are able to survive in these marginal habitats due to reduced metabolic costs. This relationship did not hold true in this study, likely because of the overall homogeneity of velocities within the pool mesohabitat of the Middle Fork Rio Ruidoso. Homogenous velocities created suitable habitat throughout the pools and likely led to reduced size related habitat partitioning. Additionally, pool mesohabitat was the predominant habitat type, further homogenizing velocities throughout the study reaches.

Mean discharge during the winter and spring seasons were more than three times that of the summer and fall seasons within the Middle Fork Rio Ruidoso. This increased discharge had a significant effect on the stream depths and velocities of available habitats. Despite the higher velocities observed during the winter, fish of all age classes displayed strong selection of deeper, lower velocity water close to cover. Similar observations of stream salmonids using deeper, slower water during the winter has been documented by others (e.g., Cunjak and Power 1986; Baltz et al. 1991; Simpkins et al. 2000) and may be in response to conserving energy from

reduced feeding efficiency at low temperatures (Smith and Li 1983) and predator avoidance (Valdimarsson and Metcalfe 1998). Swimming performance of salmonids is reduced at low temperatures causing slow acceleration (Webb 1978; Johnson et al. 1996) to escape from predators. Therefore, it is beneficial for salmonids to seek shelter during the winter to avoid predation. Additionally, selecting positions in deep pools may shelter fish from supercooled waters as deeper water may be slightly warmer thereby avoiding frazil and anchor ice (Huusko et al. 2007). Brown et al. (1999) found that juvenile Rainbow Trout exposed to supercooled waters with frazil and anchor ice had reduced levels of plasma ions and increased plasma glucose indicating a general stress response. As stress is energetically demanding for a fish (Barton and Schreck 1987), frequent frazil and anchor ice formations during the winter can affect the survival of salmonids. Additionally, small frazil ice crystals could abrade the gills of salmonids causing hemorrhage and aggregate on the gill rakers, potentially leading to suffocation (Brown et al. 1994). Therefore, it is beneficial for fish to select deep water habitats that may preclude frazil ice formations.

During the spring season, fish shifted their microhabitat use to the highest focal velocities observed of any season. Prey drift is positively correlated with velocity (Townsend and Hildrew 1976; Grant and Noakes 1987; Nislow et al. 1998). Therefore, shifts in microhabitat to faster velocities while maintaining greater depths indicates that fish were selecting foraging positions. Focal velocities used by all age classes were similar between winter, summer, and fall. However, given that winter discharge and subsequently focal velocity was more than three times that of summer

or fall suggests differences in microhabitat use between winter and summer/fall seasons.

Results from this study can be used to guide managers in future restoration and management of small headwater streams, particularly where discharge and velocities are extremely low. In light of anthropogenic changes to aquatic environments (e.g., climate change, water diversions, habitat degradation), it is important to understand fish-habitat relationships to recognize the impacts that these changes will have on salmonids. For instance, livestock grazing in riparian areas causes increased channel width and decreased channel depth (Knapp et al. 1998). This research demonstrated the importance of deep pool habitat in which fish can select stream positions, presumably to maximize their foraging radius while minimizing swimming costs from the slow focal velocities. Decreasing channel depth will decrease the foraging radius of fish and increase velocities, resulting in increased energetic costs. Additionally, fish of all age classes displayed a strong selection for cover during the winter. Presumably, this creates habitat for fish to minimize energetic costs while also minimizing risk of predation and the threat of supercooled waters. Disturbances to riparian areas such as livestock grazing can cause reductions in the amount of instream cover (Armour et al. 1991). It is important to understand the effects such management decisions will have on streams as reductions in instream cover reduces densities of salmonids (Eklov and Greenberg 1998).

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Chapter 2: A Foraging-based Bioenergetic Assessment of Microhabitat Use and Availability by Drift-feeding Rainbow Trout in a Small Headwater Stream with Implications for Climate Change

Abstract

A foraging-based bioenergetics model assessed if Rainbow Trout *Oncorhynchus mykiss* of various age classes were selecting microhabitats from available habitat that maximized their net energy intake (NEI). The model predicted that 81% of fish sampled throughout the year met maintenance growth rations while only 40% maximized their growth ration. More than 80% of all energy acquired throughout the study for age-1+ fish was predicted to occur during May, June, and September. Predictions of overwinter NEI rates were generally positive for most fish (67-86%) indicating overwinter survival was likely high. The amount of available habitat capable of supporting fish declined with fish size as larger individuals require larger amounts of prey to sustain metabolic costs. When combined with microhabitat selection, these results demonstrated that fish selecting deep pool habitat maximized their foraging area while minimizing swimming costs at low focal velocities. The bioenergetics model was used to simulate changes in available habitat suitability at various climate change scenarios. Under a scenario of a 6°C increase, the model predicted in a reduction of suitable habitat by as much as 12% during the summer and 17% during the winter. Mean NEI of available habitat declined by 67-75% during summer while NEI improved during the winter months due to increases in food ration. These results demonstrated that climate change may restrict fish populations,

increase intraspecific competition, and reduce growth potential, affecting their long term viability.

Introduction

Habitat is the combined presence of both biotic and abiotic characteristics necessary for the persistence of individuals or populations. Managers have long been interested in relating specific habitat variables (e.g., stream depth, velocity, temperature) to habitat quality to clearly define habitat requirements for effective species management and stream restoration. This is often done through a correlative approach that relates fish abundance to physical habitat variables. It is often assumed that habitat selection by fishes indicates habitat requirement, but this assumption is rarely validated (Rosenfeld 2003). Habitat selection occurs when an individual uses a habitat in greater proportion than available (positive selection) or avoids a particular habitat in greater proportion than available (negative selection). The consequence of losing a selected habitat is usually unclear because fish may be able to maintain positive growth in a habitat that is less selected. Eventually, the less selected habitat may act as a “metabolic sink” where fish lose weight and die (Sogard 1994; Rosenfeld 2003). Therefore, energetic consequences of selected microhabitat variables must be considered to understand how microhabitat variables affect fish metabolically. Bioenergetic models offer a mechanistic approach to complement microhabitat selection studies as they can contribute an understanding of the causation underpinning microhabitat selection. Bioenergetic models have been used to predict microhabitat choice of stream salmonids based on energetic costs and

benefits (e.g., Fausch 1984; Hughes and Dill 1990; Railsback and Harvey 2002; Jenkins and Keeley 2010).

Bioenergetics is the study of the processing of energy by living systems (Ivlev 1939). Bioenergetic models mathematically describe the processes that equate energy consumed with energy gained and expended (Winberg 1956). In fisheries science, bioenergetics is typically used in a variety of ways including modeling energy budgets of individuals and populations, developing projections about fish production, characterizing predator-prey dynamics, and developing assumptions about habitat use (Hartman and Kitchell 2008).

Bioenergetic models have been informative in stream drift-foraging where the mechanisms underlying foraging are relatively easily modeled. Bioenergetics can be used to model microhabitat selection of stream-dwelling salmonids by combining the energetic requirements of fish with basic foraging ecology. Stream salmonids typically face into the current to hold foraging positions near the substrate where they feed on drifting invertebrates in the water column. Stream salmonids primarily feed on invertebrate drift (Elliott 1973), and because of this, one would expect locations with high drift densities to be selected by fish over locations with low drift densities. Macroinvertebrate drift rates and current velocities are positively correlated (Townsend and Hildrew 1976; Grant and Noakes 1987; Nislow et al. 1998), suggesting that salmonids would select locations with high velocities over locations with lower velocities. However, there is an energetic tradeoff between the costs of maintaining swimming position in high velocity compared with the potential energy gained from that position. Swimming costs increase exponentially with water

velocity (Elliott 1976; Brett and Glass 1973; Stewart 1980) while rates of prey drift increase linearly with water velocity (Fausch 1984). Additionally, prey drift becomes increasingly more difficult to capture at higher water velocities, marginalizing energetic gains from these positions (Fausch 1984). Therefore, stream salmonids must select stream positions that maximize energetic benefits of prey capture while minimizing the metabolic demands of foraging.

Habitat alterations pose a significant threat to fish populations (Malmqvist and Rundle 2002) and as such understanding the effects of habitat alterations on habitat suitability is paramount. Bioenergetic models allow researchers to assess how large scale changes in environmental variables may influence habitat quality. For instance, climate change is predicted to increase mean annual air temperatures 0.3-6.4°C by 2100 (IPCC 2007). Subsequent increases in water temperatures are predicted to alter fish distributions and fragment populations by pushing temperatures outside the thermal tolerance of various species (Riemann et al. 2007; Williams et al. 2009). Less understood is how increases in temperature within thermal limits affect the habitat of a species. At various climate scenarios, bioenergetic models can be used to simulate complex interactions of temperature related changes in habitat suitability (Jenkins and Keeley 2010).

The goal of this study was to assess the energetic profitability of used and available microhabitat positions of Rainbow Trout *Oncorhynchus mykiss* over time and under varying temperature scenarios. Specific hypotheses included: 1) fish will select microhabitats that maximize their net energy intake (NEI), 2) NEI rates will

vary temporally and among size classes, and 3) habitat suitability and growth potential of available habitat will change under varying climate change scenarios.

Methods

Study Area

The study area was located within a 1.5 km reach between two natural fish barriers of the Middle Fork Rio Ruidoso on the Mescalero Apache Reservation in south-central New Mexico (Figure 2.1). The Middle Fork Rio Ruidoso is a second order stream originating within the Sacramento Mountains with a drainage area of approximately 7.2 km². Precipitation occurs largely as snow with peak runoff occurring in late March through April and additional precipitation in July and August in the form of large monsoonal rain events. Elevations of the study area range from 2,450 m at the lower barrier to 2,627 m at the upper barrier of the study area. The riparian community is dominated by a dense mixed conifer forest. There are no perennial tributaries within the study area. The Middle Fork Rio Ruidoso is characterized by a high gradient (>5%) step-pool complex with short riffles and runs. Stream temperatures within the study area frequently fell below 0°C during the winter and exceeded 20°C during the summer.

Rainbow Trout were the dominant species within the study area (100-200 fish·100 m⁻¹) with few Brook Trout *Salvelinus fontinalis* (<1 fish·100 m⁻¹) that periodically migrated downstream from above the upper barrier (Figure 2.1). Rainbow Trout within this section of the Middle Fork Rio Ruidoso were selected as they were the predominant species present and there was an absence of fishing

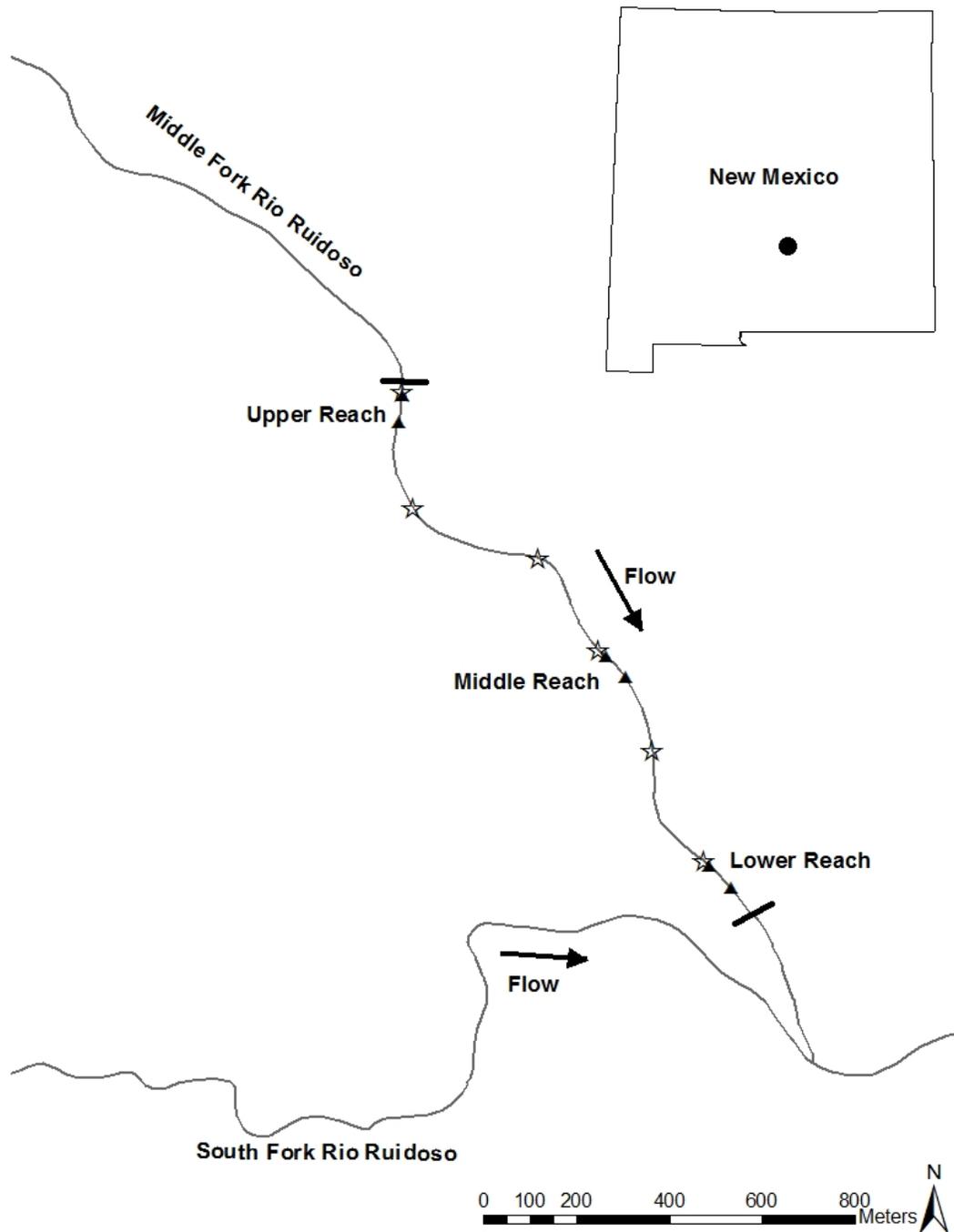


Figure 2.1. Study area illustrating the location of the lower (elevation 2,491 m), middle (2,552 m), and upper reaches (2,620 m; between solid triangles) and locations of six in-stream data loggers (open stars) within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. The solid lines represent the upper and lower terminus of the study area. Inset map indicates the location of the study area within New Mexico (black dot).

pressure that could bias fish behavior. Additionally, temperatures within the study area offered an opportunity to observe microhabitat selection at a range of temperatures typically found in many western U.S. streams (i.e., <0 to >20°C).

Three 50 m long reaches were randomly placed on the Middle Fork Rio Ruidoso for the monthly assessment of habitat use and availability by Rainbow Trout (Figure 2.1). Reaches were selected based on the location of instream data loggers. The first logger was randomly placed between 0 m and 240 m upstream from the lower barrier and subsequent loggers were systematically placed every 240 m upstream of the previous logger. Reaches were then placed downstream of the first, middle, and last data loggers.

Fish Foraging Locations

Foraging locations of Rainbow Trout were evaluated monthly at all three reaches of the Middle Fork Rio Ruidoso between December 2011 and November 2012. Shallow water precluded the use of underwater observation techniques (Heggenes et al. 1990). Therefore, fish were observed from positions along each stream bank by two observers before measuring habitat variables. Prior to observations, the observers calibrated their visual estimates of fish lengths downstream of the reach using pieces of PVC cut to known lengths and placed on the stream bottom next to fish positions to increase accuracy (Dolloff et al. 1996). Observers cautiously moved upstream to minimize disturbance to fishes. For each fish, observers allowed a minimum of 10 minutes for the fish to adjust its position for each habitat unit (i.e., run, riffle, pool, or pocket) until all fish within the habitat unit

selected a position. The observers then sketched the locations of the fish and estimated the total length (± 1 cm) and focal height of each fish (± 1 cm; taken at snout of fish). Once each habitat unit was surveyed, an observer entered the stream to place colored markers under the position of each fish with the guidance of the second observer from the stream bank. After the entire reach was surveyed for fish, the stream depth, focal height water velocity, and mean water velocity was measured at every marked fish location. Stream depth (± 0.01 m) was recorded with a meter stick, and current velocity was measured with a portable velocity meter (± 0.001 m/s, Hach model FH950, Loveland, Colorado) and wading rod at the focal velocity of the fish and at the mean water velocity. If the stream depth was < 0.50 m then the mean water velocity was taken at 60% of the stream depth and if the stream depth was ≥ 0.50 m then mean water velocity was taken at 20% and 80% of the stream depth and the two were averaged (Gordon et al. 2004).

Available Habitat

To measure available microhabitat, transects were systematically placed along the thalweg of each 50 m reach by randomly selecting the location of the first transect between 1 and 150 cm upstream of the lower end of the reach and placing subsequent transects every 1.5 m upstream of the previous transect. From December 2011 through March 2012, transects were spaced every 1.5 m. After assessing the distribution of the data, it was determined that transect intervals could be increased to 3 m with minimal loss of information thereby reducing sampling effort from April 2012 to the conclusion of the study in November 2012. Water depth, focal water

velocity, and mean water velocity were measured at 0.25 m intervals along each transect.

Bioenergetics Model Development

Foraging profitability can be evaluated in the context of bioenergetics. For stream dwelling salmonids gross energy intake (GEI) is the total energy ingested by fish from macroinvertebrates. Gross energy intake is calculated by estimating the amount of macroinvertebrate drift passing through a fish's effective foraging window, also known as the maximum capture area (MCA). The MCA can be modeled as a half circle area that is perpendicular to streamflow, within which a fish can capture prey (Figure 2.2). The radius of the MCA is defined by the maximum capture distance (MCD) from which a fish can detect a prey item and react to the item before it drifts past the fish.

To assess profitability of used and available fish positions, energetic costs were incorporated using the concept of calculating net energy intake (NEI). All energetic costs associated with foraging, losses from swimming, costs of intercepting a prey item, cost of digesting a prey item, and losses of energy through feces were subtracted from the GEI to calculate NEI. A bioenergetics foraging model of NEI was developed by Hughes and Dill (1990). This model was modified by Addley (1993) and later by Jenkins and Keeley (2010) to include estimates of fish energy requirements and distance from which fish can detect prey (from other published studies). The model of Jenkins and Keeley (2010) was further refined in this study with a maximum sustainable fish velocity obtained from Harvey and Railsback

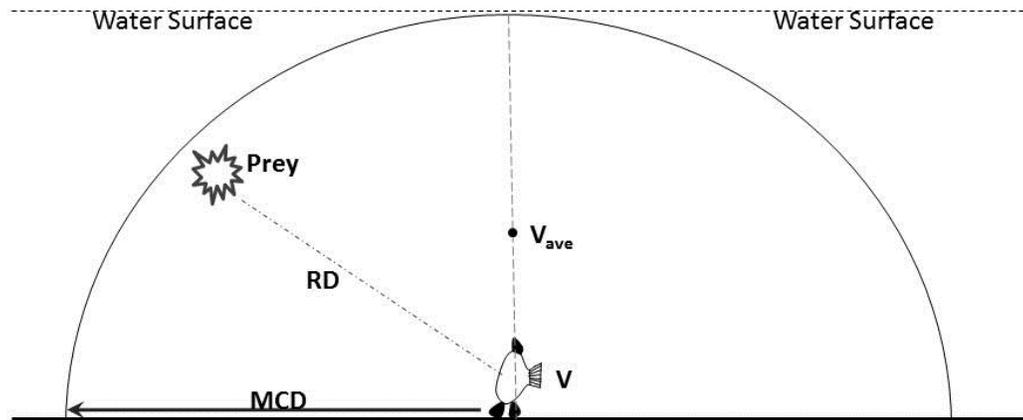


Figure 2.2. Diagram depicting the maximum capture area (MCA; half circle) with a radius equal to the maximum capture distance (MCD) of a foraging salmonid. RD = reaction distance, V_{ave} = mean velocity of the MCA, and V = focal point velocity. Adapted and modified from Hayes et al. (2000) and Guensch et al. (2001).

(2009) that used data from Rainbow Trout (Table 2.1). Minimum prey size was also modified in this study and defined as the smallest prey item in which the benefit of capturing the prey item (E_i) outweighed the cost of capture (CC; Table 2.1). Due to gape limitations of age-0 fish, an equation from Keeley and Grant (1997) was used to calculate the maximum prey size that age-0 fish can ingest (PL_{max} ; Table 2.1).

Estimates of fish bodyweight necessary for the swimming cost (SC) equation were estimated from a length:weight relationship developed from more than 500 Rainbow Trout collected throughout the study area (Table 2.1).

Fish cannot eat an infinite amount of food; thus, a maximum food ration (D ; $mg \cdot day^{-1}$) that a fish can ingest in a day was used (Elliott 1976; Appendix C). From this model, the resulting energy that a fish can consume in a day (C_{max}) was calculated and set to the upper limit to obtain GEI. Elliott's (1976) estimate of maximum daily intake was based on Brown Trout *Salmo trutta* fed discrete meals over a 24 h period. For this study, the amount of foraging time was based on the amount of daylight hours available for fish to forage at the time of sampling. Nighttime foraging was not within the scope of this study. The following equation was used to estimate C_{max} :

$$C_{max} = \frac{1}{\text{feeding hours} \cdot \text{day}^{-1}} \cdot D(mg \cdot \text{day}^{-1}) \cdot 4.438(cal \cdot mg^{-1}) \cdot 4.1868(joules \cdot cal^{-1}) \cdot 0.58.$$

Where the maximum food ration (D) was calculated from Elliott (1976; Appendix C), conversion to calories ($cal \cdot mg^{-1}$) was from Elliott (1976), and the energy assimilation fraction (0.58) was from Elliott (1976) and Brett and Groves (1979). The amount of

Table 2.1. Equations used to calculate net energy intake (NEI) of fish positions. Original model was developed by Hughes and Dill (1990) and modified by Addley (1993) and later by Jenkins and Keeley (2010).

Parameter	Equation	Comments and Source
NEI (joules·h ⁻¹)	$NEI = \frac{\sum_{i=1}^n DD_i \cdot MCA_i \cdot V_{ave} \cdot (E_i - CC) - SC}{1 + \sum_{i=1}^n t_i \cdot DD_i \cdot MCA_i \cdot V_{ave}} \cdot 3600$	Net energy intake based on the gross energy consumed minus the energy costs for each prey class (<i>i</i>), multiplied by 3600 for hourly NEI estimate
Reaction distance, RD _{<i>i</i>} (cm)	$RD_i = [12 \cdot PL_i (1 - e^{(-0.2 \cdot FL)})]$	Prey length (<i>PL_i</i> , mm) are used to calculate reaction distance for a given fish fork length (<i>FL</i> , cm); Equation from Hughes and Dill (1990)
Maximum sustainable fish velocity, V _{max} (cm·s ⁻¹)	$V_{max} = (2.8FL + 21) \cdot (-0.0029T^2 + 0.048T + 0.37)$	<i>T</i> is temperature (°C), <i>FL</i> is fish fork length (cm); Equation from Harvey and Railsback (2009)
Swimming cost, SC (joules·s ⁻¹)	$SC = \frac{1.4905 \cdot W^{0.7836} \cdot e^{0.0682T} \cdot e^{(0.0259 - 0.0005T)V}}{3600}$	<i>W</i> is individual fish weight (g), <i>T</i> is temperature (°C), <i>V</i> is focal point velocity of the fish (cm·s ⁻¹); equation from Stewart (1980)
Cost of capturing prey, CC (joules·prey ⁻¹)	$CC = 6SC_{V_{max}}$	Estimated at six times the swimming costs associated with a fishes maximum sustainable velocity; equation from Addley (1993)
Maximum capture distance, MCD _{<i>i</i>} (cm)	$MCD_i = \sqrt{RD_i^2 - \left(\frac{V_{ave} \cdot RD_i}{V_{max}}\right)^2}$	Estimated using the computed reaction distance for each prey size category (mm) and mean velocity of the maximum capture area (<i>V_{ave}</i> , cm·s ⁻¹); equation from Hughes and Dill (1990)
Maximum capture area, MCA _{<i>i</i>} (cm ²)	If stream depth ≥ MCD, then $MCA = \frac{1}{2}\pi \cdot (MCD_i)^2$ If stream depth < MCD, then $MCA_i = \left[SD \left(\sqrt{MCD_i^2 - SD^2}\right) + MCD_i^2 \cdot \arcsin\left(\frac{SD}{MCD_i}\right)\right]$	Equal to the area of a half circle with a radius equal to maximum capture distance if the stream depth (<i>SD</i> , cm) is greater than the maximum capture distance, otherwise MCA is equal to an area of less than half a circle; equation from Hughes and Dill (1990) and Jenkins and Keeley (2010)
Prey energy content, PE _{<i>i</i>} (joules·prey ⁻¹)	$PE_i = 0.3818(PL_i)^{2.46}$	<i>PL_i</i> is the mean length of prey a size category <i>i</i> (mm); equation from Smock (1980), Cummins and Wuycheck (1971), and Jenkins and Keeley (2010)
Energy assimilated, E _{<i>i</i>} (joules·prey ⁻¹)	$E_i = 0.58 \cdot (PE_i)$	Energy acquired from prey after losses from excretion (~14%) and digestion (~28%); equation from Elliott (1976) and Brett and Groves (1979)
Maximum prey length, PL _{max} (mm)	$\log_{10} PL_{max} = 0.85 \cdot \log_{10} FL + 0.039$	Maximum prey length (mm) that can be ingested by an age-0 fish where <i>FL</i> is the fork length (cm); equation from Keeley and Grant (1997)
Drift density, DD _{<i>i</i>} (mean no. of prey·cm ⁻³)	Collected in this study	Drift density of size category <i>i</i> averaged over three periods of the day (0900, 1200, 1500)
Length:weight relationship	$\log_{10} W = -4.06991 + 2.60348 \cdot \log_{10} L$	From this study where <i>W</i> is fish weight (g) and <i>L</i> is fish length (mm)
Time spent foraging, t _{<i>i</i>} (s)	Estimated to be 5 seconds	Estimated from Bachman (1984)

Note. Stream specific fish size, prey length and abundance, water temperature, focal and mean velocities, and stream depth were included in this model.

feeding hours per day was defined as the number of daylight hours from 0.5 h before sunrise to 0.5 h after sunset to the nearest 0.5 h.

Estimates of NEI for this study were computed as follows. If $GEI \geq C_{max}$, then:

$$NEI = C_{max} \cdot E_i - (SC \cdot 3600) .$$

Where E was the energy acquired from a food item of size class i , and SC was the swimming costs of maintaining a foraging position. If $GEI < C_{max}$, then:

$$NEI = \frac{\sum_{i=1}^n DD_i \cdot MCA_i \cdot V_{ave} \cdot (E_i - CC_i) - SC}{1 + \sum_{i=1}^n t_i \cdot DD_i \cdot MCA_i \cdot V_{ave}} \cdot 3600 .$$

Where DD_i was the drift density of prey of size class i that enters the fishes maximum capture area (MCA), V_{ave} was the average velocity of the water within the MCA, CC_i was the cost associated with capturing the prey item, and t_i was the time spent handling a prey item. A complete list of formulas used to derive these equations is shown in Table 2.1.

Macroinvertebrate Collections

To obtain drift density estimates for the bioenergetics model, drift nets (45 width x 27 height x 108 cm length; 500 μ m mesh) were set for one hour at each sample collection at the top end of each reach three times during the day beginning at 0900, 1200, and 1500. One drift net was secured into the substrate using metal stakes with the top of the net protruding from the water to collect surface macroinvertebrates. Mean water velocity and depth was measured at eight evenly spaced points across the drift net to calculate the volume of water passing through the

net over time. One drift net was found to be sufficient at sampling greater than 75% of the stream discharge. Specimens from each net were transferred to a plastic bag and preserved in 95% ethanol.

Macroinvertebrates were classified by taxa (order or family), measured for length (± 0.25 mm), and placed into 0.5 mm size classes. Drift density for each size class and net were calculated using the formula by Allan and Russek (1985):

$$\text{Sample Drift Density} = \frac{\text{Number captured}}{\text{Proportion of flow filtered}}$$

Where proportion of flow filtered was the volume (cm^3) of water passing through the drift net estimated by the area of the net mouth and the velocity at the net mouth, number captured was the number of macroinvertebrates captured in one hour, and sample drift density was the number of macroinvertebrates per cm^3 of water. The average drift densities of the three daily drift samples were used in the bioenergetics model for the sampling period.

Model Application

Net energy intake was estimated for individual fish at each foraging location. For each fish, the bioenergetics model used individual fish length, focal water velocity, mean water velocity, depth, and reach-specific macroinvertebrate drift density and mean temperature. Estimates of available NEI were calculated using five size classes of fish: 57, 99, 143, 177, and 210 mm. These size classes were based on back-calculated length at age data from fish scales collected throughout the study period (see Chapter 1) as follows: age-0 (≤ 78 mm), age-1 (79-119 mm), age-2 (120-

164 mm), age-3 (165-188 mm), and age-4+ (≥ 189 mm). The midpoint of each age class and the average fish length observed for the age-0 and age-4+ age classes were used for available NEI estimates. Fish size has a large influence on NEI estimates and therefore it was necessary to use multiple size classes of fish. Mean NEI values were calculated for statistical analyses at each transect based on average foraging potential at 25 cm intervals. Estimates of NEI were used to evaluate the proportion of fish and available habitat meeting maintenance ration ($NEI \geq 0$) and maximum growth ration (C_{max}) of Rainbow Trout for each month.

Temperature Simulations

Mean ambient summer and winter conditions from the Middle Fork Rio Ruidoso were used to assess how different climate change scenarios would affect the amount of available habitat capable of meeting maintenance rations of Rainbow Trout. To assess the change in suitable habitat, temperatures were increased at 1°C intervals up to 6°C for the summer (June-July) and winter (December-February) while all other variables remained constant. These warmer temperatures represent a range of predicted temperature changes from climate change models (IPCC 2007). The percent deviation in suitable habitat between ambient conditions that were measured and those simulated were used to illustrate the response in changing temperatures.

Statistical Analysis

Data from each reach were combined within each month as bioenergetic variables were similar between reaches within a month. Net energy intake was tested for normality (Shapiro-Wilk W statistic) and was determined to be non-normal ($P < 0.05$). Thus, non-parametric Mann-Whitney U tests were used to compare the median NEI values selected by fish to median NEI values available to determine if fish were selecting positions with greater profitability than available. The significance level (α) for all tests was 0.05 (Zar 1999).

Results

A total of 99 macroinvertebrate drift samples were collected throughout the study period (Appendix D). The orders Diptera and Hemiptera accounted for 62% of the invertebrates collected and consisted of adults and the families Chironomidae, Dixidae, Simuliidae, Aphididae, and Veliidae. The orders Ephemeroptera, Plecoptera, and Trichoptera collectively accounted for 13% of the drift and consisted primarily of the families Baetidae, Perlodidae, and Hydropsychidae. Nearly half (46%) of drift captured consisted of terrestrial invertebrates.

A total of 1,653 observations of fish were recorded between December 2011 and November 2012. Size of fish ranged from 38 to 305 mm with a mean length of 110 mm. Age-1 fish were most frequently observed and accounted for 51% of the fish sampled followed by age-0 (20%), age-2 (19%), age-4+ (6%), and age-3 (4%). Observations could not be completed during August 2012 due to large rain events that precluded visual observations from high turbidity.

Simulated NEI rates displayed strong seasonal variability with temperature and macroinvertebrate drift density dictating the amount of potential energy acquired at fish positions and available habitat. Mean daily temperatures varied from 0.32°C in January to 15.08°C in July (Table 2.2). Mean macroinvertebrate drift density and energy density was relatively low throughout the winter and spring months (<6 macroinvertebrates \cdot m⁻³; ≤ 46 joules \cdot m⁻³) before peaking in June (25.4 ± 8.8 macroinvertebrates \cdot m⁻³; 219 ± 109.8 joules \cdot m⁻³, mean \pm standard error; Table 2.2). Low predicted metabolic rates of fish during the winter months (December-February) led to relatively low NEI rates (Figure 2.3). However, age-0, age-1, and age-2 fish selected positions that had significantly greater simulated NEI rates than available during this period (Figure 2.3). Potential NEI rates increased for most age classes from March to June in addition to water temperature and drift density. Age-0 and age-1 fish selected foraging positions that were significantly greater than positions available during March and April while age-1 and larger age classes selected more profitable positions during the warmer months of May and June (Figure 2.3). Drift densities in March and April consisted largely of small invertebrates that created low potential NEI for larger age classes (Figure 2.3). Macroinvertebrate drift in May and June consisted of drift density of large invertebrates with high energy leading to the most energetically profitable months of the year (Figure 2.3). Although July temperatures were relatively warm ($15.08 \pm 0.32^\circ\text{C}$), low drift rates throughout the study area led to low potential NEI. Despite this, age-4+ fish located positions that were significantly more energetically profitable than available habitat (Figure 2.3). Net energy intake rates for all age classes declined throughout the fall

Table 2.2. Monthly mean \pm standard error temperature ($^{\circ}\text{C}$), discharge ($\text{m}^3 \cdot \text{s}^{-1}$), macroinvertebrate drift density ($\text{number} \cdot \text{m}^{-3}$), and macroinvertebrate drift energy density ($\text{joules} \cdot \text{m}^{-3}$) collected from all three reaches of the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Variable	Month											
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Temperature	0.32 ± 0.08	0.85 ± 0.13	1.12 ± 0.50	5.01 ± 0.55	10.32 ± 0.35	13.29 ± 0.41	14.89 ± 0.38	15.08 ± 0.32	-	11.33 ± 0.51	9.47 ± 0.26	3.47 ± 0.36
Discharge	0.004 ± 0.0006	0.008 ± 0.0007	0.007 ± 0.0005	0.013 ± 0.0010	0.006 ± 0.0005	0.003 ± 0.0004	0.002 ± 0.0005	0.002 ± 0.0005	-	0.004 ± 0.0005	0.001 ± 0.0003	0.002 ± 0.0002
Drift density	3.3 ± 1.7	0.5 ± 0.1	0.9 ± 0.3	1.3 ± 0.3	2.7 ± 0.8	5.8 ± 1.6	25.4 ± 8.8	5.0 ± 1.4	-	7.1 ± 1.4	17.6 ± 4.9	5.2 ± 1.2
Drift energy density	15 ± 4.6	4 ± 1.4	12 ± 5.3	16 ± 4.3	14 ± 4.9	46 ± 10.7	219 ± 109.8	15 ± 4.0	-	29 ± 7.9	64 ± 24.6	30 ± 6.8

“-“ indicates data could not be collected due to high turbidity

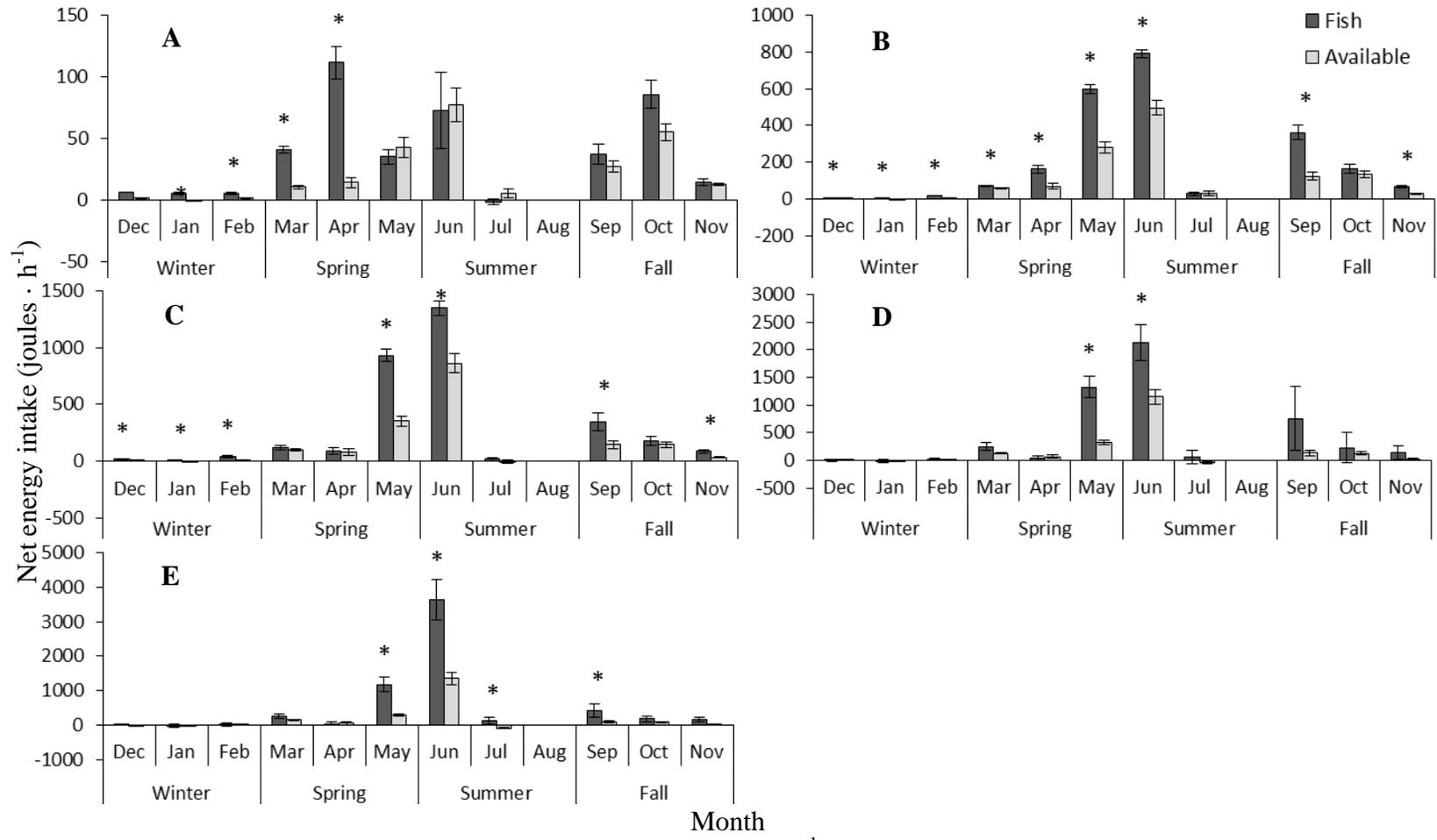


Figure 2.3. Monthly mean (± 1 SE) net energy intake values (joules · hr⁻¹) of used (dark bars) and available (light bars) stream positions for age-0 (A), age-1 (B), age-2 (C), age-3 (D), and age-4+ (E) fish combined from all three reaches of the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Asterisk (*) denotes statistical difference ($P < 0.05$) between use and availability for each month (Mann-Whitney U -test). Note: no data was collected in August due to high turbidity.

(September-November) largely due to declining temperatures. Age-1 and age-2 fish selected positions that were significantly more energetically profitable than available during September and November while age-4 fish only selected more profitable positions during November (Figure 2.3). This indicates that energetically profitable positions were more readily available to smaller bodied individuals.

Use and availability of habitat that provided maintenance ration ($NEI \geq 0$) or maximum growth ration (C_{max}) varied greatly depending on month and age class (Figure 2.4). Generally, fish of all size classes selected stream positions that met their maintenance ration or maximum growth ration at a higher proportion than available (Figure 2.4). In total, 81% of all fish observed throughout the study period were predicted to have met maintenance rations while 40% were predicted to have met maximum growth rations. No available habitat was predicted to have been capable of meeting maximum growth ration in July. Outside of July, less than 15% of available habitat in April, September, and October met maximum growth rations. With the exceptions of April and July, greater than 50% of available habitat was predicted to have been capable of meeting maintenance ration for at least one size class (Figure 2.4).

Simulated changes in temperature for both the summer and winter seasons significantly altered the amount of available habitat capable of meeting maintenance rations and the average amount of energy provided. Simulations of summer temperatures from an average of 15°C to 21°C demonstrated 7.6-12.4% less available habitat was capable of supporting fish at 21°C than 15°C (Figure 2.5a). Mean NEI of available habitat declined sharply at temperatures above 18°C and mean NEI values

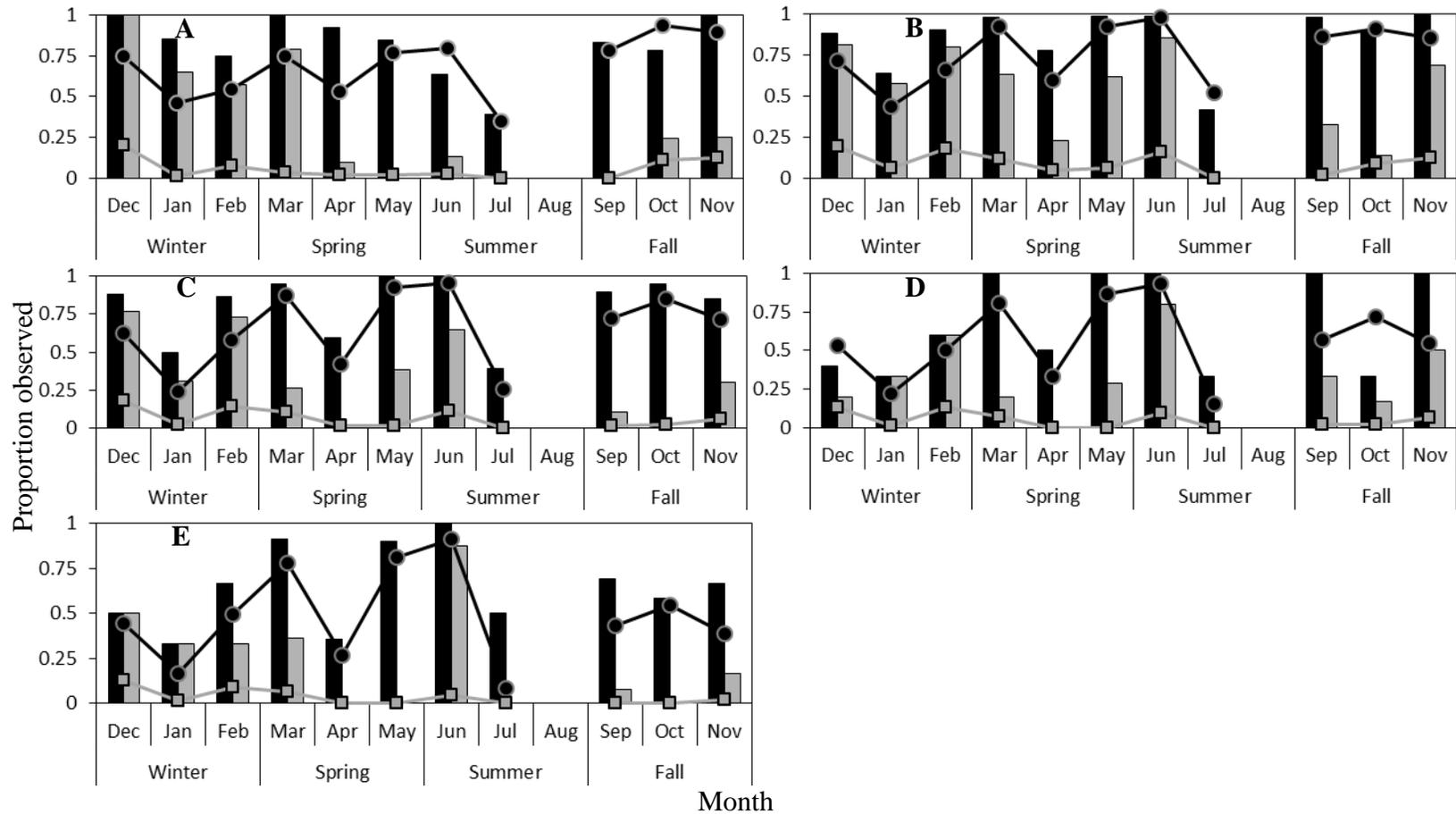


Figure 2.4. Monthly proportion of fish that met maintenance ratio ($NEI \geq 0$; black bars) and maximum ratio (C_{max} ; light bars) along with the proportion of available habitat that met maintenance ratio (black circles) and maximum growth ratio (light squares) for age-0 (A), age-1 (B), age-2 (C), age-3 (D), and age-4+ (E) fish observed within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Note: no data was collected in August due to high turbidity.

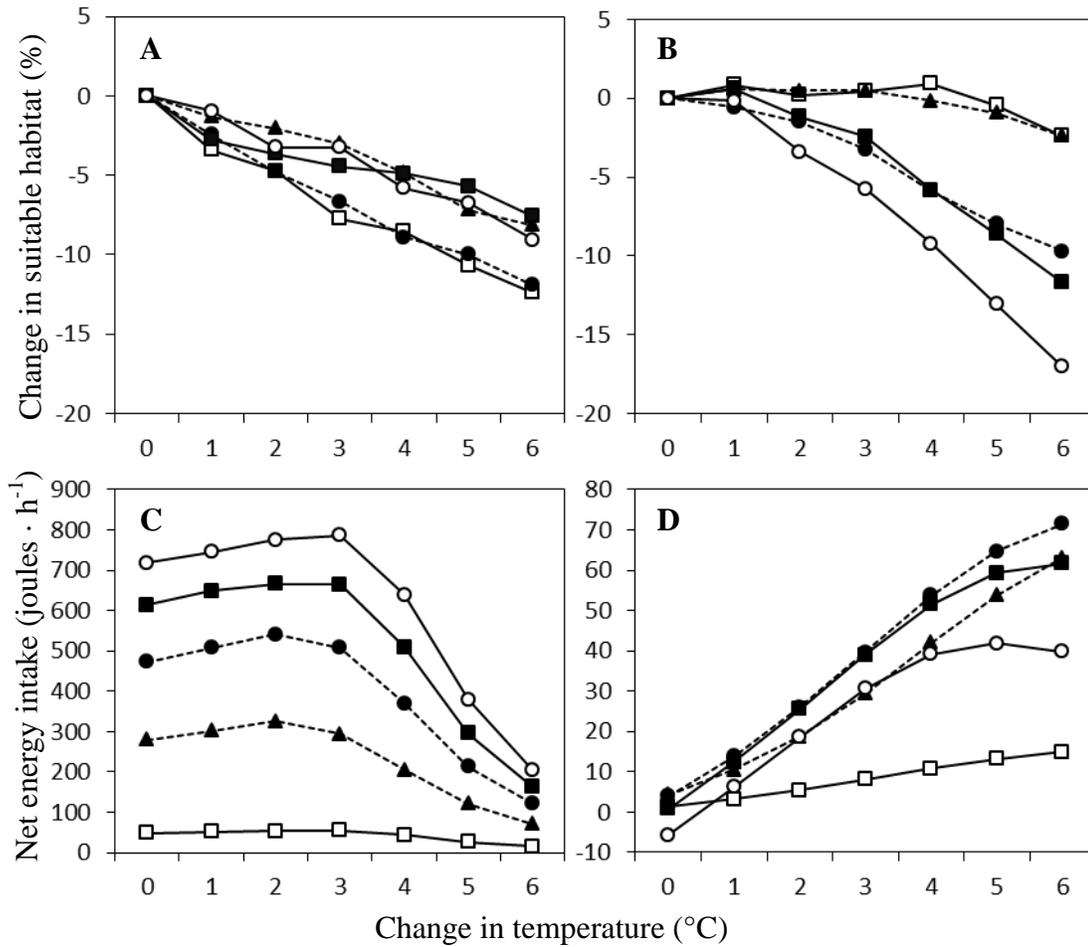


Figure 2.5. Relative change (%) in suitable habitat capable of supporting Rainbow Trout as a function of change in temperature for summer (A) and winter (B), and net energy intake (joules·h⁻¹) as a function of change in temperature for summer (C) and winter (D). Open squares represent age-0, solid triangles represent age-1, solid circles represent age-2, solid squares represent age-3, and open circles represent age-4+ available habitat for Rainbow Trout within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

at 21°C were 67-75% less compared to 15°C (Figure 2.5b). Simulations of winter temperatures also demonstrated that habitat suitability declined for all age classes (Figure 2.5c). Age-4+ fish would experience the largest decline (17%) in habitat suitability (Figure 2.5c). Age-0 and age-1 fish would experience a slight increase in habitat availability at increases in temperature from 1 to 3°C before a decline in available habitat at higher temperatures (Table 2.5c). Despite the loss of suitable habitat, mean NEI of available habitat increased over simulated temperatures culminating in NEI values that were as much as 70 times that of initial temperatures (Figure 2.5d).

Discussion

Fish of all size classes selected foraging positions that were more energetically profitable than available for many months of the year. This substantiates previous bioenergetic studies in fishes that indicate choice of stream position was largely a function of energetics. Results from Chapter 1 demonstrated that all size classes of Rainbow Trout selected the deepest area of the stream throughout the year. Greater depths allow fish to maximize their capture area, resulting in a high prey encounter rate. Fish selecting greater depths would also have access to lower focal velocities (Chapter 1). While lower velocities decrease the prey encounter rate, the benefit of higher velocity is negated as swimming costs become greater and capture distances shrink. It is important to note that selection of stream position also relies on variables unrelated to energetics. Cover distance was strongly selected by fish of all size classes during the winter months (Chapter 1). Therefore,

bioenergetics and microhabitat variables should be assessed together when observing selection of stream position of salmonids because neither adequately describes fish behavior alone.

Macroinvertebrate drift rates in this study changed seasonally and drastically influenced the amount of energy available to fish. When drift and energy densities were high (e.g., May and June), estimates of NEI were more sensitive to water temperature as fish approached or achieved maximum growth ration (Filbert and Hawkins 1995; Jenkins 2004). When drift densities were relatively low (e.g., January and July), estimates of NEI were more sensitive to prey abundance than water temperature (Addley 1993; Hayes 2000). Jenkins and Keeley (2010) observed relatively high drift densities throughout their study (17.7-52.0 macroinvertebrates · m⁻³) and determined that temperature was the primary driver of NEI estimates because drift rates were high. In this study, high drift and energy densities in June resulted in relatively large NEI rates due to temperature because food was abundant. As drift rates declined in July, NEI rates declined, illustrating NEI rates were more sensitive to drift rates than temperature when drift rates were low.

Rainbow Trout of all age classes displayed varying amounts of NEI rates throughout the year. Young-of-year fish had greater difficulty meeting maintenance rations during the year when older individuals were successful. For instance, 63% of young-of-year fish were predicted to have met maintenance rations in June while all older individuals were predicted to have met maintenance rations during same month. This was most likely due to gape limitations of young-of-year fish unable to capture large prey items (Keeley and Grant 1997) that were found in June drift samples.

Throughout the winter months, young-of-year and age-1 fish were observed actively foraging throughout the daytime hours. This led to more than half of these fish predicted to meet maximum growth ration while larger fish, that were frequently observed far under cover, experienced difficulty meeting maintenance ration. Young-of-year salmonids are more vulnerable to mortality than older individuals due to relatively higher metabolic costs per body size and subsequently more rapid depletion of energy reserves (Shuter and Post 1990). Thus, it benefits smaller bodied fish to actively forage during daylight hours when prey encounter and success rates are high. The observation of younger individuals actively foraging during daylight hours is unique in this study. Other studies cite fish switching to a nocturnal foraging behavior with the onset of winter (e.g., Cunjak 1988; Heggenes et al. 1993; Jakober et al. 2000; Robertson et al. 2003). It is believed this switch in behavior is in response to fish hiding during the day to avoid predation and foraging at night when risk of predation is minimal (Huusko et al. 2007). The decrease in foraging efficiency at night may be mitigated by reduced predation risk (Fraser and Metcalfe 1997; Valdimarson and Metcalfe 1998). Nighttime foraging was outside the scope of this study, however, warrants further investigation.

The amount of available habitat capable of supporting maintenance growth rations declined as fish size increased. This was not surprising given that metabolic demands of salmonids increase exponentially with fish size (Brett and Glass 1973). To meet the increased metabolic demands, larger individuals must shift their microhabitat use to the head of pools, near the center of the current to take advantage of higher prey encounter rates than smaller individuals within the pool (Fausch 1984;

Hughes 1992). Thus, available habitat capable of supporting larger individuals becomes increasingly restricted. Reductions in suitable habitat, such as seen in this small headwater stream, limit the growth potential and abundance of large individuals in the stream.

Energy acquired by age-1 and older fish during the months of May, June, and September was predicted to account for more than 80% of all energy assimilated for these age classes throughout the study period. This indicates that the growing season of Middle Fork Rio Ruidoso consists largely of these three months. Overwinter survival of young-of-year salmonids is directly related to the body size of the individual (Shuter and Post 1990). Recently emerged young-of-year fish in this study were not observed in sample collections until September and achieved positive growth throughout the fall and winter months. Jenkins (2004) determined that NEI rates of all size classes were negative beginning in October and assumed that trend continued throughout the winter. Further investigation by Jenkins (2004) revealed that many fish were maximizing their food intake (C_{max}), however, swimming costs outweighed gross energy intake. Velocity rates in this study were less than 25% of that of Jenkins (2004) which led to positive NEI rates from reduced swimming costs. This illustrates the complexity of bioenergetic assessments as stream mechanics can drastically change predicted results.

Understanding the effects of climate change on fish habitat is critical for predicting fish distribution and abundance. Studies that have incorporated physiological parameters of ectothermic animals have demonstrated that climate change is much more complex than simply an additive effect of temperature (Clark et

al. 2001; Buckley 2008). This study demonstrated that the amount of available habitat capable of supporting fish declined by as much as 12% between 15°C and 21°C, while suitable available winter habitat declined by as much as 17%. The highest recorded daily mean temperature during this study was 18.2°C, or less than 3°C of the maximum modeled temperature of 21°C. These results indicate that if all other variables remain constant then fish populations will become increasingly restricted and competition for resources will increase. It is difficult to determine how increased temperatures will affect macroinvertebrate populations; however, climate change will increase incidence and severity of drought (IPCC 2007). Therefore, it is likely that the decline in suitable habitat for salmonids modeled here is conservative as reduced velocities will result in reduced prey encounter rates.

This study also demonstrated that NEI rates declined rapidly at temperatures above 18°C. Mean NEI of available habitat at 21°C was 25-33% of NEI at 15°C for all age classes. This further demonstrated the effect climate change will have on stream salmonids by reducing growth rates and increasing stress on individuals. Results of modeled increases in winter temperatures revealed that although the amount of suitable habitat would be reduced, mean NEI of available habitat would increase. This illustrates the complexity of modeling temperature related changes to fish populations. Higher temperatures reduced the amount of suitable habitat, and while overwinter growth and survival may improve, stressful summer conditions may limit the long-term viability of the population.

Bioenergetic models can be a productive area of research because of the linkage between physical habitat characteristics and prey availability to estimate fish

growth and habitat quality. When combined with the results from Chapter 1, this study demonstrated the functional relationships that underpin microhabitat selection. For instance, fish of all size classes selected the deepest areas of pools where capture area would be maximized and swimming costs would be minimized. Although I believe the trends observed in this study were biologically relevant, there were components of the bioenergetics model that could be improved upon in future studies. Few studies have attempted to estimate activity budgets, prey size limitations, maximum rations, or swimming costs and prey drift in complex flow patterns. It is possible with further investigation of these features that bioenergetic models can be further refined to aid researchers in teasing apart complex fish-habitat relationships.

An intriguing aspect of bioenergetics models is that the process links biotic and abiotic factors into a single unit of measure which may allow comparisons of habitat quality throughout a watershed with different environmental conditions. For example, habitat quality may be compared above and below various land-use practices such as logging or grazing to determine how fish were impacted energetically. In addition, specific variables can be altered to simulate how changing land-use or management scenarios may affect fish demographics. Other areas of research could simulate modifications to flow regimes or modifications to prey drift from increased nutrient inputs.

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Chapter 3: Evidence of Seasonal Behavioral Thermoregulation of Resident Rainbow Trout in a Small Headwater Stream

Abstract

Until the development of archival temperature recorders, our understanding of thermoregulation in fish was limited by intermittent observations of fish position and current water temperature. While warming trends associated with a changing climate has focused our attention on upper thermal limits in fishes, less attention has been given to temperature selection during periods of supercooling. Behavioral thermoregulation of Rainbow Trout *Oncorhynchus mykiss* was characterized during summer and winter months using radio telemetry and archival temperature implants to compare selected water temperatures with ambient stream water temperatures. Instream data loggers placed longitudinally in the stream provided reference points for ambient stream temperatures. Despite ambient water temperatures that never exceeded the thermal tolerances of Rainbow Trout during the summer, fish were observed using localized coolwater refugia that were 3°C cooler for short durations (2-4 h). Prolonged use of coolwater refugia were on average $0.16 \pm 0.03^\circ\text{C}$ cooler than ambient stream temperatures for the warmest 18 days of the year. Supercooled water ($<0^\circ\text{C}$) occurred at four of six ambient temperature sites. Despite supercooling conditions, average daily fish temperatures were never below 0°C and occasionally fish found and selected warmwater refugia that were 3°C warmer than ambient stream temperatures. While fish selected water temperatures that were only slightly warmer than ambient (mean, 0.04°C), a small increase in temperature is all that is necessary

to escape supercooled waters. Thermal refuges within the Middle Fork Rio Ruidoso are from groundwater upwelling and highlight the importance of protecting these areas, especially in light of current climate change.

Introduction

Salmonids are coldwater fish usually found in water less than 20°C; optimal growth occurs in a narrower range and is species-dependent (Beitinger and Fitzpatrick 1979). Temperatures in streams, however, can range from below 0°C in winter to temperatures well above 25°C during the summer months. These extreme temperatures can limit the longitudinal distribution of fish (Torgersen et al. 1999), restrict seasonal migration patterns (Richter and Kolmes 2005), and fragment populations by isolating suitable thermal habitats (Rieman and McIntyre 1995). Fish are ectothermic, and because of this, their metabolic rate increases exponentially with water temperature (Elliott 1976). Prolonged exposure to suboptimal temperatures without significant amounts of energy intake can lead to mortality (Dickerson and Vinyard 1999). For instance, the critical thermal maxima (CT maxima; maximum temperature a fish experiences before losing equilibrium) in Rainbow Trout *Oncorhynchus mykiss* is between 28°C and 29.8°C (Currie et al. 1998). A higher or lower CT maxima will depend on the acclimation temperature, life history, and age of the fish (Rodgers and Griffiths 1983; Currie et al. 1998).

Less understood are the effects of chronic exposure to extremely low water temperatures on salmonids. Although relatively few laboratory studies have assessed critical thermal minima (CT minima), most studies agree that Rainbow Trout can

withstand water temperatures near 0°C and even supercooled waters (<0°C) for a short period of time (Becker et al. 1977; Currie et al. 1998; Brown et al. 1999). The freezing temperature of blood plasma in salmonids is between -0.7 and -0.9°C (Fletcher et al. 1988) resulting in freezing of fish a rare event unless trapped in ice.

Supercooled waters occur in high gradient, turbulent streams exposed to air temperatures below 0°C. When water is supercooled, small (0.1-1.0 mm) discoid or spicule shaped ice crystals (known as frazil ice) can form. Frazil ice crystals grow by attaching to one another to form aggregates. Frazil ice can also stick to any substrate or other submerged objects in the water column creating blankets of ice on stream bottoms known as anchor ice.

Supercooled water and the subsequent formation of frazil and anchor ice can have detrimental effects on salmonids. Brown et al. (1999) found that juvenile Rainbow Trout exposed to supercooled waters with frazil and anchor ice had reduced levels of plasma ions and increased plasma glucose indicating a general stress response. As stress is energetically demanding for a fish (Barton and Schreck 1987), frequent frazil and anchor ice formations during the winter affect the survival of salmonids that may already have difficulties meeting metabolic demands during the winter (Cunjak et al. 1987). Small frazil ice crystals could abrade the gills of salmonids causing hemorrhage and aggregate on the gill rakers, potentially leading to suffocation (Brown et al. 1994). Significant downstream migration of salmonids occurred with the onset of frazil and anchor ice formations in headwater streams when habitats became uninhabitable (Jakober et al. 1998; Brown et al. 2000; Simkins et al. 2000). To escape frazil and anchor ice, fish seek thermal refugia such as

groundwater upwellings or springs that are relatively warmer and preclude the formation of ice (Cunjak 1996; Power et al. 1999; Huusko et al. 2007).

Observations of relationships between stream temperatures and fish densities are often used to describe selection of thermal refugia. For example, Ebersole et al. (2001) observed Rainbow Trout near ground water upwellings during warmer portions of summer. The authors noted that not all Rainbow Trout moved into these refugia and presumed fish were utilizing other thermal refuges. Baird and Krueger (2003) used a more direct approach to measure thermal refuge use of salmonids by implanting fish with a temperature sensitive radio transmitter and compared water temperatures experienced by the fish with the ambient water temperature of the river. To relate the temperature of the fish with its location, however, observations had to be made in person making the number of observations per fish small (median, 8 observations; range, 2-22 observations). The mean distance between the locations of where fish temperatures were recorded and the locations where ambient water temperatures were recorded was also large (mean, 1.6 km; range, 0-9.6 km), and likely resulted in skewed results as water temperatures can vary longitudinally (Tague et al. 2007).

Recent technological advances have resulted in the development of archival temperature sensors that can be surgically implanted into fishes to allow researchers to obtain water temperatures directly experienced by the fish. These devices can record water temperatures at a predefined interval from months to years and have become especially popular by researchers to identify water temperatures that trigger spawning movements and migration of salmonids (Reddin et al. 2004; Goniea et al.

2006; Howell et al. 2010). The goal of this study was to characterize summer and winter behavioral thermoregulation of Rainbow Trout in a small headwater stream in south central New Mexico. I hypothesized that Rainbow Trout would display behavioral thermoregulation as ambient stream temperatures exceed thermal optimum of the species. This would be evident by selection of cooler water temperatures than ambient stream temperature during the warmest periods of the year, and selection of warmer water temperatures than ambient stream temperature during the coldest periods of the year.

Methods

Study Area

The study area was located within a 1.5 km reach between two natural fish barriers of the Middle Fork Rio Ruidoso on the Mescalero Apache Reservation in south-central New Mexico (Figure 3.1). The Middle Fork Rio Ruidoso is a second order stream originating within the Sacramento Mountains with a drainage area of approximately 7.2 km². Precipitation occurs largely as snow with peak runoff occurring in late March through April and additional precipitation in July and August in the form of large monsoonal rain events. Elevations of the study area range from 2,450 m at the lower barrier to 2,627 m at the upper barrier of the study area. The riparian community is dominated by a dense mixed conifer forest. There are no perennial tributaries within the study area and discharge measured during 2012 ranged from 0.001 m³·s⁻¹ in October to 0.013 m³·s⁻¹ in March. The Middle Fork Rio Ruidoso is characterized by a high gradient (>5%) step-pool complex with short

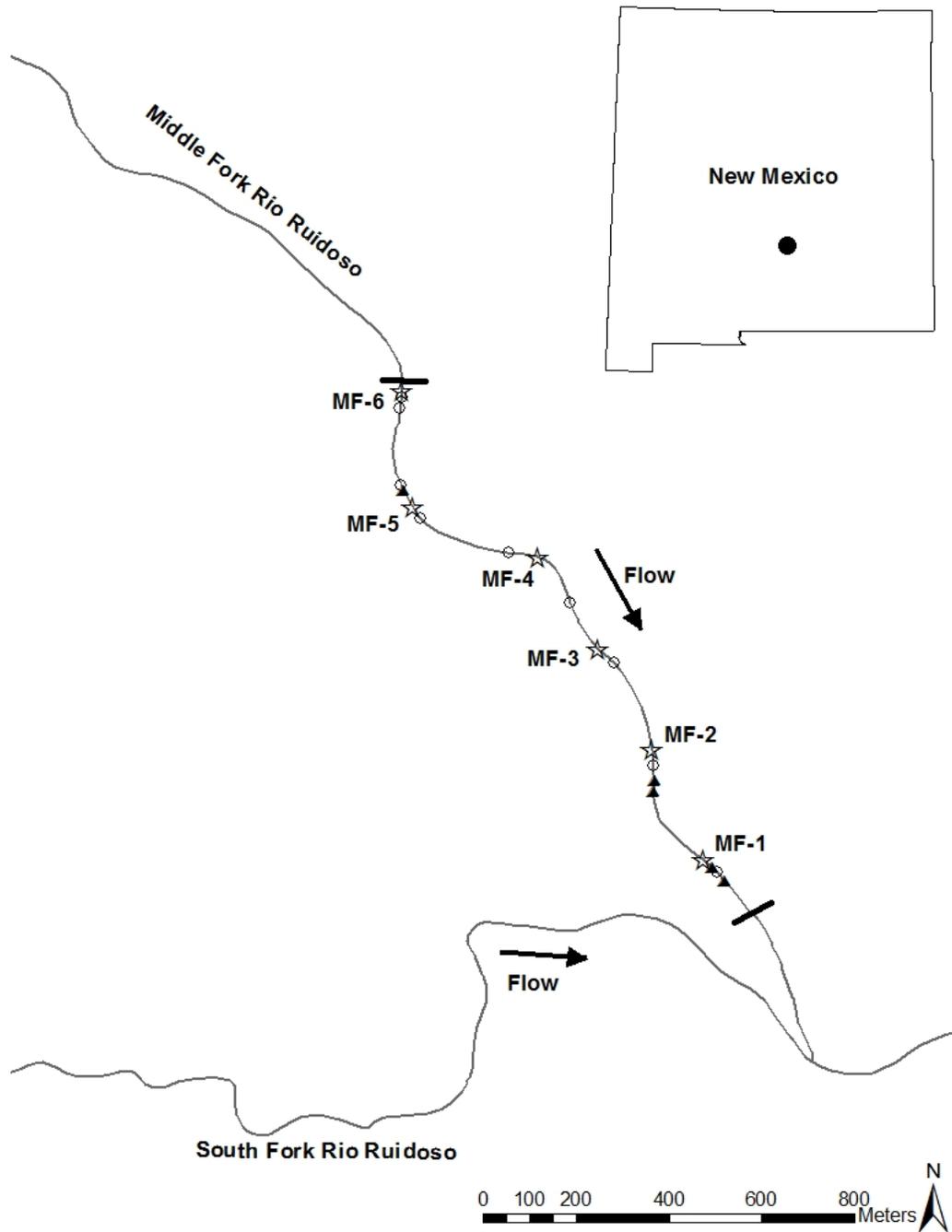


Figure 3.1. Study area illustrating the location and names of the six instream data loggers (open stars), the tagging location of five Rainbow Trout recovered during the summer (solid triangles), and the locations of the nine recovered Rainbow Trout during the winter months (open circles). The solid lines represent the upper and lower terminus of the study area of the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Inset map indicates the location of the study area within New Mexico (black dot).

riffles and runs. Stream temperatures within the study area frequently fell below 0°C during the winter and exceeded 20°C during the summer.

Rainbow Trout were the dominant species within the study area (100-200 fish·100 m⁻¹) with few Brook Trout *Salvelinus fontinalis* (<1 fish·100 m⁻¹) that periodically migrated downstream from above the upper barrier (Figure 3.1). Rainbow Trout within this section of the Middle Fork Rio Ruidoso were selected as they were the predominant species present and there was an absence of fishing pressure that could bias fish behavior. Additionally, temperatures within the study area offered an opportunity to observe microhabitat selection at a range of temperatures typically found in many western U.S. streams (i.e., <0 to >20°C).

Ambient Water Temperatures

Six instream data loggers (HOBO U22 Pro v2 Water Temperature Data Loggers; resolution ±0.02 °C, accuracy ±0.2°C; Onset Computer Corporation, Bourne, Massachusetts) were placed approximately 240 m apart longitudinally along the study reach (Figure 3.1). The first logger was randomly placed between 0 m and 240 m upstream of the start of the study segment and subsequent loggers were systematically placed every 240 m upstream of the previous logger. Instream temperature loggers were programmed to record ambient stream temperature at 1 h intervals. Before deployment, the loggers were calibrated to ensure that the loggers were within the manufacture's stated accuracy using water baths at 0°C and 25°C.

Selected Fish Temperatures

Rainbow Trout (>80 g) were captured with a Smith-Root LR-24 backpack electrofishing unit (Smith-Root, Vancouver, Washington) May 2012 and September and October 2012 for tag implantation. Upon capture, fish were anesthetized using tricaine methanesulfonate (MS-222; 80 mg/L) until loss of equilibrium, and then measured for total length (mm) and weight (g). Fish were transferred to a V-shaped surgical board where the gills were continuously flushed with anesthetic (20 mg/L) and then freshwater approximately one minute before completion of the surgery to begin the recovery process. Briefly stated, an incision approximately 10 mm long was cut into the abdominal cavity slightly to one side of the midventral line halfway between the pectoral and pelvic fins. A grooved director was then inserted into the cavity to direct the placement of the exit hole for the antenna of the radio transmitter just anterior to the pelvic girdle and about 1/3 the distance from the ventral surface to the lateral line. The body wall was then pierced with an 18-gauge hypodermic needle into the grooved director and pulled through to the original incision. The transmitter antenna was then threaded through the anterior end of the hypodermic needle and both the grooved director and hypodermic needle were removed. The antenna was then gently pulled posterior while the transmitter was simultaneously inserted into the body cavity. The incision was closed using three evenly spaced sutures with 4-0 Vicryl™ Plus Antibacterial absorbable braided monofilament suture material and a 1/2 circle tapered needle (Ethicon Inc., San Angelo, Texas). A colored floy tag was inserted into the dorsal musculature of the fish prior to being transferred to a live car in the stream. When the fish was fully recovered (approximately 0.5 h), it was

released at the initial place of capture. All instruments were sterilized in Cidex™ OPA solution (Ethicon Inc., San Angelo, Texas) between each surgery.

Prior to implantation, a VHS radio transmitter (model F1555, 216 d battery life, 1.2 g in air; Advanced Telemetry Systems, Isanti, Minnesota) was glued to an archival temperature tag capable of recording the internal body temperature of the fish every hour for 218 days (model DST nano-T, resolution ± 0.032 °C, accuracy ± 0.2 °C between -1 °C and 40 °C, 1 g in air; Star-Oddi, Gardabaer, Iceland). Due to the short battery life of the tags, it was necessary to tag one group of fish to observe summer thermoregulatory behavior and another group to observe winter thermoregulatory behavior. Total transmitter weights were no more than 3% of the body weight for all fish. While this was higher than 2% body weight recommended by Winter (1996), the author provided no empirical evidence to support the maximum of 2%. Brown et al. (1999) demonstrated that juvenile Rainbow Trout implanted with a transmitter between 6-12% of their body weight had no effect on their swimming performance. Another study by Moore et al. (1990) demonstrated tags up to 5% body weight had no effect on the growth, feeding, or swimming behavior of juvenile Atlantic Salmon *Salmo salar*. A linear regression analysis of tag percent body weight to change in body weight was used to test if tag weight had a significant effect on fish growth.

Statistical Analyses

To assess behavioral thermoregulation of Rainbow Trout, the coldest 5% (18 days) and warmest 5% (18 days) of the year were calculated from the recovered

thermal logger because this represents the most thermally challenging periods when fish are likely to seek thermal refuge. A daily mean was used for each day rather than finer temporal measurements (e.g., daily maximum, daily minimum, hourly) to indicate prolonged continuous use. Daily means were calculated from temperatures recorded between 00:00 and 11:00 during the coldest periods and between 12:00 and 23:00 during the warmest periods because these periods likely include the daily minimum and maximum, respectively, and are therefore most likely to be the periods of time when fish would seek thermal refuge (Howell et al. 2010).

The distribution of the differences between selected and ambient temperatures was normal (Shapiro-Wilk W statistic). Thus, a one-tailed paired t -test was used to compare the mean difference between mean temperatures selected by fish and mean ambient stream temperatures of the nearest paired instream data logger to the fish. A one-tailed test was used as it was hypothesized that fish would select cooler water during summer and warmer water during the winter. Significant differences indicated that fish were utilizing either a coolwater or warmwater refuge. The significance level (α) for all tests was assessed at 0.05 (Zar 1999).

Results

Ambient Stream Temperatures

Ambient stream temperatures varied considerably throughout the study. The warmest reach was MF-4 during the summer months with the highest recorded daily maximum temperature of 25.7°C and the highest average weekly maximum (AWMax) of 23.7°C (Table 3.1). Ten days had mean daily (12:00-23:00)

temperatures that exceeded 20°C. Logger MF-1 was the coolest reach during the summer months with the highest AWM_{max} of 20.7°C. Logger MF-6 was the coolest reach during the winter months with 41 days that had mean daily (00:00-11:00) temperatures below 0°C while MF-1 and MF-5 never had temperatures below 0°C (Table 3.1).

Tagging and Recapture of Fish

A total of 16 Rainbow Trout were implanted with radio transmitters and archival temperature tags May 2012. Tagged fish averaged 249 ± 6 mm (mean \pm SE) TL (range, 210 to 287 mm) and 158 ± 11 g mass (range, 110 to 261 g). Five of the tagged fish were recaptured in September and October 2012. The remaining fish were lost presumably to predation, radio tag failure, or expelling tags out of the body cavity. Of the five fish recaptured, one fish gained 6 mm length and all fish averaged -2.4 ± 13.6 g (range, -38 to 39 g) change in mass (Table 3.2). Linear regression analysis showed tag percent body weight had no significant effect on change in weight ($t = -0.36$, $df = 4$, $P = 0.74$). Two fish moved from their initial point of capture while the remainder was sedentary throughout this portion of the study. Despite moving, the nearest instream temperature logger was unchanged. Recaptured fish averaged 56 ± 11 m (range, 25 to 88 m) from the nearest instream temperature logger.

Another 14 fish were tagged in September and October 2012 with radio transmitters and archival temperature tags. Tagged fish averaged 217 ± 4 mm TL (range, 205 to 258 mm) and weighed 106 ± 4 g (range, 96 to 149 g) (Table 3.2). Of

Table 3.1. Instream data loggers (Middle Fork, MF) and corresponding highest average weekly maximum temperature (AWMax), lowest average weekly minimum temperature (AWMin), number of days when the maximum daily temperature exceeded 20°C, number of days when the daily mean (12:00-23:00) temperature exceeded 20°C, number of days when the minimum daily temperature was below 0°C, and the number of days when the minimum daily mean (00:00-11:00) temperature was below 0°C between 1 May 2012 and 28 February 2013 within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Instream data logger	AWMax (°C)	AWMin (°C)	Maximum daily temperature > 20°C	Daily mean temperature > 20°C	Minimum daily temperature < 0°C	Daily mean temperature < 0°C
MF-1	20.7	0.06	9	0	0	0
MF-2	22.0	-0.02	22	0	32	1
MF-3	21.4	-0.02	29	0	27	8
MF-4	23.7	0.01	48	10	8	0
MF-5	21.8	0.04	37	0	0	0
MF-6	21.0	-0.03	19	0	63	41

Table 3.2. Details for Rainbow Trout implanted and recaptured with radio transmitters and archival temperature tags in the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. The % BW column represents the percent body weight of the total tag weight to fish weight. Changes in total length (mm) and weight (g) are reflected by delta (Δ). Movement distance represents the distance the fish moved from its point of initial capture to when the fish was recovered.

Season	Fish	Sex	Initial capture			After recapture		Movement (m)	Distance to nearest instream logger (m)
			Length (mm)	Weight (g)	% BW	Δ Length (mm)	Δ Weight (g)		
Summer	1	F	287	181	1.3	0	+39	0	66
	2	M	221	121	2.0	+6	+17	70	41
	3	M	210	118	2.0	0	-12	0	88
	4	F	228	110	2.2	0	-18	0	60
	5	M	253	172	1.4	0	-38	63	25
Winter	6	M	258	149	1.6	0	+2	0	41
	7	M	209	97	2.5	0	+1	0	109
	8	M	230	120	2.0	+8	-7	0	54
	9	F	210	98	2.4	+5	+1	0	27
	10	F	212	102	2.4	-	-	0	51
	11	M	211	102	2.4	0	-8	0	45
	12	F	210	96	2.5	0	-7	0	36
	13	M	213	105	2.3	+2	+1	0	33
	14	F	220	103	2.3	+1	-1	0	18

“-“ indicates fish was not recaptured but data from recovered tag was used until the date last observed to be alive

the 14 tagged fish, 11 were recaptured in March 2013 to assess winter thermoregulation. Two of the archival temperature tags were corrupted and not included in subsequent analyses. One fish was observed alive with tags inside the fish in early February 2013 but in March 2013, the archival temperature tag was found on the side of the stream near the last sighting. Data retrieved from this device were included in the analysis up to the date the fish was last observed alive. Of the eight fish recaptured and used in the analysis, fish gained an average of 2.0 ± 1.1 mm (range, 0 to 8 mm) of growth and averaged -2.3 ± 1.5 g (range, -8 to 2 g) change in mass. Linear regression analysis revealed that tag percent body weight had no significant effect on change in body weight during the study ($t = -0.47$, $df = 8$, $P = 0.66$). All fish were recaptured near the point of initial capture and averaged a distance of 46 ± 8 m (range, 18-109 m) from the nearest instream temperature logger.

Behavioral Thermoregulation

During the summer, fish made periodic (2-4 h) use of refugia throughout the day that were cooler than the ambient stream temperature by at least 0.5°C . Of the 216 hourly observations (12:00-23:00) for each fish on the warmest 18 days, an average of $17 \pm 4.3\%$ (range, 2-25%) of observed fish temperatures were cooler than the ambient stream temperature by at least 0.5°C . Deviations of greater than 1.0°C were observed for $6 \pm 2.7\%$ (range, 0-15%) of observations obtained for each fish. One fish periodically selected temperatures where prolonged use of coolwater refugia (daily means, 12:00-23:00) was much less than other fish (Figure 3.2). When that fish was included in analysis, fish selected temperatures that were an average of

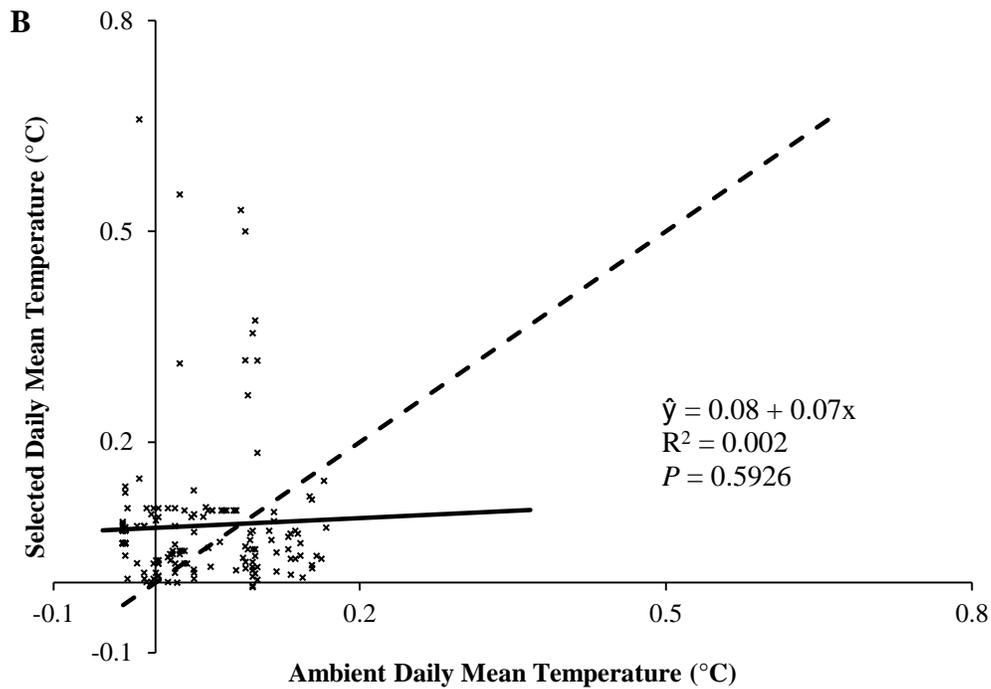
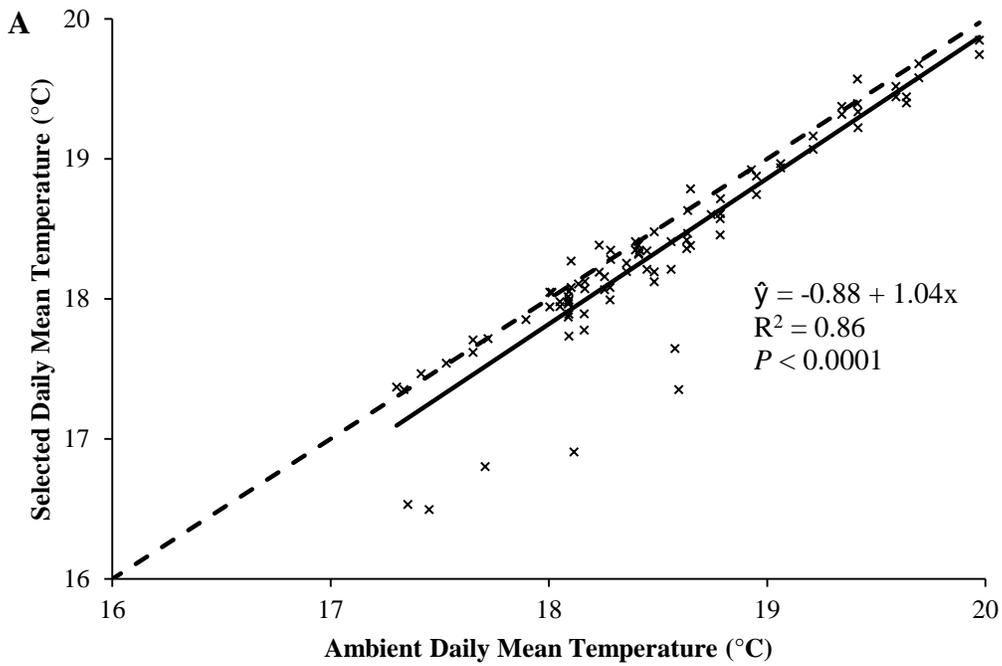


Figure 3.2. Relationship between ambient daily mean stream temperature and the daily mean water temperature selected by the fish (solid line) for the warmest 18 days of summer (A) and coolest 18 days of winter (B) within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. The dashed line represents a hypothetical 1:1 relationship where selected water temperatures are equal to the ambient stream temperature.

-0.16 ± 0.03°C cooler than ambient temperatures of the warmest 18 days (one-tailed paired *t*-test, *t* = -5.85, d.f. = 89, *P* < 0.0001; Figure 3.2). Removal of that fish from analysis revealed that fish were still selecting temperatures -0.11 ± 0.01°C cooler than ambient stream temperatures (one-tailed paired *t*-test, *t* = -7.71, d.f. = 71, *P* < 0.0001).

Archival temperature loggers recovered from fish during the winter months revealed that of the 216 hourly observations (0:00-11:00) made for each fish for the coolest 18 days, 2 ± 0.9% (range, 0-8%) of the fish observations were at least 0.5°C warmer than the ambient stream temperature while less than 1% deviated by at least 1.0°C. Fish occasionally selected water temperatures that were as much as 3°C warmer than the ambient stream temperature for short periods (usually less than 4 h) throughout the winter months. Overall, fish selected water temperatures with mean daily temperatures that were significantly warmer (0.04 ± 0.01°C) than the mean daily ambient stream temperature during the coolest 18 days of the year (one-tailed paired *t*-test, *t* = 4.51, d.f. = 161, *P* < 0.0001; Figure 3.2). Additionally, no fish selected supercooled water when the ambient stream temperature was supercooled indicating fish were avoiding such temperatures (Figure 3.2).

Discussion

Within a small headwater stream, Rainbow Trout demonstrated short term behavioral thermoregulation during the warmest and coolest periods of the year. Although summer water temperatures never approached CT maxima for Rainbow Trout (>28°C) and rarely approached the upper incipient lethal limit (26.0°C, 7 d; Bear et al. 2007), fish were still observed spending nearly 25% of their time in

temperatures that were at least 0.5°C cooler than the ambient stream temperature. Throughout the summer months, fish frequently moved between coolwater refugia and ambient stream temperatures throughout the day with fish occasionally occupying areas that were 3°C cooler than the ambient temperatures. Fish were periodically observed moving into the main channel to make feeding forays before returning to coolwater refugia. Similar behavior was observed by Baird and Krueger (2003) for stream dwelling Brook Trout moving to and from coolwater areas. The authors suggested that feeding opportunities were limited in coolwater areas, and the majority of feeding forays were in the warmer main river flow. Brett (1971) found that juvenile Sockeye Salmon *O. nerka* fed in the epilimnion of lakes where consumption rates were maximized before returning to the cooler hypolimnion to maximize food conversion efficiency and minimize maintenance metabolism. As demonstrated in Chapter 2, changing temperature affected net energy intake (NEI) of available habitat. Mean NEI of Rainbow Trout decreased rapidly at temperatures above 18°C which supports the benefit of thermoregulating. Based on the relationship of standard metabolic rate to temperature, a 150 g Rainbow Trout moving from 20°C to 19°C water would result in a 6.6% decrease in standard metabolism while a 2°C decrease to 18°C would result in a 12.8% reduction in standard metabolism (see Chapter 2).

Rainbow trout exhibited some evidence of behavioral thermoregulation, albeit minimally, during the winter months. While mean differences between fish and stream temperatures were small (0.04°C), it is important to note that only a small increase in temperature (<0.1°C) is needed for fish to escape supercooled waters. Observations of mean daily ambient temperatures less than 0°C revealed fish were

not selecting temperatures less than 0°C indicating that fish were finding warm water refugia. Rainbow trout frequently selected temperatures that were less than 0.5°C warmer than ambient stream temperatures, however, fish were rarely observed selecting temperatures greater than 0.5°C. Fish occasionally selected temperatures that were 2°C warmer than ambient temperatures for several hours at a time indicating that fish actively sought out thermal refugia that were warmer but may have rarely chosen to do so. Cunjak (1996) observed that Brook Trout typically held positions very close to sources of groundwater while Brown Trout *Salmo trutta* aggregated downstream of the point source where temperatures have cooled but still remained above freezing. He suggested that Brown Trout may not be adapted physiologically to effectively utilize warmer water as well as Brook Trout during the winter and distancing themselves from the groundwater source may preclude ice formation while still minimizing metabolic costs. Metabolic demands increase exponentially as temperature increases, therefore fish selecting warmer temperatures must compensate with increased food intake. If an abundant supply of food is available it may be beneficial for fish to select warmer habitats to take advantage of increased growth rates from higher consumption rates and better conversion efficiency (see Chapter 2). Presumably, the fish used warmer temperatures during feeding forays before returning to thermal refugia.

Thermal refugia were likely created by groundwater discharge occurring throughout the study area. Tributaries to the study area of the Middle Fork Rio Ruidoso were ephemeral with flows only occurring for short periods after snowmelt and substantial rainfall resulting in insignificant effects. Thermal refugia from

groundwater discharge often deviate from ambient stream temperatures by more than 5°C (Cunjak 1996). The effect of groundwater discharge from the hyporheic zone has been well documented in aquatic macroinvertebrates and spawning areas of stream salmonids (see Boulton and Hancock 2006 for review). Additionally, young-of-year salmonids have even been observed burrowing and moving through interstitial spaces of coarse substrates during the winter to take advantage of the warmer groundwater exchanged through the hyporheic zone (Erkinaro et al. 1994; Meyer and Griffith 1997). Larger individuals that are unable to fit into these spaces are often observed congregating in areas near an upwelling (Power et al. 1999). It is likely that Rainbow Trout within the Rio Ruidoso were able to thermoregulate by locating these groundwater sources. The size and proximity of the source, however, likely determined the degree that each fish observed in this study could deviate from ambient temperatures. For instance, one fish during the summer months periodically selected mean daily temperatures that were much less than any other fish (Figure 3.2). During the winter, several fish periodically selected much warmer mean daily temperatures than other fish (Figure 3.2).

While fish tagged in this study were among the smallest reported in thermoregulation studies, limitations due to tag size and weight precluded the use of smaller fish (<200 mm) that exhibit different patterns of microhabitat use and energetic requirements (see Chapters 1 and 2). Cunjak and Power (1986) noted young Brook Trout typically preferred to position themselves closer to sources of groundwater than older individuals. Smaller fish have reduced metabolic demands and could potentially meet those demands compared to larger fish. With time,

advancement in engineering of smaller and lighter tags could result in a better understanding of behavioral thermoregulation of smaller fish.

Interpretation of the statistical results from this study should be done cautiously due to the small number of fish observed, autocorrelation, and a lack of independence between observations. Further, some fish may have had access to more prominent thermal refugia or may have been excluded from using thermal refugia by more dominant fish. However, the pattern of selection for cooler temperatures during the summer and warmer temperatures during the winter by Rainbow Trout was repeated over multiple fish.

While studies have documented thermoregulation of salmonids during the summer months, few studies have described temperature selection during the winter months. Some studies have found large downstream movements of salmonids with the onset of anchor ice (e.g., Jakober et al. 1998; Brown et al. 2000; Simkins et al. 2000) while other studies observed fish remained sedentary, presumably because appropriate overwinter conditions existed (Huusko et al. 2007). As evidenced in Chapter 2, conditions within the study area were favorable for high overwinter survival. Studies that provided evidence of salmonids selecting warmwater winter refuges were achieved through visual observations of fish congregating in areas of warmwater inputs (e.g., groundwater upwelling, springs). For instance, Cunjak and Power (1986) observed large numbers of Brook and Brown Trout near ground water upwelling while Swales et al. (1986) observed juvenile Coho Salmon *O. kisutch* preferred to overwinter in side channels where groundwater maintained warmer water temperatures. While these studies provided anecdotal evidence of thermoregulation

in salmonids, they are merely “snapshots”. Fish in this study varied their thermoregulatory behavior considerably within a day and among days; thus, much of the information would have been lost by observing fish only several times throughout the winter. Future studies should focus on using archival temperature loggers to assess use of thermal refugia and integrate the information with bioenergetics to better understand when and why fish move in and out of refuge areas and how these patterns explain energetic benefits to the fish.

Summer temperatures within the Rio Ruidoso remained surprisingly cool despite its southern geography and low discharge. During the study, the southwest was experiencing one of the worst droughts on record

(<http://www.droughtmonitor.unl.edu/archive.html>, accessioned August 5, 2012).

Thermal refugia will become increasingly important within the watershed in light of potential further increases in temperatures resulting from climate change. The effects of climate change on stream temperatures within the Rio Ruidoso cannot be known with certainty; however, studies have shown correlations of recent increases in air temperatures resulting in increases in stream temperatures throughout the U.S. (Isaak et al. 2012; Zeigler et al. 2012). Considering Rio Ruidoso stream temperatures are already approaching the upper incipient lethal limits of Rainbow Trout there is little margin for human induced (e.g., removal of riparian vegetation, fire) increases in temperature and protection of coolwater refugia will be even more important.

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APPENDICES

APPENDIX A
SUBSTRATE DATA

Table A.1. Substrate type use and availability (%) for young-of-year (YOY), juvenile, and adult Rainbow Trout for each season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Season		Substrate type					
		Silt	Sand	Gravel	Pebble	Cobble	Boulder
Winter	Available	31.5	15.0	8.6	2.5	20.4	22.0
	Observed use						
	YOY	63.5	22.2	4.8	0.0	6.3	3.2
	Juvenile	53.3	24.0	5.7	0.4	6.6	10.0
	Adult	53.5	28.2	1.4	0.0	7.0	9.9
Spring	Available	38.8	10.2	9.0	3.3	14.8	23.9
	Observed use						
	YOY	44.9	17.8	10.2	0.0	9.3	17.8
	Juvenile	65.3	9.3	10.0	0.0	3.6	11.8
	Adult	50.6	14.4	12.6	0.6	1.7	20.1
Summer	Available	43.9	11.5	6.8	2.1	15.6	20.1
	Observed use						
	YOY	64.1	22.6	3.8	0.0	3.8	5.7
	Juvenile	62.1	13.4	6.5	0.0	6.0	12.0
	Adult	72.9	10.5	6.1	0.0	4.4	6.1
Fall	Available	56.8	4.9	7.1	2.1	8.5	20.6
	Observed use						
	YOY	74.5	3.2	6.4	0.0	2.1	13.8
	Juvenile	81.7	4.0	2.4	0.8	4.8	6.3
	Adult	73.9	6.1	1.7	0.0	3.5	14.8

APPENDIX B
LOGISTIC REGRESSION MODELS

Table B.1. All logistic regression models with Akaike information criterion corrected for small sample sizes (AIC_c) for young-of-year, juvenile, and adult Rainbow Trout microhabitat selection during the winter season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Microhabitat variables included in the models are total depth (TD), focal velocity (FV), and cover distance (CD). ΔAIC_c is the difference in AIC_c between the considered model and the best model, K is the number of parameters included in the model, and w_i is the Akaike weight. Models in bold were considered competing models and were used in the final model.

Age class	Model	AIC_c	ΔAIC_c	K	Log likelihood	w_i
Young-of-year	TD, FV, CD	157.08	0	4	-74.5	0.91
	TD, CD	161.95	4.87	3	-77.9	0.08
	TD, FV	167.34	10.26	3	-80.6	0.00
	TD	173.86	16.78	2	-84.9	0.00
	FV, CD	222.69	65.61	3	-108.3	0.00
	FV	253.27	96.19	2	-124.6	0.00
	CD	282.53	125.45	2	-173.3	0.00
Juvenile	TD, FV, CD	367.11	0	4	-179.5	0.99
	TD, CD	376.17	9.06	3	-185.1	0.01
	TD, FV	395.22	28.11	3	-194.6	0.00
	TD	408.52	41.41	2	-202.3	0.00
	FV, CD	582.95	215.84	3	-288.5	0.00
	FV	608.43	241.32	2	-302.2	0.00
	CD	705.18	338.07	2	-350.6	0.00
Adult	TD, FV, CD	241.79	0	4	-116.8	1.00
	TD, FV	252.52	10.73	3	-123.2	0.00
	TD, CD	257.86	16.07	3	-125.9	0.00
	TD	271.12	29.33	2	-133.5	0.00
	FV, CD	278.83	37.04	3	-136.4	0.00
	FV	296.08	54.29	2	-146.0	0.00
	CD	338.93	97.14	2	-167.4	0.00

Table B.2. All logistic regression models with Akaike information criterion corrected for small sample sizes (AIC_c) for young-of-year, juvenile, and adult Rainbow Trout microhabitat selection during the spring season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Microhabitat variables included in the models are total depth (TD), focal velocity (FV), and cover distance (CD). ΔAIC_c is the difference in AIC_c between the considered model and the best model, K is the number of parameters included in the model, and w_i is the Akaike weight. Models in bold were considered competing models and were used in the final model.

Age class	Model	AIC_c	ΔAIC_c	K	Log likelihood	w_i
Young-of-year	TD, FV, CD	328.60	0	4	-160.2	0.50
	TD, FV	329.35	0.75	3	-161.6	0.34
	TD, CD	331.99	3.39	3	-163.0	0.09
	TD	332.47	3.87	2	-164.2	0.07
	FV	407.74	79.14	2	-201.9	0.00
	FV, CD	408.74	80.14	3	-201.3	0.00
	CD	456.67	128.07	2	-226.3	0.00
Juvenile	TD, FV, CD	399.45	0	4	-195.7	1.00
	TD, FV	413.41	13.96	3	-203.7	0.00
	TD, CD	414.35	14.90	3	-204.2	0.00
	TD	427.70	28.25	2	-211.8	0.00
	FV, CD	586.32	186.87	3	-290.1	0.00
	FV	595.63	196.18	2	-295.8	0.00
	CD	709.50	310.05	2	-352.7	0.00
Adult	TD, FV	303.82	0	3	-148.9	0.32
	TD	304.11	0.29	2	-150.0	0.28
	TD, FV, CD	304.64	0.82	4	-148.3	0.21
	TD, CD	304.91	1.09	3	-149.4	0.19
	FV, CD	493.61	189.79	3	-243.9	0.00
	FV	497.27	193.45	2	-246.6	0.00
	CD	561.95	258.13	2	-279.0	0.00

Table B.3. All logistic regression models with Akaike information criterion corrected for small sample sizes (AIC_c) for young-of-year, juvenile, and adult Rainbow Trout microhabitat selection during the summer season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Microhabitat variables included in the models are total depth (TD), focal velocity (FV), and cover distance (CD). ΔAIC_c is the difference in AIC_c between the considered model and the best model, K is the number of parameters included in the model, and w_i is the Akaike weight. Models in bold were considered competing models and were used in the final model.

Age class	Model	AIC_c	ΔAIC_c	K	Log likelihood	w_i
Young-of-year	TD, FV	85.69	0	3	-39.8	0.35
	TD	85.90	0.21	2	-40.9	0.31
	TD, FV, CD	86.97	1.28	4	-39.3	0.18
	TD, CD	87.35	1.66	3	-40.6	0.15
	FV, CD	155.71	70.02	3	-74.8	0.00
	FV	160.27	74.58	2	-78.1	0.00
	CD	187.45	101.76	2	-91.7	0.00
Juvenile	TD, FV	209.02	0	3	-101.5	0.53
	TD, FV, CD	209.35	0.33	4	-100.6	0.45
	TD	216.37	7.35	2	-106.2	0.01
	TD, CD	217.19	8.17	3	-105.6	0.01
	FV	306.00	96.98	2	-151.0	0.00
	FV, CD	306.41	97.39	3	-150.2	0.00
	CD	374.45	165.43	2	-185.2	0.00
Adult	TD	140.20	0	2	-68.1	0.37
	TD, FV	140.41	0.21	3	-67.1	0.33
	TD, TD, CD	141.93	1.73	4	-66.9	0.15
	TD, CD	141.95	1.75	3	-67.9	0.15
	FV	231.97	91.77	2	-114.0	0.00
	FV, CD	233.20	93.00	3	-113.5	0.00
	CD	282.57	142.37	2	-139.3	0.00

Table B.4. All logistic regression models with Akaike information criterion corrected for small sample sizes (AIC_c) for young-of-year, juvenile, and adult Rainbow Trout microhabitat selection during the fall season within the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico. Microhabitat variables included in the models are total depth (TD), focal velocity (FV), and cover distance (CD). ΔAIC_c is the difference in AIC_c between the considered model and the best model, K is the number of parameters included in the model, and w_i is the Akaike weight. Models in bold were considered competing models and were used in the final model.

Age class	Model	AIC_c	ΔAIC_c	K	Log likelihood	w_i
Young-of-year	TD, CD	146.30	0	3	-70.1	0.38
	TD, FV, CD	146.66	0.36	4	-69.2	0.31
	TD	147.90	1.60	2	-71.9	0.17
	TD, FV	148.24	1.94	3	-71.1	0.14
	FV, CD	256.68	110.38	3	-125.3	0.00
	FV	263.07	116.77	2	-129.5	0.00
	CD	316.57	170.27	2	-156.3	0.00
Juvenile	TD	113.23	0	2	-54.6	0.53
	TD, CD	115.06	1.83	3	-54.5	0.21
	TD, FV	115.27	2.04	3	-54.6	0.19
	TD, FV, CD	117.12	3.89	4	-54.5	0.07
	FV	309.42	196.19	2	-152.7	0.00
	FV, CD	311.24	198.01	3	-152.6	0.00
	CD	379.00	265.77	2	-187.5	0.00
Adult	TD, CD	173.19	0	3	-83.5	0.40
	TD	173.77	0.58	2	-84.9	0.30
	TD, FV, CD	174.83	1.64	4	-83.3	0.18
	TD, FV	175.54	2.35	3	-84.7	0.12
	FV, CD	316.95	143.76	3	-155.4	0.00
	FV	317.77	144.58	2	-156.9	0.00
	CD	359.05	185.86	2	-177.5	0.00

APPENDIX C

EQUATION FOR MAXIMUM GROWTH RATION

Table C.1. Estimates of food required for maximum rations using the equation $D = aW^{b_1}e^{b_2T}$ (Elliott 1976), where maximum food ration (D) is $\text{mg} \cdot \text{day}^{-1}$, W is fish weight (g), T is temperature ($^{\circ}\text{C}$), and values of a , b_1 , and b_2 are constants given here depending on temperature range.

Temperature ($^{\circ}\text{C}$)	a	b_1	b_2
<6.6	2.902	0.762	0.418
6.6-13.3	15.018	0.759	0.171
13.3-17.8	26.433	0.767	0.126
17.8-21.7	3.241×10^7	0.753	-0.662

APPENDIX D

MACROINVERTEBRATE DRIFT DATA

Table D.1. Monthly counts of macroinvertebrates, separated by order and life stage, collected from drift samples from all three reaches of the Middle Fork Rio Ruidoso, Mescalero Apache Reservation, New Mexico.

Order	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Total
Ephemeroptera													
Larvae	0	0	0	0	4	10	4	0	-	13	14	1	46
Adult	14	8	10	42	17	5	7	3	-	26	6	50	188
Plecoptera													
Larvae	5	1	4	14	5	5	9	3	-	1	3	0	50
Adult	0	0	8	0	0	8	5	1	-	3	3	0	28
Trichoptera													
Larvae	20	25	30	54	27	28	24	13	-	29	20	11	281
Adult	0	0	0	1	0	0	2	0	-	0	0	0	3
Diptera													
Chironomidae (larvae & pupae)	46	29	66	193	23	46	75	7	-	8	8	3	504
Other larvae & pupae	39	11	11	19	14	6	23	3	-	12	4	2	144
Adult	44	10	38	133	189	185	165	24	-	271	109	35	1,203
Coleoptera	3	4	1	15	14	19	84	12	-	126	27	33	338
Hymenoptera	0	0	1	5	28	48	20	15	-	244	109	33	503
Orthoptera	0	0	1	3	6	8	6	1	-	12	18	50	105
Hemiptera	59	20	11	14	62	94	82	117	-	205	314	73	1,051
Other (acariformes, collembola, aranea, lepidoptera, odonata)	15	9	11	62	45	32	8	20	-	25	4	9	240
Total	245	117	192	555	434	494	514	219	-	975	639	300	4,684

“-“ indicates no data collected due to high turbidity