DIEL SUMMER HABITAT USE BY BULL TROUT, *Salvelinus confluentus,*

IN EASTERN CASCADES STREAMS

by

NOLAN PAUL BANISH

Under the Direction of James T. Peterson

ABSTRACT

Diel habitat use by bull trout was assessed at the micro- and mesohabitat scale in Eastern Cascades streams during the summers of 2001 and 2002. Most bull trout observations occurred at night. Bull trout exhibited an affinity for the streambed, suggesting benthic behavior. Bull trout were found in deep, low velocity microhabitats with small substrata during the day and night. However, small bull trout were found shallower than were large and adult bull trout. Bull trout often were located in pool mesohabitats formed by large woody debris. Logistic regression models indicated bull trout distributions were influenced by microhabitat, mesohabitat, and stream-level variables. Bull trout distribution was positively related to stream depth, fine substratum, and pool mesohabitats, but negatively related to current velocity, rubble substratum, stream temperature, and the presence of brook trout. Successful management of bull trout might be best applied at a mesohabitat level to preserve summer rearing areas.

INDEX WORDS: Bull trout, *Salvelinus confluentus*, Microhabitat, Mesohabitat, Logistic Regression, Principal Component Analysis, Akaike Information Criteria

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DEDICATION

To my father, G. Jeffrey Banish, for instilling me with a passion for the out-of-doors, and to my mother, Janis M. Bond, and stepfather, Charles T. Bond, for unwavering love and encouragement while I pursued my goals.

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CHAPTER 1

INTRODUCTION

Bull trout *Salvelinus confluentus* are vulnerable to local extinction throughout their range (Rieman et al. 1997). Historically, bull trout were distributed latitudinally from the Oregon-California border (41° N) north to the Yukon River drainage (61° N) and longitudinally from northwestern British Columbia (133° W) east to Alberta and Montana (114° W; Cavender 1978; Haas and McPhail 1991). The current distribution of bull trout has been reduced to less than half of their former range with much of that loss occurring throughout their southern extent (Rieman et al. 1997). Anthropogenic activities have caused much of the decline in bull trout distributions (Rieman and McIntyre 1993; Rieman et al. 1997). Habitat loss and fragmentation have greatly reduced bull trout populations (Rieman and McIntyre 1995). Logging and road construction, mining, agricultural practices, and urbanization have degraded watersheds, while irrigation and hydroelectric dams or water diversions have reduced the quantity and quality of bull trout habitats (Dunham and Rieman 1999). Genetic introgression, associated with the introduction and establishment of exotic species, such as brook trout *S. fontinalis*, also have negatively affected bull trout distributions (Thurow et al. 1997; Rieman and Allendorf 2001). The subsequent population decline has led to the listing of bull trout as a threatened species under the Endangered Species Act (Office of the Federal Register 63[June 10, 1998]: 31647).

Recognizing and understanding how fishes and habitat interact is paramount for management of stream-dwelling fishes (Lobb and Orth 1991; Orth and White 1993; Grossman and Ratajczak 1998; Peterson and Rabeni 2001). Successful management of stream-dwelling fishes requires knowledge of fish-habitat relationships at several spatial scales to determine where conservation or restoration efforts might best be most effective (Rabeni and Sowa 1996). Studying habitat use at fine (i.e., microhabitat) spatial scales provides information about fish affinities for characteristics such as depth and substratum at a specific point within the stream (LaCroix et al. 1995; Petty and Grossman 1996). Microhabitat studies also have discovered seasonal (Baltz et al. 1991) and diel (Bonneau and Scarnecchia 1998) variations in habitat use, which are important to understanding the life history requirements of fishes.

At larger spatial scales, channel units (henceforth, mesohabitats) are relatively discrete habitats with characteristic current velocities, depths, and substrata (Frissell et al. 1986). Fishes are known to associate with mesohabitats (e.g., pools, riffles) during different life history stages or at different times of the year. For example, stream margins provide important rearing habitat for juvenile cutthroat trout because of their reduced current velocities (Moore and Gregory 1988). Deep pools with low current velocity and large substrata provide critical overwintering habitats for salmonids by reducing energy expenditure (Cunjak and Power 1986; Thurow 1997; Muhlfeld et al. 2001). As well, mesohabitat characteristics influence the distribution of different fish guilds (Lobb and Orth 1991) and fish assemblages (Peterson and Rabeni 2001). Mesohabitat characteristics are directly influenced by interactions between hydraulic processes and the surrounding landscape (Leopold et al. 1964; Frissell et al. 1986). Thus, it may be possible to predict how changes in the landscape affect stream habitats and, in turn, fish populations.

Conservation and restoration of bull trout requires identifying and conserving habitats necessary for the persistence of the species. Successful protection of these habitats can only be accomplished if managers have an understanding of the specific habitats used by bull trout. Moreover, managers must focus on diel and spatial variation of habitat use to be effective (Kershner et al. 1991). Therefore, the objectives of my study were to (1) identify diel micro- and mesohabitat use by stream-dwelling bull trout, and (2) compare diel micro- and mesohabitat use by different size classes of stream-dwelling bull trout.

CHAPTER 2

LITERATURE REVIEW

Bull Trout Life History

Bull trout populations have two distinct life history forms: resident and migratory. Both resident and migratory bull trout spawn in small headwater (second to fourth order) streams, typically from August through November (Rieman and McIntyre 1993). Bull trout spawning occurs in low gradient areas that contain loose, clean gravel (Fraley and Shepard 1989). Females create a nest, or redd, in which eggs are deposited and fertilized. Redds are often made in stream sections near springs or other inputs of groundwater (Rieman and McIntyre 1996). Because groundwater is typically warmer than surface water (i.e., runoff) during the winter, egg survival is generally higher for redds located near an upwelling (Baxter and McPhail 1999). Eggs incubate over the winter and hatch between early April and May (Meehan and Bjornn 1991). Growth differs little between forms during their first two years of life in headwater streams, but diverges as migratory fish move into larger, more productive waters where their growth is greater (Rieman and McIntyre 1993).

Resident forms of bull trout complete their life history in headwater streams (Rieman and McIntyre 1993). Migratory forms live in headwater streams for 1-3 years during their juvenile life stage before migrating downstream to a larger river (fluvial) or lake (adfluvial; Rieman and McIntyre 1993; Saffel and Scarnecchia 1995). Migratory bull trout generally remain in downstream areas for 2-4 years before maturing and returning to their natal stream to spawn (Fraley and Shepard 1989; Rieman and McIntyre 1996). Both life history forms of bull trout are considered adults when they become sexually mature at 5-7 years of age (Rieman and McIntyre 1993). Resident adults range from 150-300 mm total length, whereas adult migratory fish commonly exceed 600 mm (Rieman and McIntyre 1993). Thus, bull trout that measure over 300 mm in total length are regarded as migratory (Rieman and McIntyre 1993). Although resident and migratory forms inhabit different areas during development, both require quality spawning and juvenile rearing habitat in smaller, headwater streams (Rieman and McIntyre 1993).

Anthropogenic Influences on Bull Trout Populations

Various anthropogenic activities, such as logging, mining, and agriculture can affect stream habitat (Meehan 1991). Logging, particularly in riparian zones, can cause vegetative and hydrologic changes that alters stream channel form (Hauer et al. 1999). Logging of riparian zones can reduce the shading of a stream, causing high temperature fluctuations (Meehan 1991). Logging activities often require the construction of roads to provide vehicular and equipment access to remote areas. Roads can increase erosion, alter stream channel morphology, change flow regimes, and increase human access (Trombulak and Frissell 2000), adversely affecting bull trout populations (Baxter et al. 1999). Road construction also contributes to sediment loading in streams (Trombulak and Frissell 2000), resulting in an increase of fine soil particles that can cover spawning substrata for bull trout (Fraley and Shepard 1989).

Mining activities can degrade the aquatic habitat by altering hydrochemistry, changing stream morphology and flow, and by introducing sediments (Quigley and Arbelbide 1997). Platts and Martin (1978) suggest that mining causes fish to become stressed above natural levels resulting in population instability. Exposure to acid mine drainage can cause reduced growth rates, reproductive failure, or mortality (Haines 1981; Hansen et al. 2002) that may lead to declines in salmonid populations (Nelson 1982).

Agricultural practices, such as farming and grazing, affect bull trout habitats and other aquatic resources because they are often located on historic flood plains and stream valley bottoms (Quigley and Arbelbide 1997). Grazing alters the streamside riparian vegetation and compacts soil surfaces, increasing groundwater runoff, lowering streambank stability, and reducing fish cover (Platts 1991). Platts (1991) noted that grazing activity may alter riparian areas via channel widening, channel aggrading, or lowering of the water table.

Water diversions and impoundments alter habitat by transforming lotic systems into lentic systems. Dams and irrigation diversion barriers can decrease or fragment bull trout habitat by restricting immigration or emigration (Dunham and Rieman 1999; Neraas and Spruell 2001). Migratory life history forms are particularly susceptible to barriers because they prevent access to spawning, rearing, and overwintering areas. Barriers also reduce the gene flow among local subpopulations, isolating bull trout populations and restricting naturally occurring gene flow (Neraas and Spruell 2001; Rieman and Allendorf 2001). Water diversion and impoundment also can raise stream temperatures (Petts 1984), which may be detrimental to thermally sensitive bull trout (Selong et al. 2001).

Stream discharge and the frequency and timing of both low and high flows are important to interannual variation in reproductive success and early survival of bull trout (Rieman and McIntyre 1996). High flows during the winter incubation period can influence survival of bull trout by increasing bedload scour where eggs remain concealed (Rieman and McIntyre 1996). Fluvial and adfluvial bull trout migrate upstream to spawning grounds in stream tributaries in response to temperature and stream discharge (Swanberg 1997). Similarly, resident bull trout move in response to decreasing water temperatures (Swanberg 1997; Bonneau and Scarnecchia 1998; Jakober et al. 1998). Reduced temperatures, and subsequent formation of stream ice, led to the movement of resident bull trout to more suitable overwinter habitats, such as deep pools associated with large woody debris (Jakober et al. 1998).

Conservation and restoration of bull trout will require protecting remaining populations and their habitats. The majority of watersheds occupied by bull trout are predominately managed by Federal agencies, such as the U.S. Forest Service, the National Park Service, and the Bureau of Land Management (Quigley and Arbelbide 1997). Currently, Federal law requires public lands to be managed for multiple purposes, including mining, logging, ranching, and recreation (Ferson and Burgman 2000). Thus, the future management of bull trout and their habitats must be balanced within the context of a multiple land-use approach. As such, it will be increasingly important for management agencies to identify habitats important to the survival of bull trout and incorporate this knowledge into conservation and restoration strategies. Towards this end, this project will develop a greater understanding of the habitat requirements of bull trout in Eastern Cascades streams.

CHAPTER 3

METHODS

Study Sites

I studied diel habitat use of stream-dwelling bull trout in ten streams east of the Cascade Range in Washington and Oregon during the summers of 2001 and 2002 (Figure 1). During 2001, I sampled an eleventh stream, Canyon Creek, but I dropped this site from analysis because Leary and Allendorf (1997) found that it contained a morphologically similar, but behaviorally different congener, Dolly Varden *S. malma*. I chose streams based on the Washington Department of Fish and Wildlife (WDFW) Stream Net database (Paul Mongillo, WDFW, personal communication). I observed diel bull trout habitat use from July to September when water levels had receded from spring and summer snowmelt and visibility was best. Study sites were chosen to incorporate a variety of habitats and averaged 203.1 m (range 189.0 – 233.6 m) in length. All streams had low temperatures and conductivities but varied habitat characteristics (Table 1).

Fish Sampling

Snorkeling is a common method of assessing habitat use by stream-dwelling fish (Petty and Grossman 1996). However, training is necessary to obtain the skills needed to identify species and visually estimate fish body length during snorkel surveys (Thurow 1994; Dolloff et al. 1996). Prior to sampling each year, I received instruction in

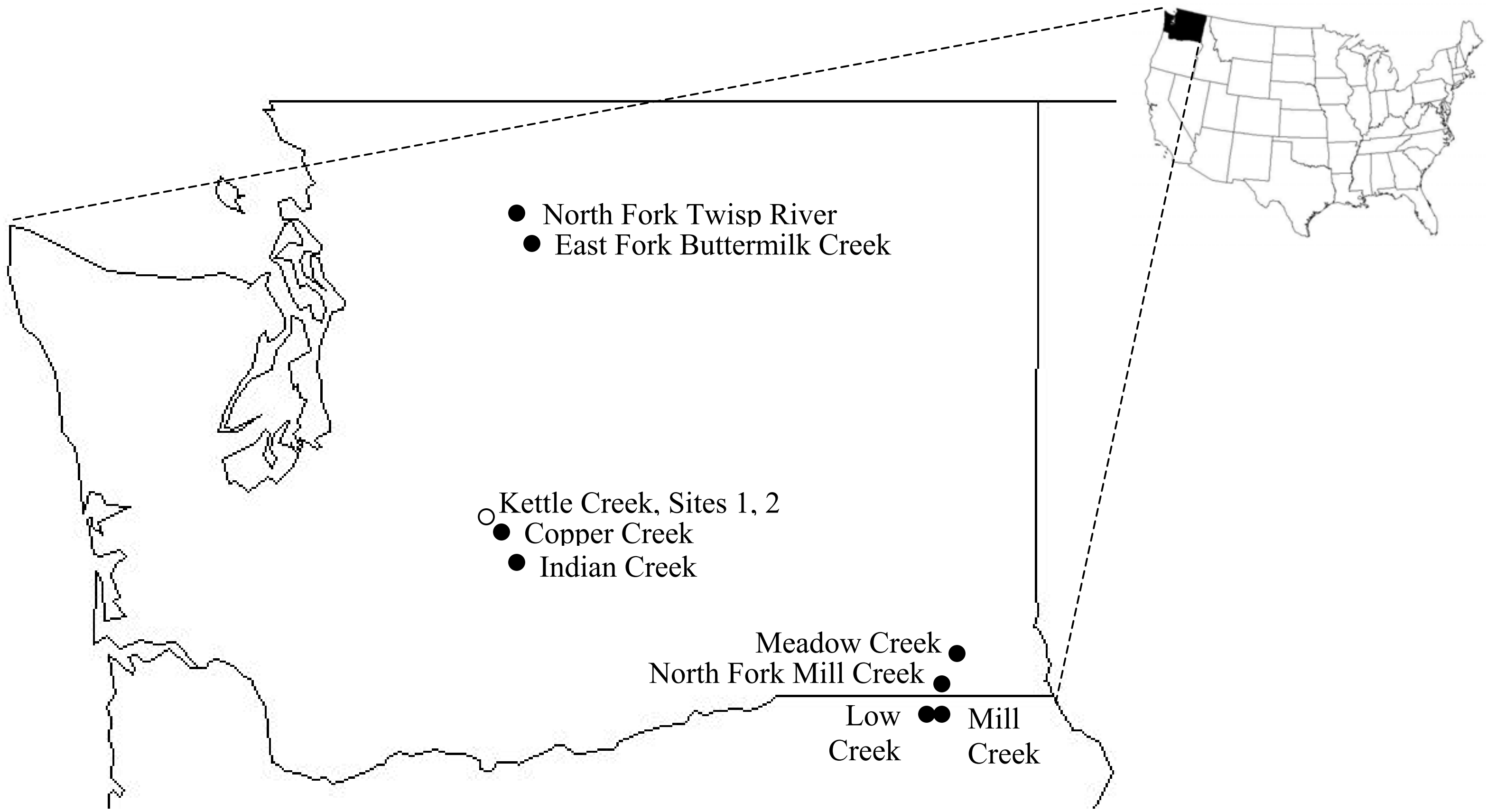

Figure 1. Location of study sites from Eastern Cascades streams during the summers of 2001 and 2002. Circles that are filled in represent single sample locations. An open circle represents two study sites in proximity.

Table 1. Location, survey date, and physiochemical characteristics of study sites from Eastern Cascades streams.

Stream	Date	Latitude and Longitude	Unit Length (m)	Mean Width (m)	Mean Depth (m)	Conductivity (µS)	Mean Temperature (°C)	LWD [a] (no./m²)
Copper Creek	08/21/02	46° 48' 49"N 121° 18' 24"W	192.7	5.27	0.14	40	8.5	0.031
East Fork Buttermilk Creek	08/15/02	48° 19' 19"N 120° 17' 55"W	207.5	5.90	0.14	60	10.0	0.034
Indian Creek	07/17/01	46° 39' 44"N 121° 17' 04"W	200.0	3.78	0.09	20	7.0	0.004
Kettle Creek Site 1	08/28/02	46° 56' 28"N 121° 19' 34"W	233.6	4.00	0.14	50	8.0	0.029
Kettle Creek Site 2	08/29/02	46° 56' 22"N 121° 19' 33"W	194.9	4.80	0.16	70	8.5	0.027
Low Creek	08/01/02	45° 59' 33"N 118° 02' 03"W	189.0	3.23	0.13	70	12.5	0.021
Meadow Creek	07/25/02	46° 09' 39"N 117° 43'42"W	191.7	3.48	0.11	40	12.0	0.036
Mill Creek	08/01/02	45° 59' 34"N 118° 02' 05"W	221.3	8.37	0.35	70	12.0	0.009
North Fork Mill Creek	08/07/02	46° 01' 19"N 117° 59' 42"W	200.2	2.92	0.11	70	7.5	0.014
North Fork Twisp River	09/05/02	48° 27' 41"N 120° 34' 39"W	200.3	6.57	0.19	40	7.0	0.009

[a] Density of large woody debris

snorkeling techniques and safety using methods detailed in Thurow (1994). Briefly, U.S. Forest Service biologists placed fish of known species and sizes in cages within a hatchery raceway. I carefully snorkeled through the raceway and identified species and estimated sizes of the fishes. My observations then were compared to the known species and corresponding sizes to determine my accuracy. Observations were repeated until all fish were accurately identified and estimated within 25 mm of the true fish length.

I completed day and night snorkeling at each stream study site except at Mill Creek, where only day snorkeling was completed, and at North Fork Twisp River, where only night snorkeling was completed. Each study site was randomly assigned to either day or night snorkeling as the primary survey method. Study sites were marked with flagging tape at the up- and downstream ends prior to snorkeling. Prior to snorkeling, I measured stream temperature with a calibrated hand-held thermometer. I completed single-pass day snorkeling between 1000 and 1500 h to maximize underwater visibility. I entered the stream at the downstream end of the study site and snorkeled slowly and deliberately upstream in order to minimize disturbance and prevent bull trout from swimming upstream after observing them. An assistant on land followed me at all times. The assistant provided me with a light for viewing undercut banks or other poorly lit areas when necessary and metal washers that were marked with colored flagging tape representing different size classes of bull trout. Washers also were marked to indicate day or night observations. When bull trout were located, I visually estimated bull trout total length (TL) to the nearest size class (1 = 70-99 mm, 2 = 100-199 mm, 3 = 200-299 mm, 4 = $\geq$ 300 mm) and recorded lengths on a wrist slate. I noted other fish within 200 mm of bull trout focal point during the survey. The assistant then provided me with the appropriately flagged washer to place at bull trout focal point (anterior portion of the fish) and recorded presence of other fish species. I snorkeled to the upstream end of the study site and exited the stream. Bull trout observation data were later transferred from the wrist slate to data sheets.

I completed night snorkel sampling using the same procedures as day snorkeling. However, night surveys were completed between 2230 and 0430 h. I also used a halogen dive light to aid in observation of bull trout. The halogen light did not appear to disturb fish, as I was often able to maneuver within one meter of bull trout before they would flee. Previous studies also have reported a low fright response to dive lights (Bonneau and Scarnecchia 1996; Jakober et al. 1998). I calculated average stream temperature from day and night temperature readings.

Habitat Measurements

My study was a multi-scale investigation of habitat use by bull trout. I measured both micro- and mesohabitat characteristics at areas used by bull trout (henceforth, habitat use) and of the study sites as a whole (henceforth, habitat availability). I collected all habitat availability data during daylight hours after both snorkel surveys were completed. I defined microhabitat as a 20 x 20 cm square below bull trout focal points (point beneath the anterior portion of the fish; Grossman and Freeman 1987). Microhabitat measurements included focal point velocity, average current velocity, depth, distance from substrata, distance to cover, and substrata composition below focal points. Focal point and average velocities were measured with a calibrated Geopacks Basic Flowmeter (Geopacks 2000). When water column depth was less than 75 cm, I recorded average velocity at 0.6 depth. For depths greater than 75 cm, I recorded average velocity as the mean of readings taken at 0.2 and 0.8 depth. I used a delineated 1.44 m PVC tube to measure water column depth, distance from substratum, and distance to cover. I visually estimated percent composition of four substrata categories at fish focal points: rubble (> 150 mm), cobble (75-150 mm), gravel (<75 mm and > 6 mm), and fines (≤ 6 mm). I defined cover as objects able to conceal 50% of the bull trout's body following Grossman and Freeman (1987).

I classified mesohabitats as discrete channel unit habitats where each bull trout was observed. I categorized mesohabitats as riffle, pool, pocket water, or run following Platts et al. (1983). Riffles were shallow (mean = 0.20 m) and steep areas with swift, turbulent water and rubble or cobble substratum. Pools were the deepest (range 0.52 – 1.15 m) depressions in the streambed with slower water velocity and typically with depositional substrata. Pocket water mesohabitats were relatively shallow and had swift flowing water containing numerous boulders that created low current velocity eddies, or pockets, behind obstructions. Runs were areas of moderate depth (mean = 0.30 m) with swiftly flowing water, little surface disturbance, no major flow obstructions, and typically contained gravel, cobble, and rubble.

After habitat use data were recorded, I measured habitat availability via a line transect method. Beginning at the lower end of each study site, I established a minimum of 13 transects (mean = 15) perpendicular to the flow at 10 m intervals. At each transect, I used a delineated tape to measure the study site along the centerline of the stream perpendicular to flow. Habitat measurements were recorded in an upstream direction, starting on the left bank, and proceeding to the right bank to provide a consistent frame of reference. At each transect, I measured wetted width using a delineated tape and recorded depths at ¼, ½, and ¾ of wetted width with a delineated 1.44 m PVC tube. I visually estimated substratum composition in a 1 m wide band centered across each transect. Finally, I classified mesohabitat type at each transect. Mesohabitats were recorded as discrete channel unit types described above. I calculated mean wetted width for sites by averaging wetted widths for all transects. I added depths at ¼, ½, and ¾ of wetted width and divided by four to acquire mean depth at each transect (Platts et al. 1983). I calculated areas of study sites as mean wetted width multiplied by length. Thurow et al. (2001) found that 13 transects would result in measurements that were 40% of the true mean values with 95% confidence. A summary of habitat availability and habitats used by bull trout can be found in the appendix.

Statistical Analysis

I was unable to measure available distance to cover to compare to observed distance to cover. Therefore, I did not include distance to cover in the logistic regression modeling procedure (detailed below). To examine differences in bull trout distance to cover between day and night, I computed mean differences and 95% confidence intervals (CI) that provided information of the magnitude and precision of differences (Johnson 1999). I used Statistical Analysis Software (SAS) version 8.02 for all statistical analyses (SAS Institute 2001).

Habitats often consist of combinations of physiochemical variables that can be physically correlated (Hawkins et al. 1993). Principal Component Analysis (PCA) can be used to describe the variation in a dataset in terms of an uncorrelated set of variables

(Everitt and Dunn 1992). I used PCA to create uncorrelated components representing microhabitats (e.g., Grossman and Freeman 1987). Prior to PCA, microhabitat variables were standardized using Pearson correlations. I retained all principal components with eigenvalues > 1.0 (Kaiser 1960). Each principal component > 1.0 was interpreted for ecological meaning by examining the principal component loadings, which are Pearson correlations between component scores and microhabitat variables (Stevens 1992). I interpreted components using the variables with the largest loadings (absolute value). Separate PCA were conducted for different size classes of bull trout and day and night habitat use.

Chi-square tests are used to compare two or more data distributions (Ott 1993), such as the distribution of habitat availability and habitat use data. I used chi-square tests to compare micro- and mesohabitat availability and micro- and mesohabitat use by different size classes of bull trout during the day and at night following methods detailed in Grossman and Freeman (1987). Briefly, I first created frequency distributions of the principal component scores for both habitat availability and habitat use data. I then tested for non-random habitat use by superimposing the habitat use distributions on the habitat availability distributions. The frequency distributions for habitat availability and habitat use were compared using a chi-square test (Ott 1993) using the habitat availability data for expected frequencies. A statistically significant ($P \leq 0.05$) chi-square test would indicate bull trout did not use habitats in proportion to their availability, which I interpreted as a non-random habitat use pattern. If I found a significant result, I used a partitioned chi-square test to determine which individual distributions were statistically significant. I then created frequency distribution histograms for habitat availability and habitat use to allow visual inspection of the distributions.

Logistic regression is a statistical method used to assess the relationships between predictor variables and a binary response, such as species presence or absence (Hosmer and Lemeshow 2000). I used logistic regression with observed bull trout presence (1) and habitat availability within a stream (0) as the binary response and physiochemical characteristics (Table 2) as model predictors. Observations with missing values were omitted prior to analysis. I dummy coded (0, 1) mesohabitats with pocket water as the baseline. Presence of brook trout also was dummy coded (0 = absent). Presence of brook trout and stream temperature were used as model predictors to account for dependence among observations within streams when non-independence was detected (detailed below). I fit separate logistic regression models for each bull trout size class and day and night habitat use. I calculated Pearson correlations for all pairs of predictor variables (i.e., multi-scale habitat characteristics) prior to analyses. To avoid multicollinearity, I excluded correlated ($r^2 \geq 0.20$) predictor variable pairs from the logistic regression modeling procedure.

I used an information-theoretic approach (Burnham and Anderson 1998) to evaluate the fit of logistic regression models relating bull trout distribution to physiochemical characteristics of streams. Initially, I developed a global (saturated) logistic regression model that contained several uncorrelated multi-scale habitat variables (Table 2) as predictors that I believed to influence bull trout distributions within streams. I then constructed ecologically meaningful candidate models that were subsets of the global model.

I used Akaike's Information Criteria (AIC; Akaike 1973) with the small sample bias adjustment (AIC_c; Hurvich and Tsai 1989) to evaluate the fit of each candidate model. After all AIC_c were calculated, the relative plausibility of each candidate model was assessed using Akaike's weights (Burnham and Anderson 1998). The best-fitting candidate model will have the greatest Akaike weight that can range from 0 to 1. The Akaike weights can be interpreted as the probability that a particular model is the best model, given the candidate set of models (Burnham and Anderson 1998). Thus, I constructed a confidence set of the candidate models, similar to a confidence interval of a mean. The confidence set included models with Akaike weights within 10% of the best fitting model, which is similar to Royall's (1997) cutoff point of 12.5% for evaluating strength of evidence.

The Akaike weights are equivalent to verification that a model appears to be the best approximating model, given the data and set of candidate models (Buckland et al. 1997). However, parameter estimates and their associated standard errors for each candidate model may differ. Uncertainty exists as to which parameter estimates and associated standard errors among the candidate models are the best approximators of the true relationship. To incorporate this uncertainty, I used Akaike weights to calculate model-averaged parameter estimates and unconditional standard errors following Burnham and Anderson (1998). I also calculated importance weights to examine the relative strength of individual model parameters by summing the Akaike weights for each candidate model that contained the parameter of interest.

Observations of bull trout within streams may not be independent of each other. To test for violation of the independence assumption among observations within streams,

Table 2. Category and description of multi-scale habitat variables used to evaluate bull trout distribution within streams during the summers of 2001 and 2002 by size class and time of day.

Category	Model Variable	Description of Model Variable
Microhabitat	Depth	Depth (m) of fish in water column
	Fine	Percent composition of fines (< 6 mm) in 400 cm^2 quadrat at focal point
	Gravel	Percent composition of gravel (6-75 mm) in 400 cm^2 quadrat at focal point
	Cobble	Percent composition of cobble (75-150 mm) in 400 cm^2 quadrat at focal point
	Rubble	Percent composition of rubble (> 150 mm) in 400 cm^2 quadrat at focal point
	Velocity	Velocity (m/s) at fish focal point
Mesohabitat[a]	Pool	Dummy coded as 1 for presence in pool, otherwise 0
	Riffle	Dummy coded as 1 for presence in riffle, otherwise 0
	Run	Dummy coded as 1 for presence in run, otherwise 0
Stream Level[b]	Brook Trout	Dummy coded as 1 for brook trout presence in sample site, otherwise 0
	Temperature	Stream temperature (ºC) during sampling

[a] Pocket water used as baseline

[b] Included in model procedure to account for dependence among observations within streams

I used analysis of variance (ANOVA) using deviance residuals from the global model as predictors and streams as the dependent variable. When ANOVA $P \geq 0.10$, I assumed that observations within streams were independent of each other (Snijders and Bosker 1999). Low *P*-values ($P < 0.10$) suggested dependence among observations within streams. To account for dependence, I included a stream-level characteristic, such as temperature or the presence of brook trout in the logistic regression models. I assessed goodness-of-fit of the global model via the Hosmer-Lemeshow goodness-of-fit (GOF) test (Hosmer and Lemeshow 2000). Low *P*-values ($P < 0.10$) indicated lack-of-fit. I assumed the subset of candidate models fit well if the global model fit sufficiently (Burnham and Anderson 1998).

Odds ratios (OR) can be used to describe the degree to which logistic regression model predictors affect the response variable (Hosmer and Lemeshow 2000). To allow for ease of interpretation, I calculated scaled OR using units of change I deemed to be biologically meaningful. The scaled OR allowed for biologically meaningful interpretation rather than the single unit of change interpretation. For example, I scaled the percent fines OR using 15 because I believed that a 15% change in percent fines is biologically meaningful compared to a single unit change (i.e., 1%). I constructed 90% CI of the scaled OR, which provided additional information on the precision of the parameter effect (Hosmer and Lemeshow 2000). A biologically important relationship between bull trout distributions and model predictors was inferred if the 90% CI of a scaled OR contained values whose magnitudes were considered meaningful, whereas a 90% CI containing one indicated imprecise results (Thompson and Lee 2000).

It has been suggested that the presence of brook trout within streams may lead to displacement of bull trout (Gunckel et al. 2002; B. Rieman *personal communication*) and, hence, a change in habitat use by bull trout. To examine whether brook trout may have influenced habitat use by bull trout, I calculated mean habitat availability for streams containing brook trout and non-brook trout streams. I also was interested in how stream temperature varied between streams containing brook trout and non-brook trout streams. Therefore, I computed mean temperature between streams containing brook trout and non-brook trout streams and a 95% confidence interval (CI) of the difference that provided information of the magnitude and precision of differences (Johnson 1999).

CHAPTER 4

RESULTS

Thirty bull trout were observed in 2001 and 183 bull trout were observed in 2002 with 26 and 187 observed during the day and night, respectively. In 2001, 3% of bull trout observations were from size class one (70 – 99 mm) and 97% from size class two (≥ 100 – 199 mm). No bull trout from size class three (≥ 200 – 299 mm) or four (≥ 300 mm) were observed during 2001. In 2002, 25% of bull trout observations were from size class one, 69% from size class two, 4% percent (N = 7) from size class three, and 2% (N = 4) from size class four. Given that few bull trout from size classes three and four were observed in either year, I combined size classes three and four resulting in three size classes for all analyses that I defined as small (70 – 99 mm TL), large (100 – 199 mm TL), and adult (200 - 499 mm TL).

Microhabitat Use

All bull trout were observed < 10 cm from the stream bottom; hence no analyses were necessary to test for differences in distance from stream bottom because I believed testing for differences within the range of 10 cm were not biologically important (*sensu* Johnson 1999).

Few fish species were observed within 20 cm of bull trout focal points. During the course of sampling, three rainbow trout *Oncorhynchus mykiss* (1% of observations) were observed within 20 cm of bull trout focal points. Hence, there was insufficient data to test for effect of other fish species on habitat use by bull trout.

Bull trout tended to use microhabitats closer to cover during the day (mean = 0.18 m) than at night (mean = 0.25 m), but the 95% CI (-0.20, 0.05) of the difference between the two means contained zero indicating an imprecise estimate of the difference.

Principal Component Analysis

PCA of day habitat use and availability indicated three components had eigenvalues $\geq$ 1.0 and accounted for 73.6% of the variance in the microhabitat data. Component one accounted for 29.1% of the variance and was positively associated with percent rubble and negatively with percent fines and gravel (Table 3). Component two accounted for 26.5% of the variance and positively associated with velocity and percent cobble and negatively with percent fines (Table 3). Component three accounted for 18.0% of the variance and was positively associated with depth and percent cobble (Table 3).

Table 3. Principal component loadings for microhabitat availability and use by small and large bull trout during the day from Eastern Cascades streams during the summers of 2001 and 2002. Bold numbers represent loadings used for interpretation.

	Principal Component		
Variable	1	2	3
Velocity	0.0846	**0.6019**	-0.2093
Depth	0.4032	-0.3718	**0.4913**
Fines	**-0.6081**	**-0.6008**	0.2817
Gravel	**-0.6961**	0.2532	-0.3929
Cobble	0.1938	**0.7616**	**0.5780**
Rubble	**0.8272**	-0.2874	-0.4771

PCA of night habitat use and availability indicated four components with eigenvalues $\geq$ 1.0 accounted for 86.4% of the variance in the microhabitat data. Component one accounted for 27.7% of the variance and was positively associated with percent fines and gravel and negatively with percent rubble (Table 4). Component two accounted for 22.8% of the variance and was positively associated with percent rubble and negatively with percent cobble (Table 4). Component three accounted for 18.6% of the variance and was positively associated with percent gravel and negatively with percent fines (Table 4). Component four accounted for 17.3% of the variance and was positively associated with velocity and negatively with percent cobble (Table 4).

Table 4. Principal component loadings for microhabitat availability and use by small and large bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Bold numbers represent loadings used for interpretation.

	Principal Component			
Variable	1	2	3	4
Velocity	-0.3437	-0.2667	-0.0748	**0.7033**
Depth	0.3325	0.4040	0.3965	-0.4089
Fines	**0.4957**	0.1747	**-0.8310**	-0.0427
Gravel	**0.7404**	-0.2216	**0.4934**	0.3634
Cobble	-0.4361	**-0.7433**	0.0356	**-0.4799**
Rubble	**-0.6689**	**0.7067**	0.1427	0.1189

Chi-square tests indicated that small bull trout used areas with significantly (χ^2 = 16.96, 5 df, P < 0.01) greater amounts of fines and gravel but less rubble, which are characteristic of pool and pocket water mesohabitats, than was available during the day (Figure 2). Adult bull trout, in contrast, used areas with significantly (χ^2 = 21.87, 6 df, P < 0.01) more rubble but less fines and gravel than was available during the day

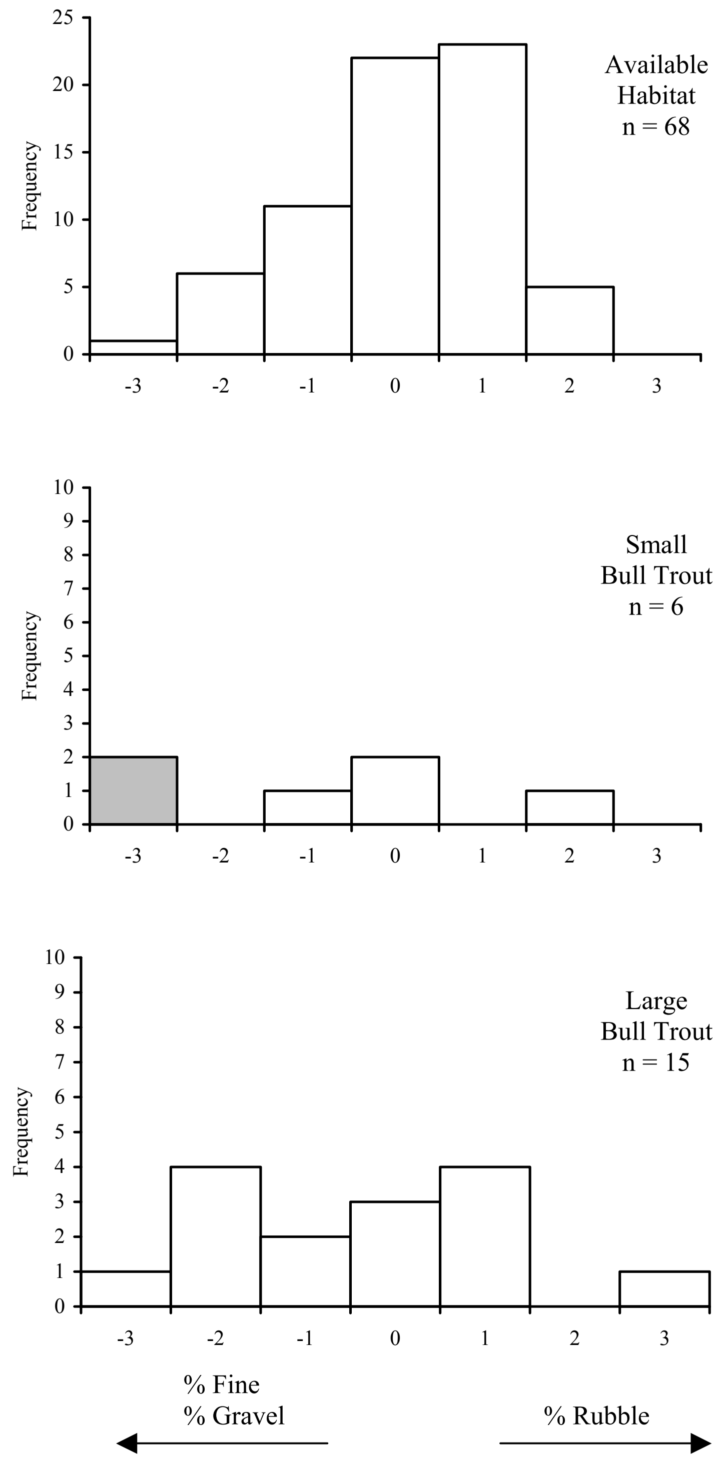

Figure 2. Frequency distribution histograms of principal component one for microhabitat availability and use by small and large bull trout during the day from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

(Figure 3). Large bull trout used significantly ($\chi^2 = 42.76$, 6 df, $P < 0.01$) slower areas with more fines and less cobble (i.e., pool mesohabitats) than was available during the day (Figure 4). Adult bull trout did not use microhabitats that varied from available on principal component two (Figure 5). Small bull trout used significantly ($\chi^2 = 12.87$, 4 df, $P = 0.01$) deeper microhabitats with more cobble, typical of pool mesohabitats, than was available during the day (Figure 6). However, small bull trout also were found in shallower areas with fewer cobbles, which is characteristic of pocket water mesohabitats, than was available during the day (Figure 6). Large bull trout used significantly ($\chi^2 = 24.69$, 5 df, $P < 0.01$) deeper microhabitats with more cobble than was available during the day (Figure 6). Adult bull trout also used significantly ($\chi^2 = 10.89$, 4 df, $P = 0.03$) deeper microhabitats with more cobble than was available during the day (Figure 7).

All size classes of bull trout used areas with significantly (small: $\chi^2 = 17.53$, 6 df, $P < 0.01$; large: $\chi^2 = 29.03$, 6 df, $P < 0.01$; adult: $\chi^2 = 19.05$, 5 df, $P < 0.01$) more small substrata and less large substrata, which are typical of pool and pocket water mesohabitats, than were available at night (Figures 8, 9). Small and large bull trout did not use deep areas with more rubble or cobble substratum than was available (Figure 10). However, adult bull trout used areas with significantly ($\chi^2 = 26.64$, 5 df, $P < 0.01$) more rubble and less cobble than was available at night (Figure 11). Small bull trout used areas with significantly ($\chi^2 = 22.12$, 6 df, $P < 0.01$) more fines and less gravel as well as areas with more gravel and less fines (Figure 12). The use of areas with gravel and fine substrata are indicative of low velocity areas, such as pool or pocket water mesohabitats. Likewise, large bull trout used significantly ($\chi^2 = 39.02$, 7 df, $P < 0.01$) more gravel and less fines than were available at night (Figure 12). Adult bull trout, however, did not use

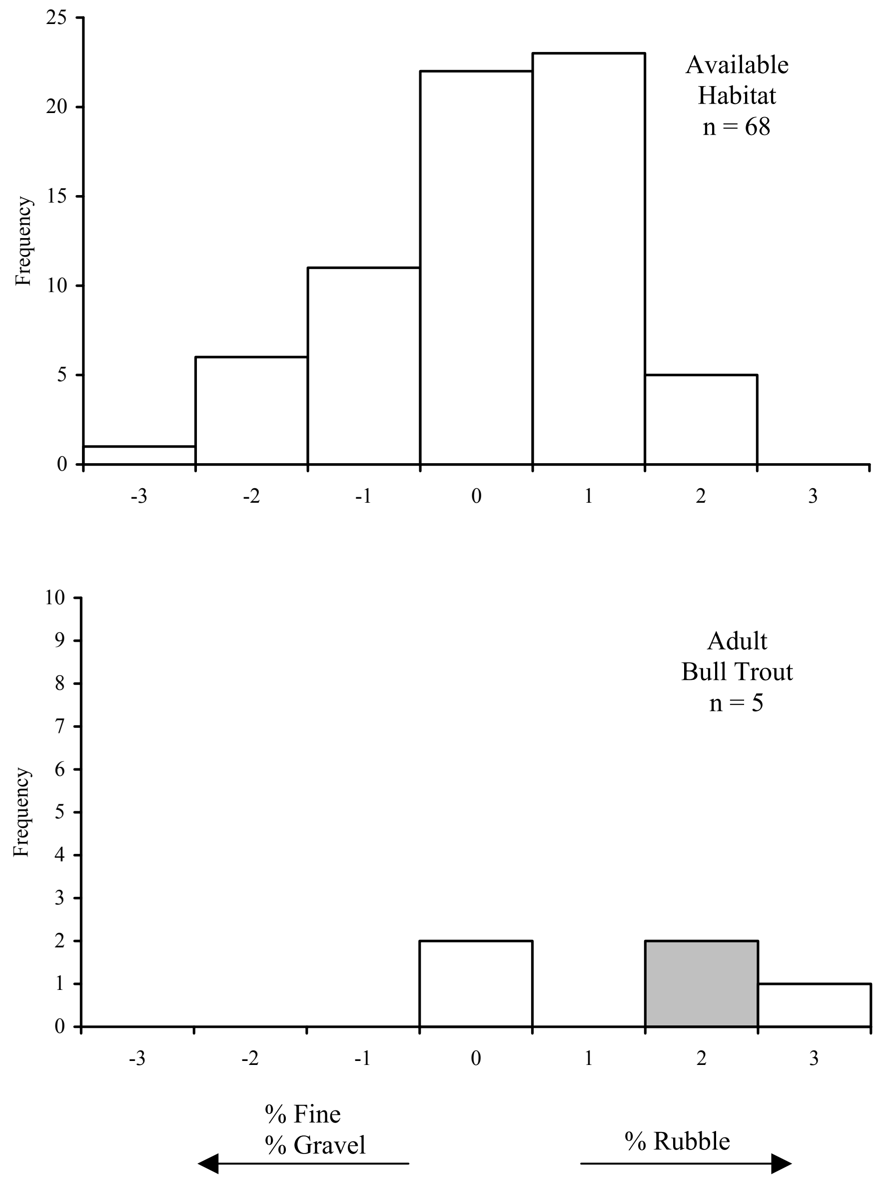

Figure 3. Frequency distribution histograms of principal component one for microhabitat availability and use by adult bull trout during the day from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

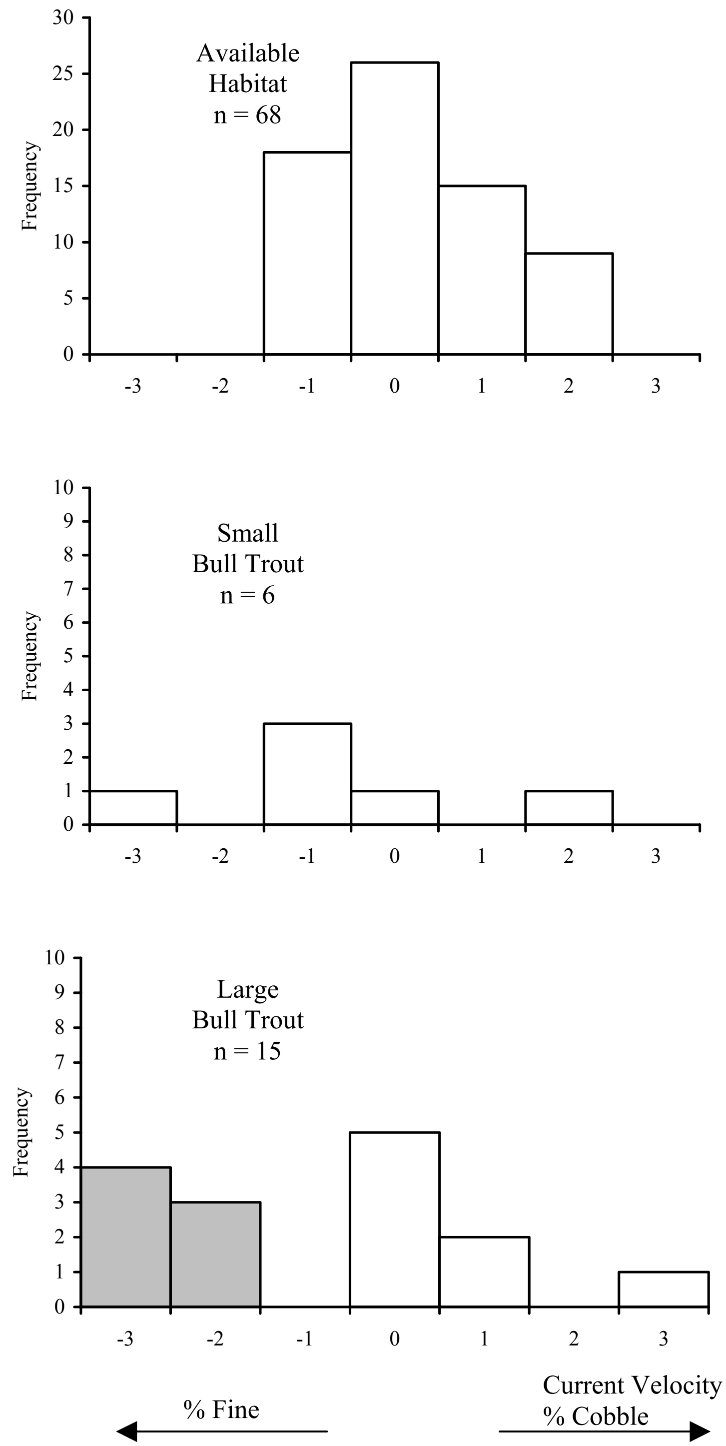

Figure 4. Frequency distribution histograms of principal component two for microhabitat availability and use by small and large bull trout during the day from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

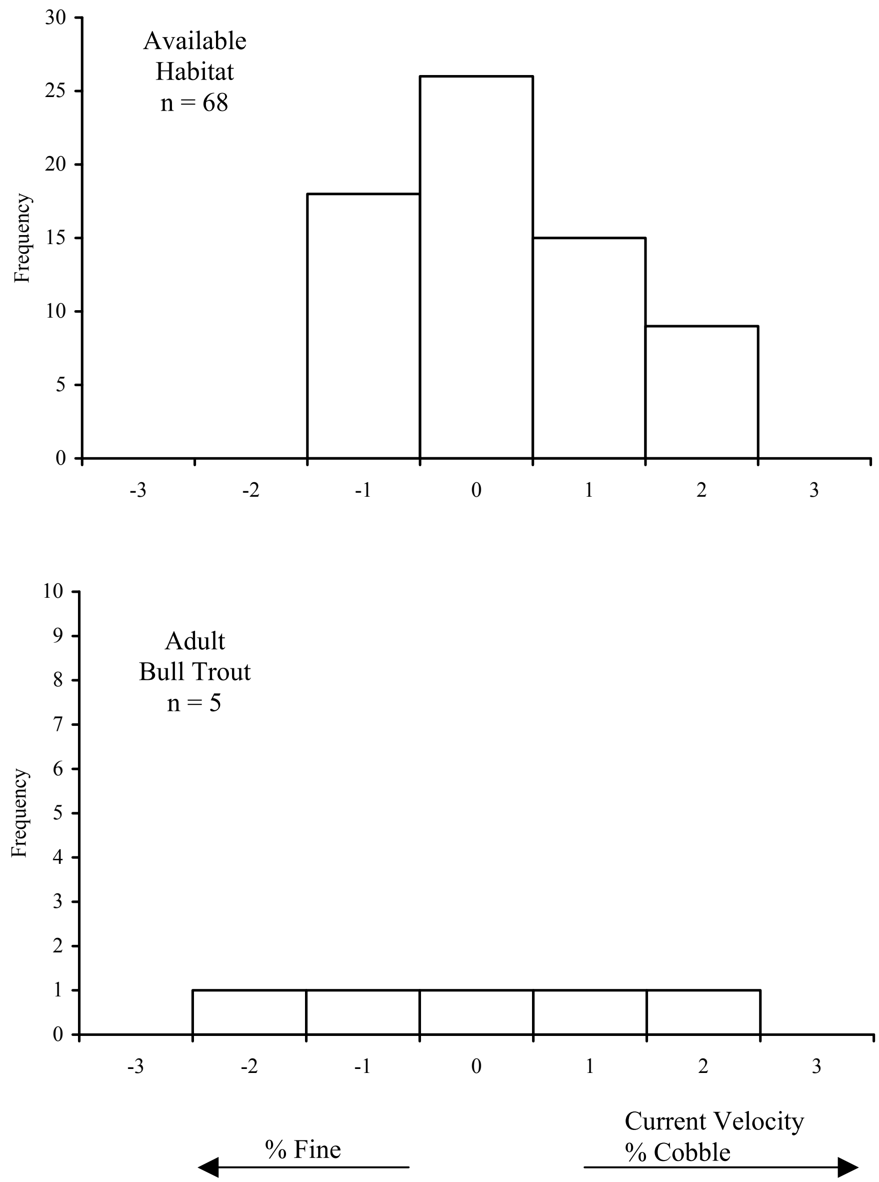

Figure 5. Frequency distribution histograms of principal component two for microhabitat availability and use by adult bull trout during the day from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components.

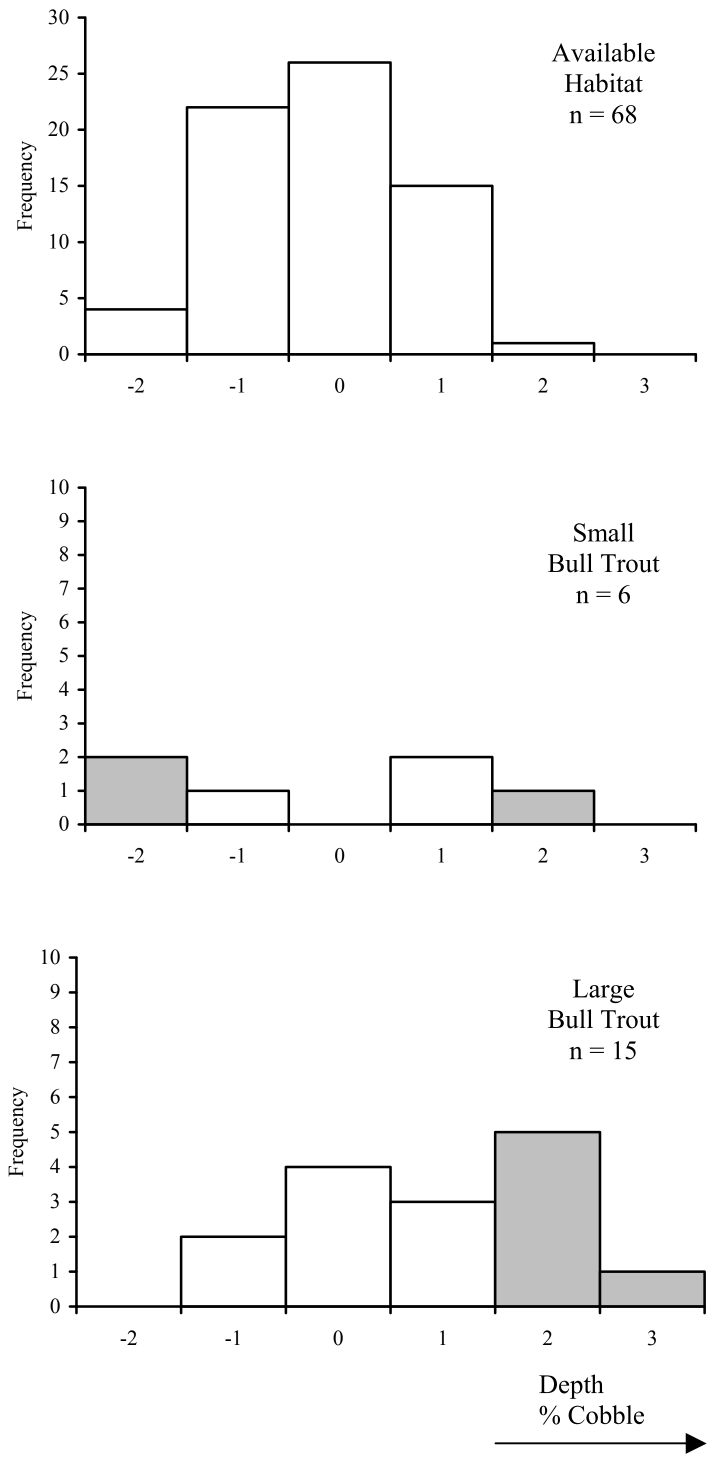

Figure 6. Frequency distribution histograms of principal component three for microhabitat availability and use by small and large bull trout during the day from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

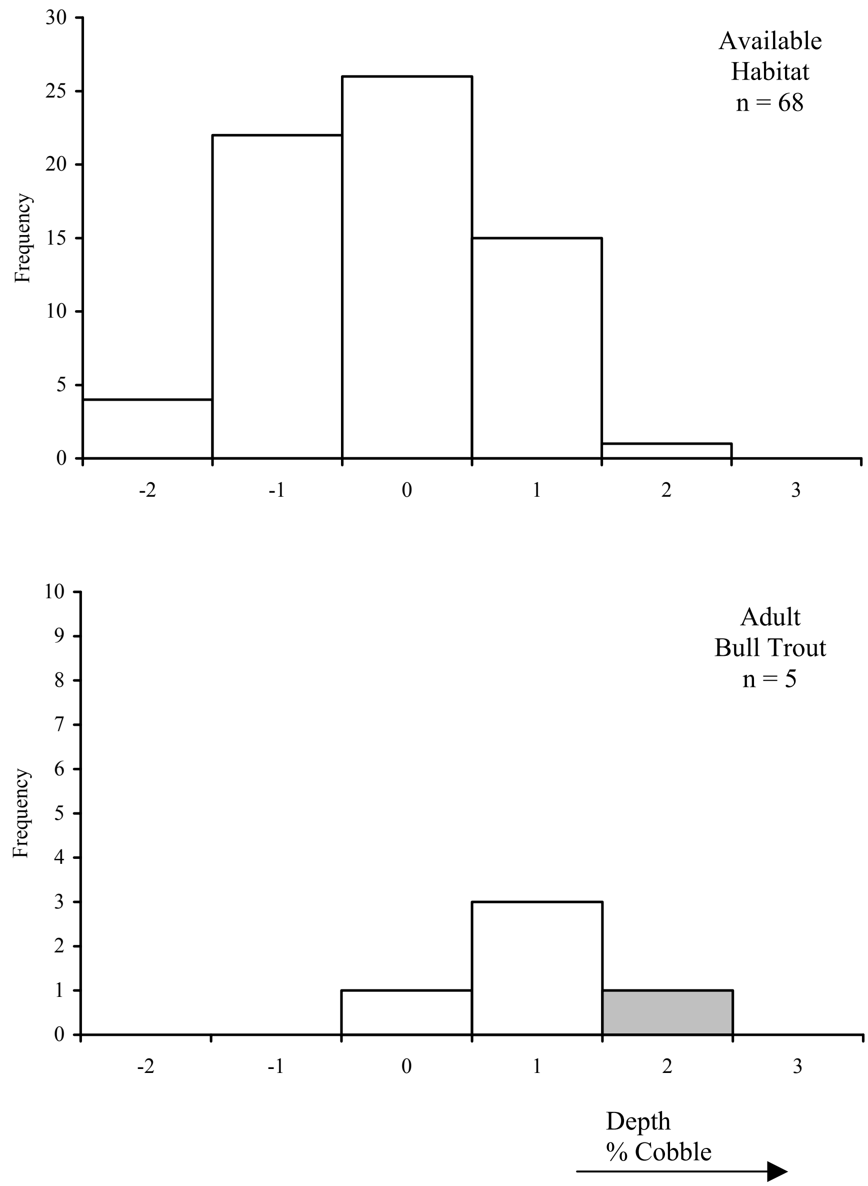

Figure 7. Frequency distribution histograms of principal component three for microhabitat availability and use by adult bull trout during the day from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

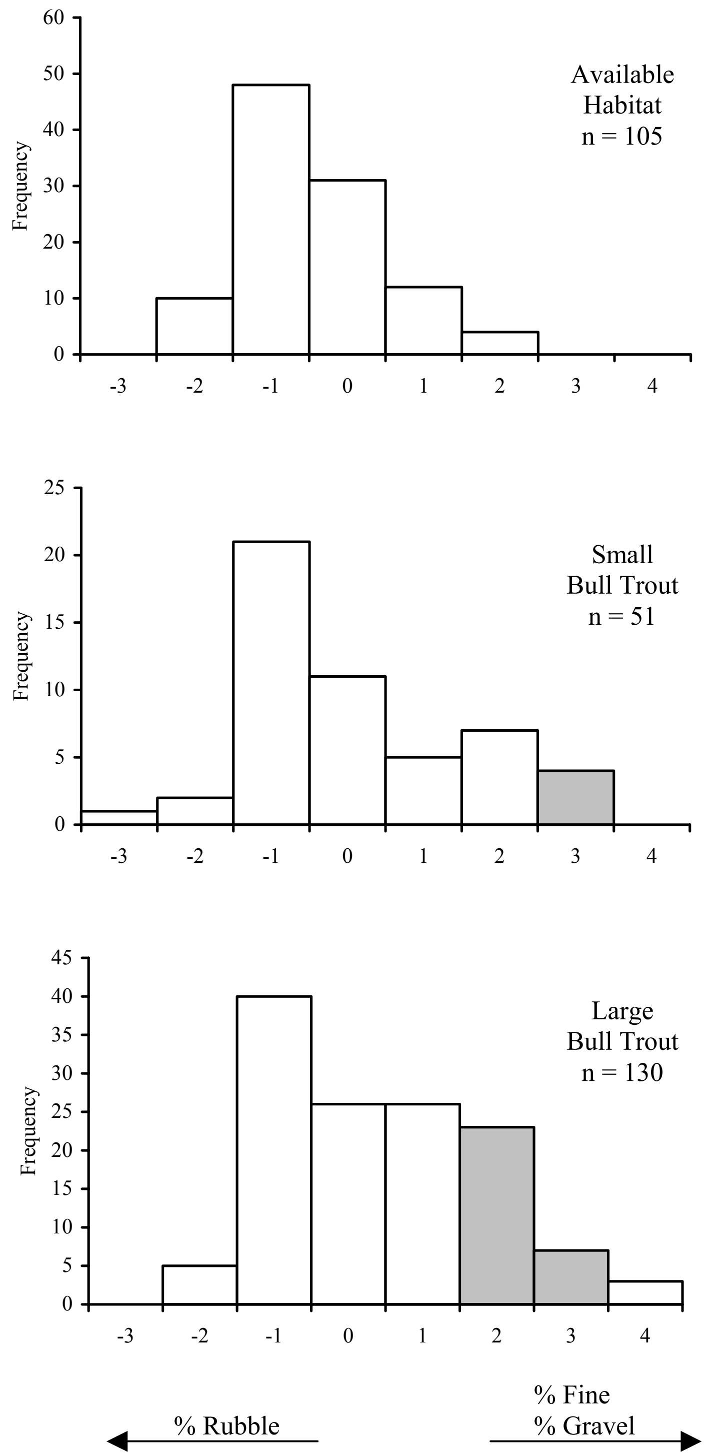

Figure 8. Frequency distribution histograms of principal component one for microhabitat availability and use by small and large bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

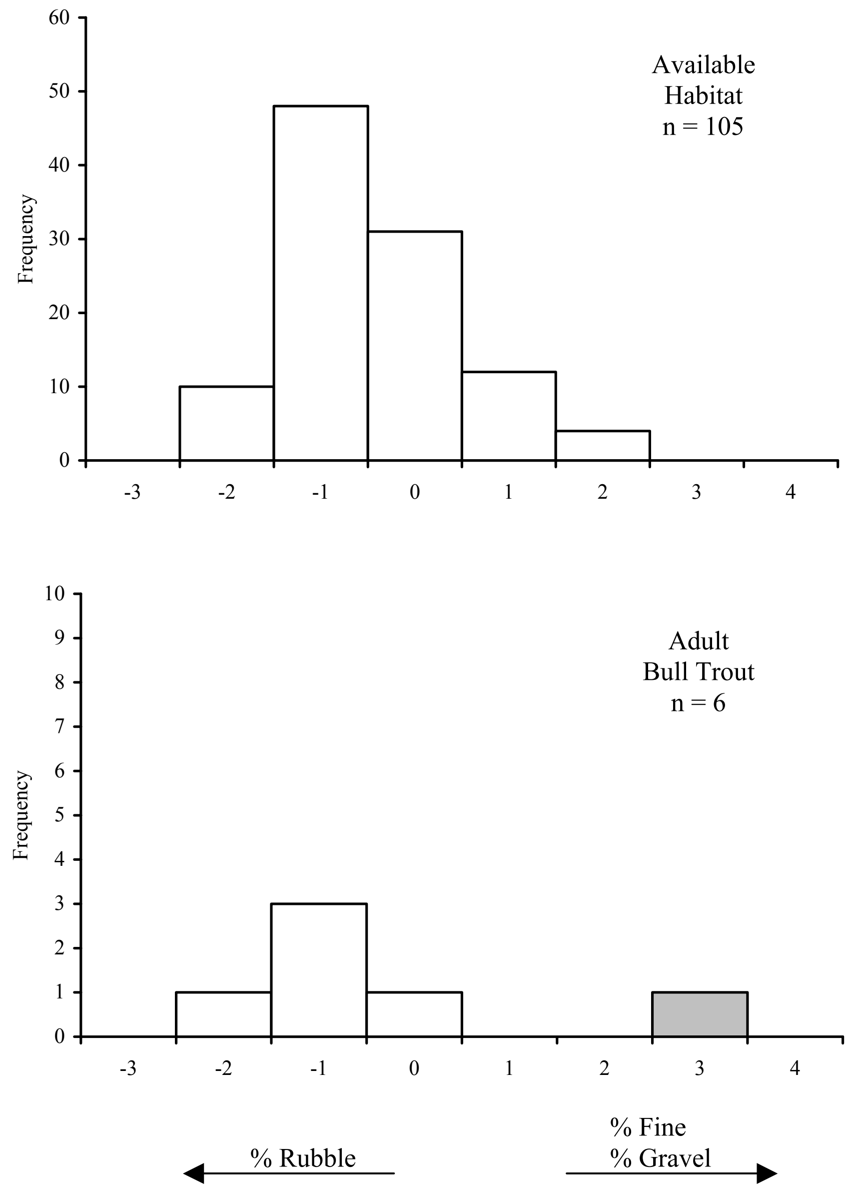

Figure 9. Frequency distribution histograms of principal component one for microhabitat availability and use by adult bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

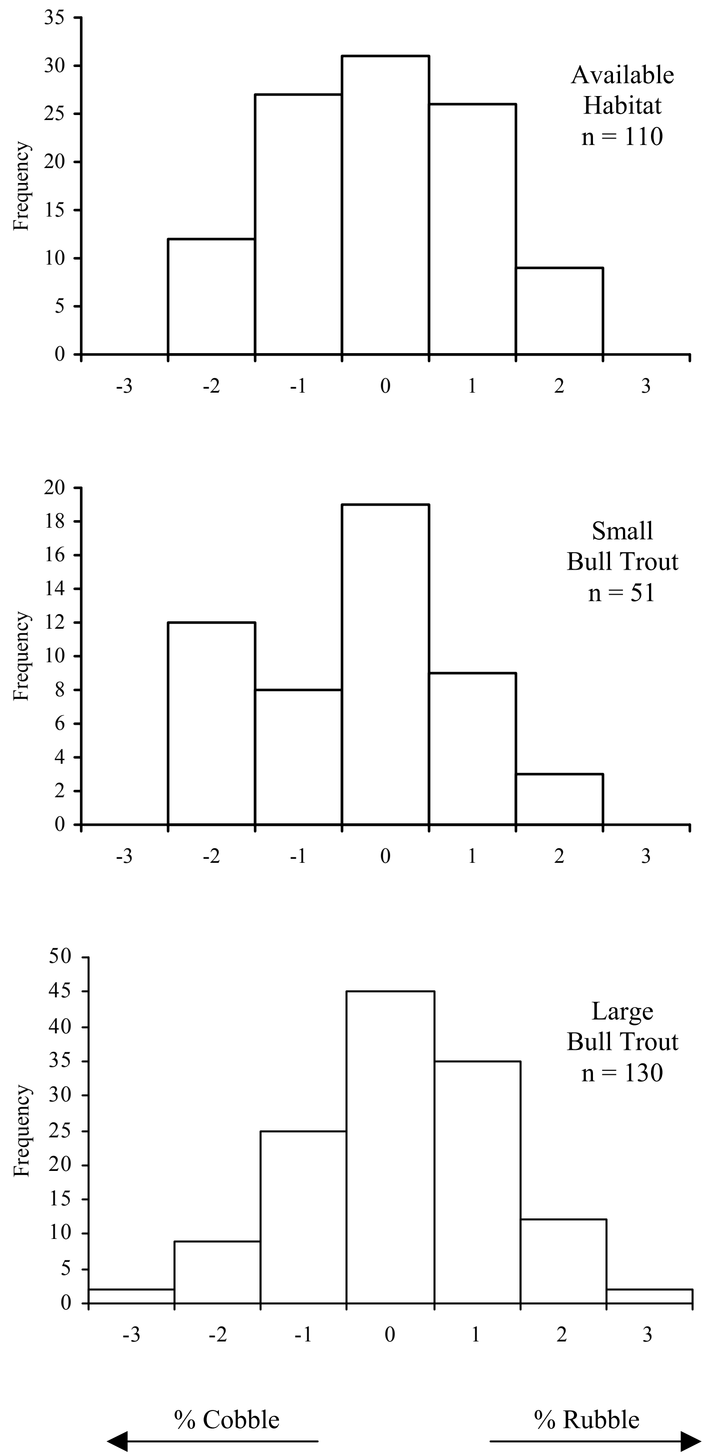

Figure 10. Histogram of frequency distributions from principal component two for microhabitat availability and use by small and large bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components.

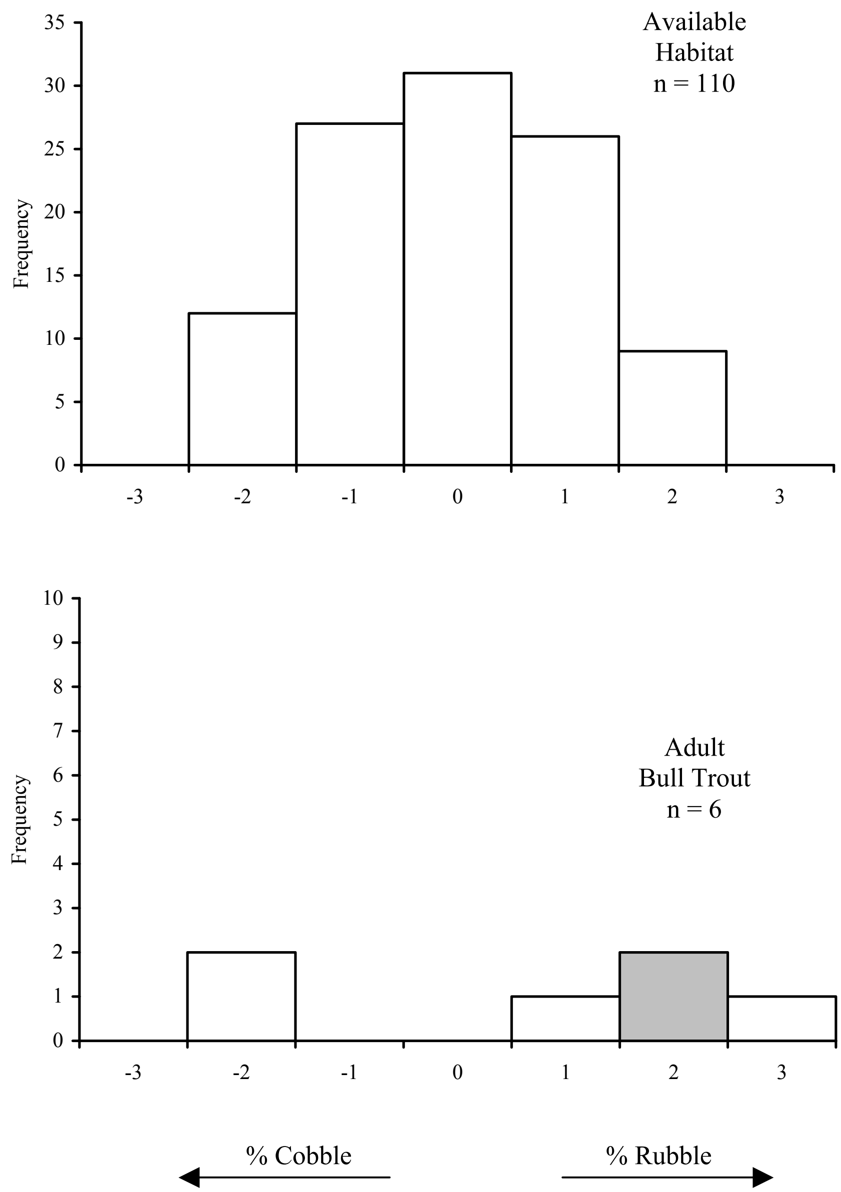

Figure 11. Histogram of frequency distributions from principal component two for microhabitat availability and use by adult bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

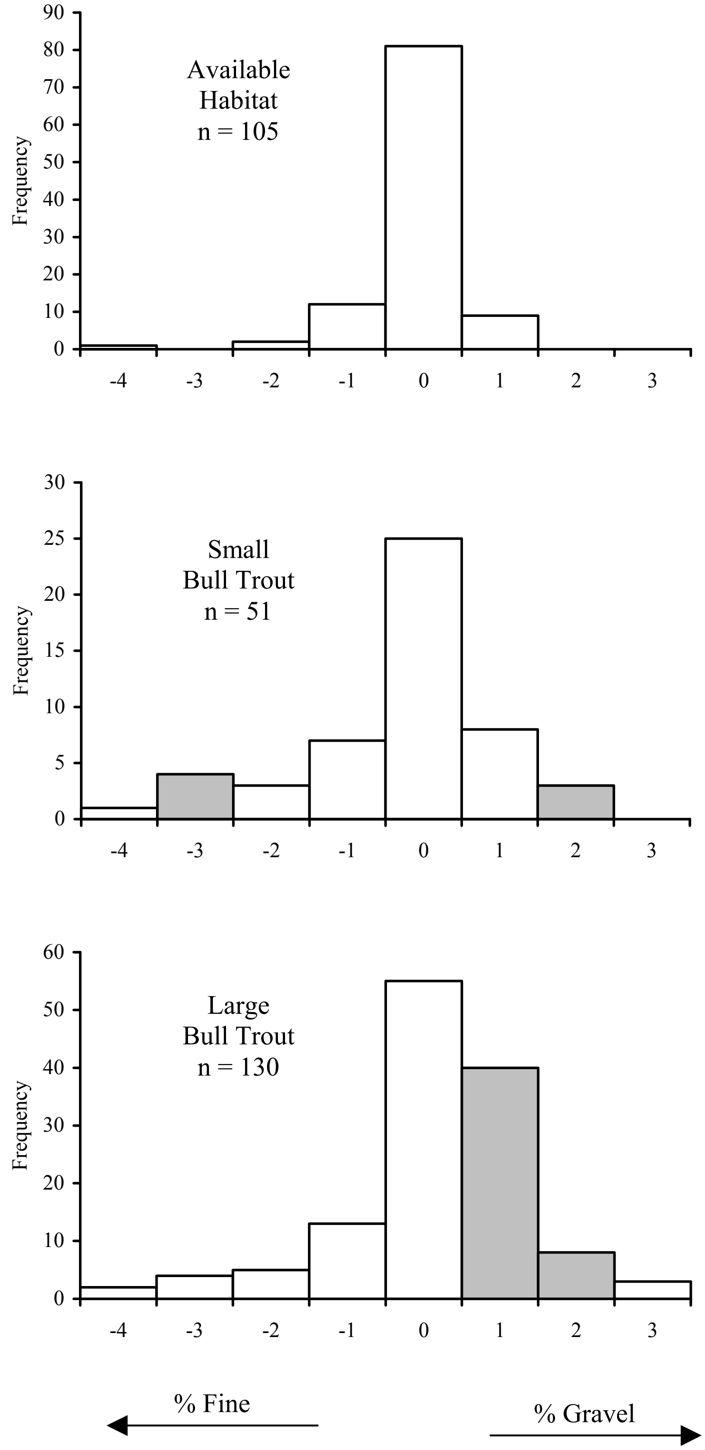

Figure 12. Histogram of frequency distributions from principal component three for microhabitat availability and use by small and large bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

areas with more fines or gravel that differed from available (Figure 13). All size classes of bull trout used significantly (small: $\chi^2 = 16.47$, 7 df, $P = 0.02$; large: $\chi^2 = 16.89$, 7 df, $P = 0.02$; adult: $\chi^2 = 19.12$, 6 df, $P < 0.01$) lower velocity microhabitats with more cobble (i.e., pool and pocket water mesohabitats) than was available at night (Figures 14, 15).

Mesohabitat Use

Small bull trout used pocket water mesohabitats significantly ($\chi^2 = 9.31$, 3 df, $P = 0.03$) more than were available during the day (Figure 16). Large bull trout used pool mesohabitats significantly ($\chi^2 = 9.77$, 2 df, $P = 0.01$) more than were available during the day (Figure 17). Adult bull trout did not use mesohabitats that varied statistically ($\chi^2 = 0.50$, 2 df, $P = 0.78$) from available during the day (Figure 18). At night, small bull trout used pocket water and pool mesohabitats significantly ($\chi^2 = 35.70$, 3 df, $P < 0.01$) more than were available (Figure 19). Similarly, large bull trout used pocket water and pool mesohabitats significantly ($\chi^2 = 53.42$, 3 df, $P < 0.01$) more than were available at night (Figure 20). Adult bull trout also used both pocket water and pool mesohabitats significantly ($\chi^2 = 29.72$, 3 df, $P < 0.01$) more than were available at night (Figure 21).

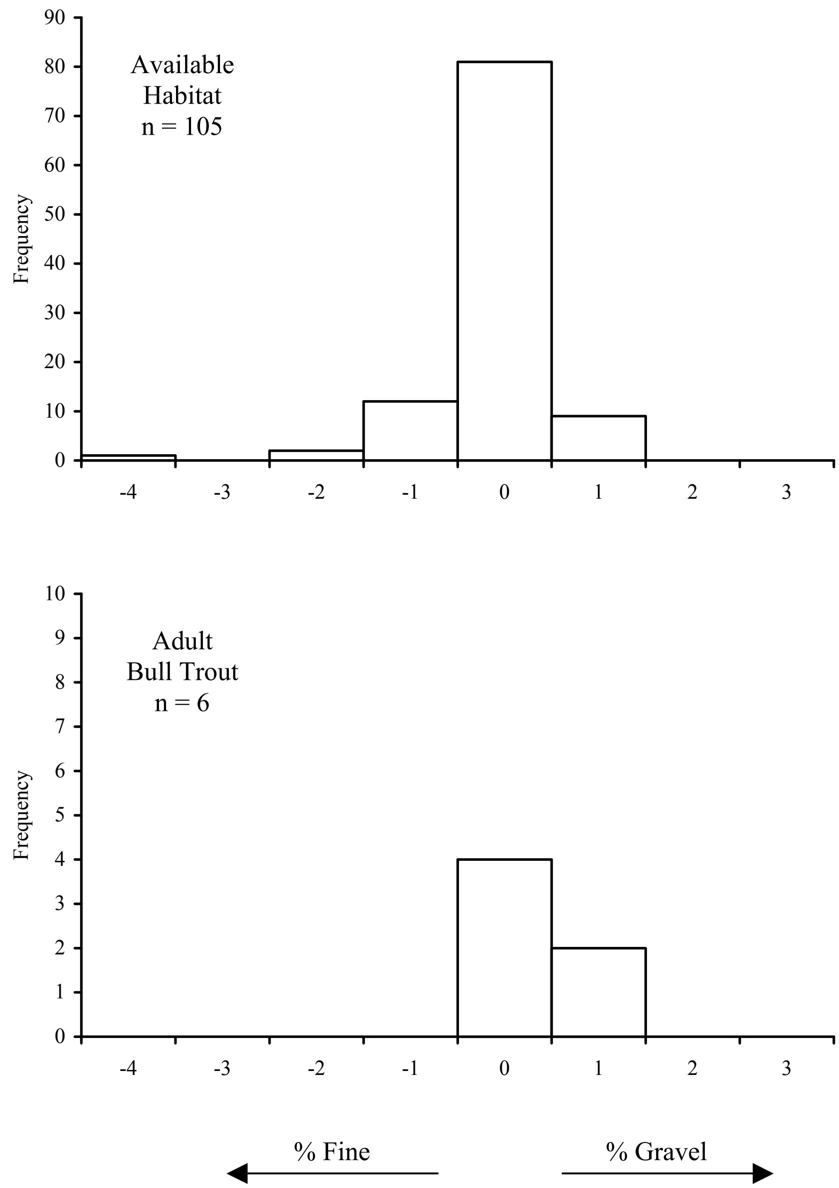

Figure 13. Histogram of frequency distributions from principal component three for microhabitat availability and use by adult bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components.

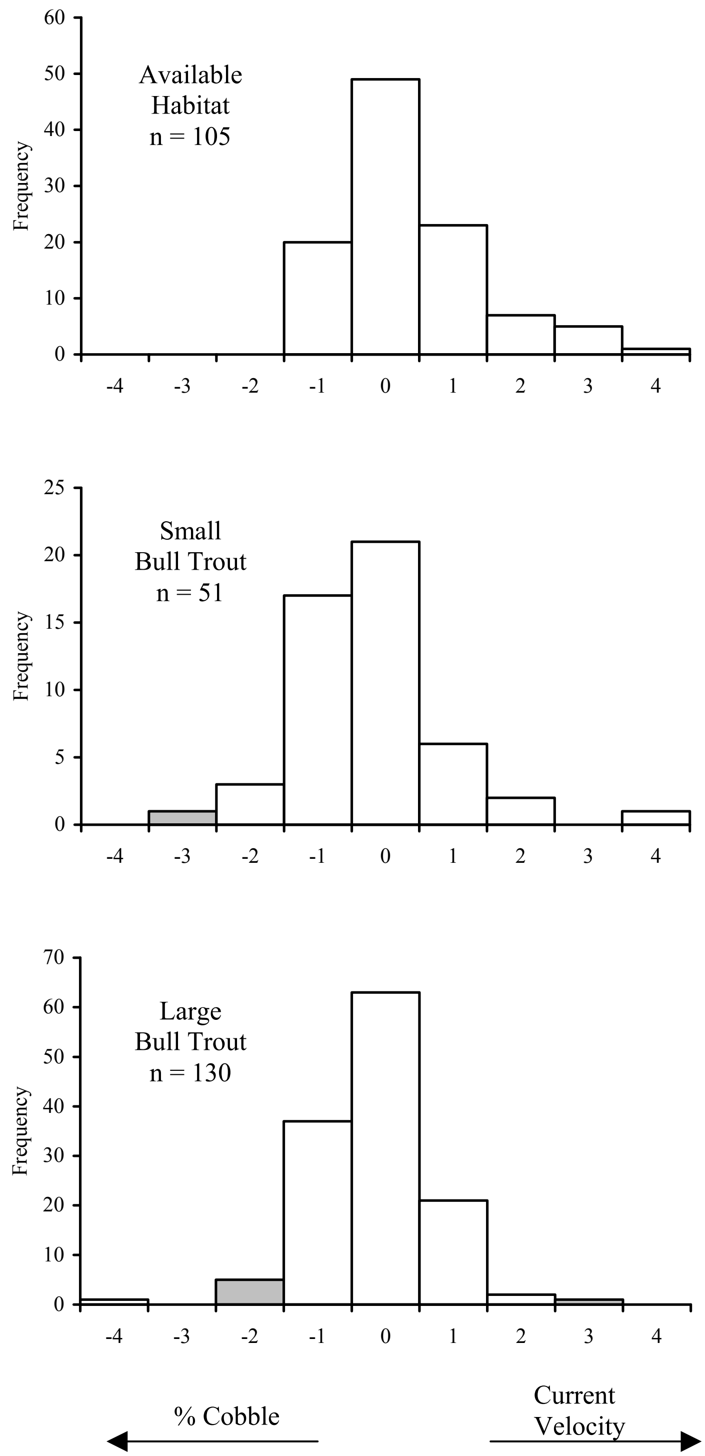

Figure 14. Histogram of frequency distributions from principal component four for microhabitat availability and microhabitat use by small and large bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

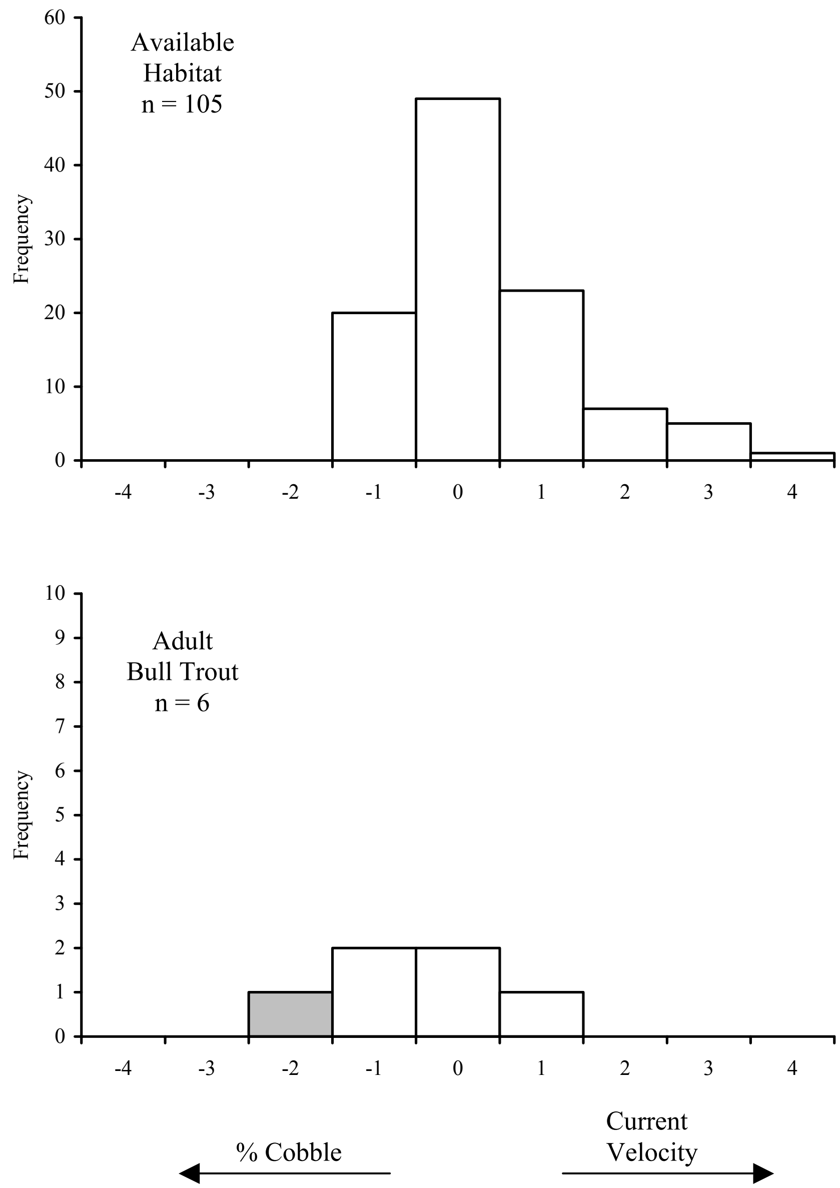

Figure 15. Histogram of frequency distributions from principal component four for microhabitat availability and microhabitat use by adult bull trout at night from Eastern Cascades streams during the summers of 2001 and 2002. Arrows represent interpretation of components. Shaded bars represent microhabitat use by bull trout that differed significantly ($P \leq 0.05$) from available.

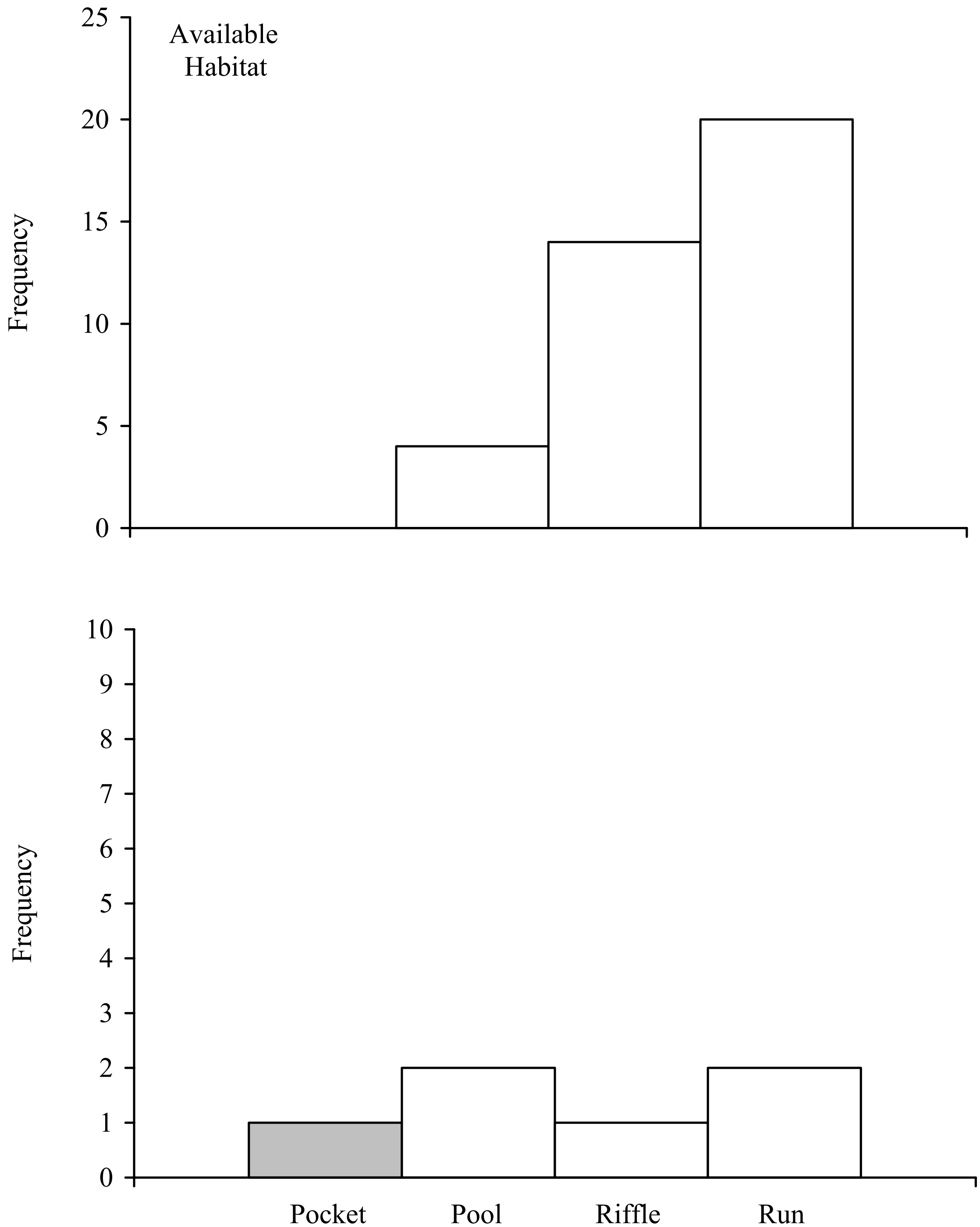

Figure 16. Mesohabitat availability (top) and use (bottom) by small bull trout during the day in Eastern Cascades streams during the summers of 2001 and 2002. Histograms represent frequency of occurrences for available mesohabitat (top; N = 38) and mesohabitat use by small bull trout (bottom; N = 6). Shaded bars represent mesohabitat used by bull trout that differed significantly ($P \leq 0.05$) from available.

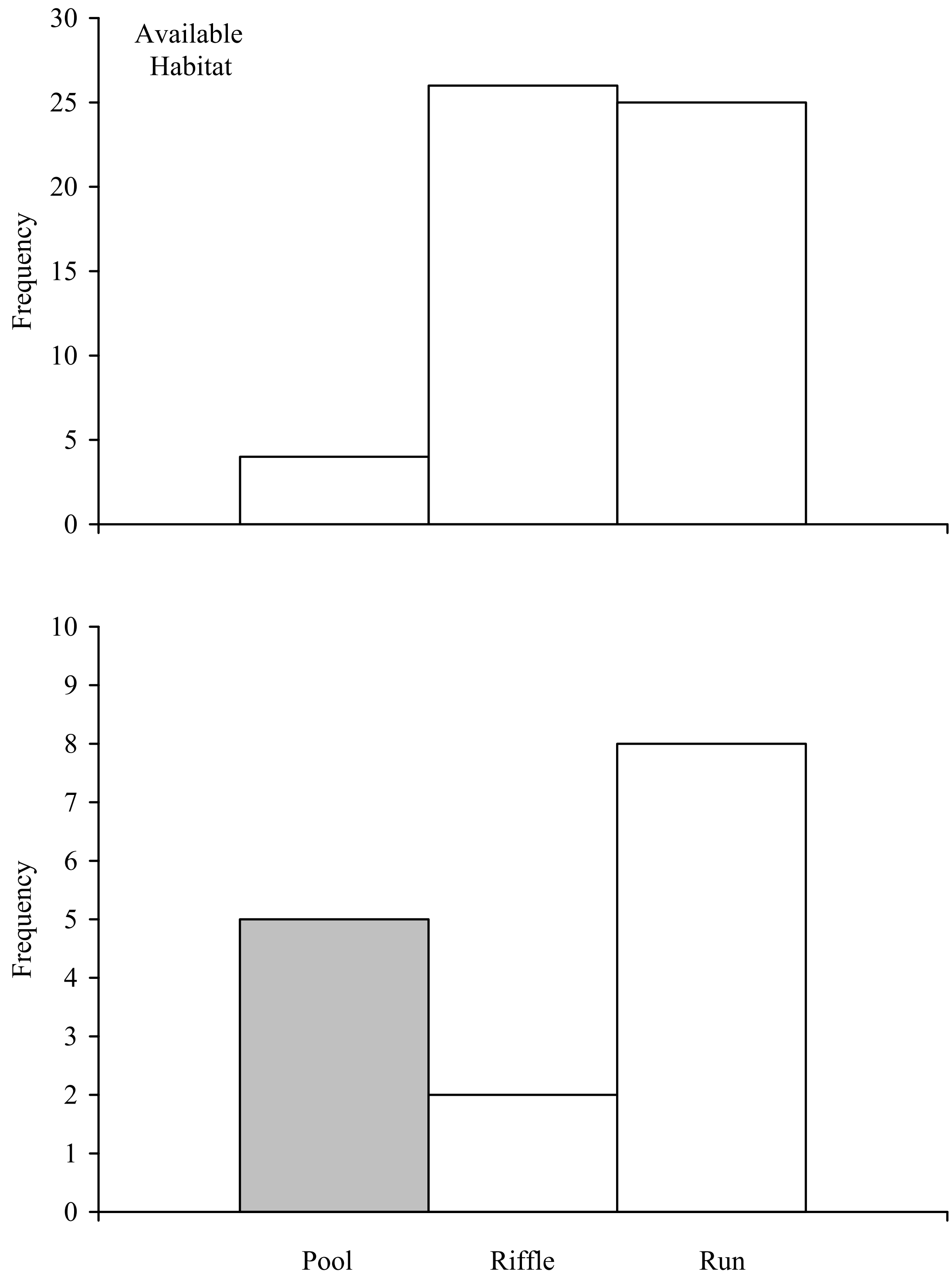

Figure 17. Mesohabitat availability (top) and use (bottom) by large bull trout during the day in Eastern Cascades streams during the summers of 2001 and 2002. Histograms represent frequency of occurrences for available mesohabitat (top; N = 55) and mesohabitat use by large bull trout (bottom; N = 15). Shaded bars represent mesohabitat used by bull trout that differed significantly ($P \leq 0.05$) from available.

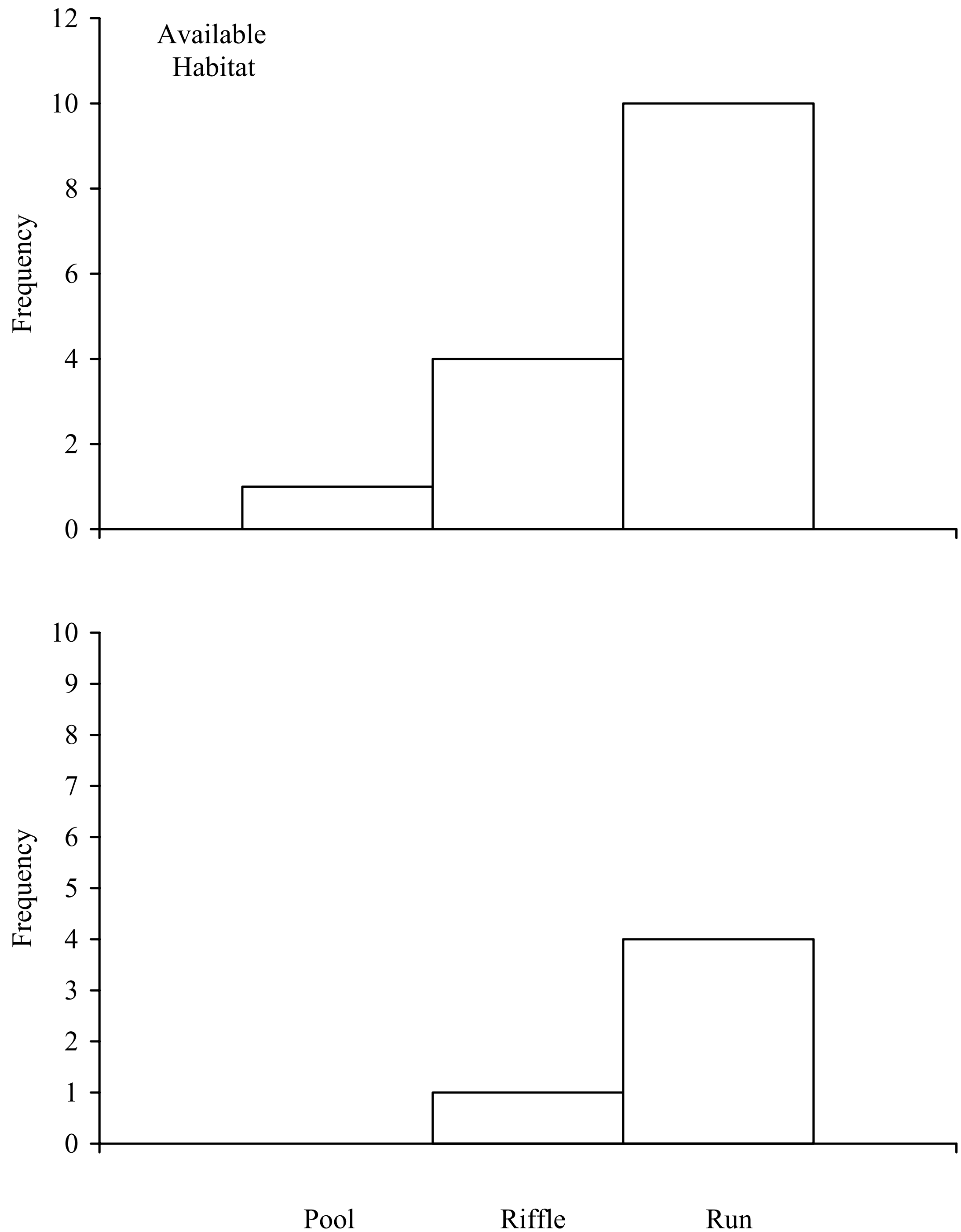

Figure 18. Mesohabitat availability (top) and use (bottom) by adult bull trout during the day in Eastern Cascades streams during the summers of 2001 and 2002. Histograms represent frequency of occurrences for available mesohabitat (top; N = 15) and mesohabitat use by small bull trout (bottom; N = 5).

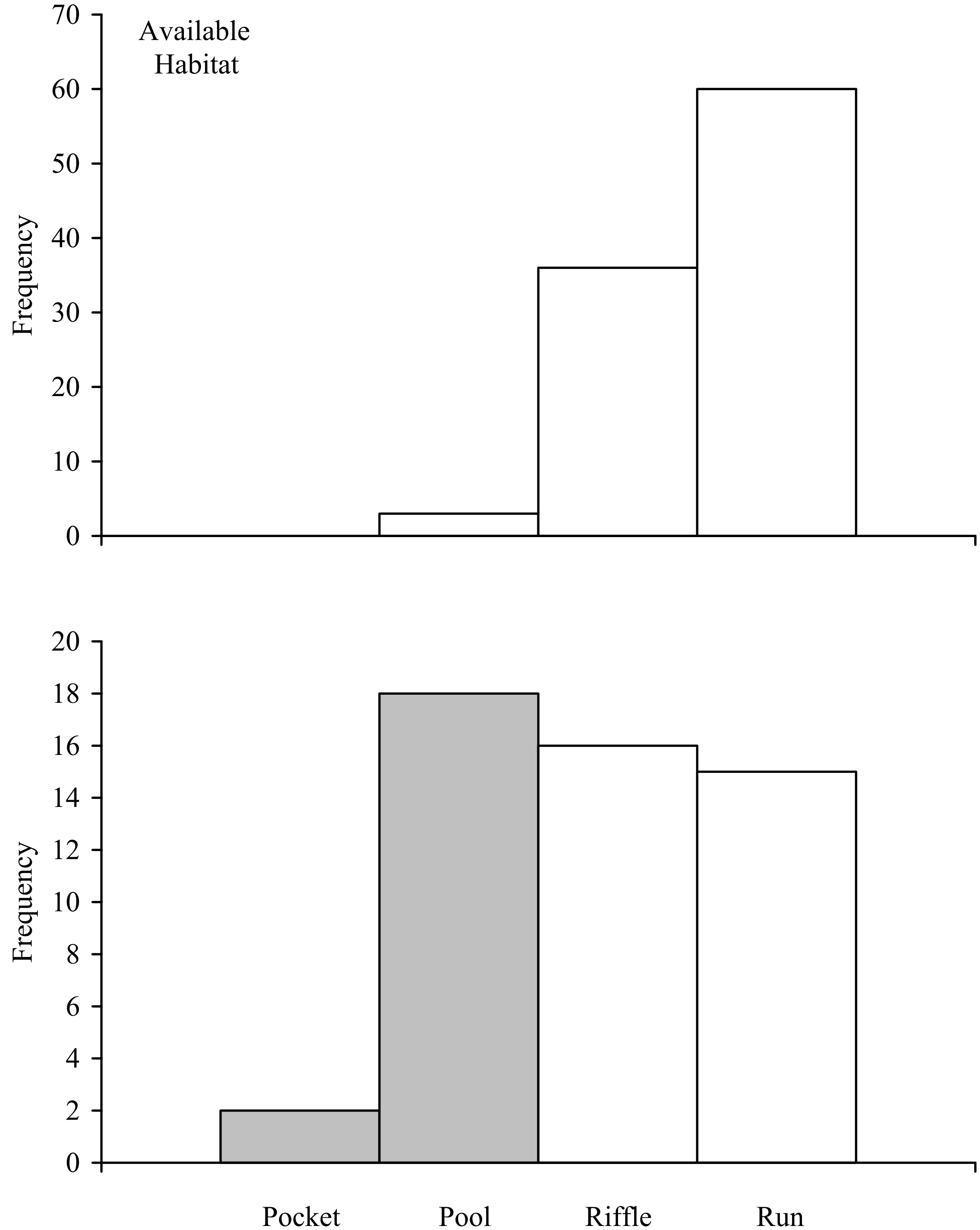

Figure 19. Mesohabitat availability (top) and use (bottom) by small bull trout at night in Eastern Cascades streams during the summers of 2001 and 2002. Histograms represent frequency of occurrences for available mesohabitat (top; N = 102) and mesohabitat use by small bull trout (bottom; N = 51). Shaded bars represent mesohabitat used by bull trout that differed significantly ($P \leq 0.05$) from available.

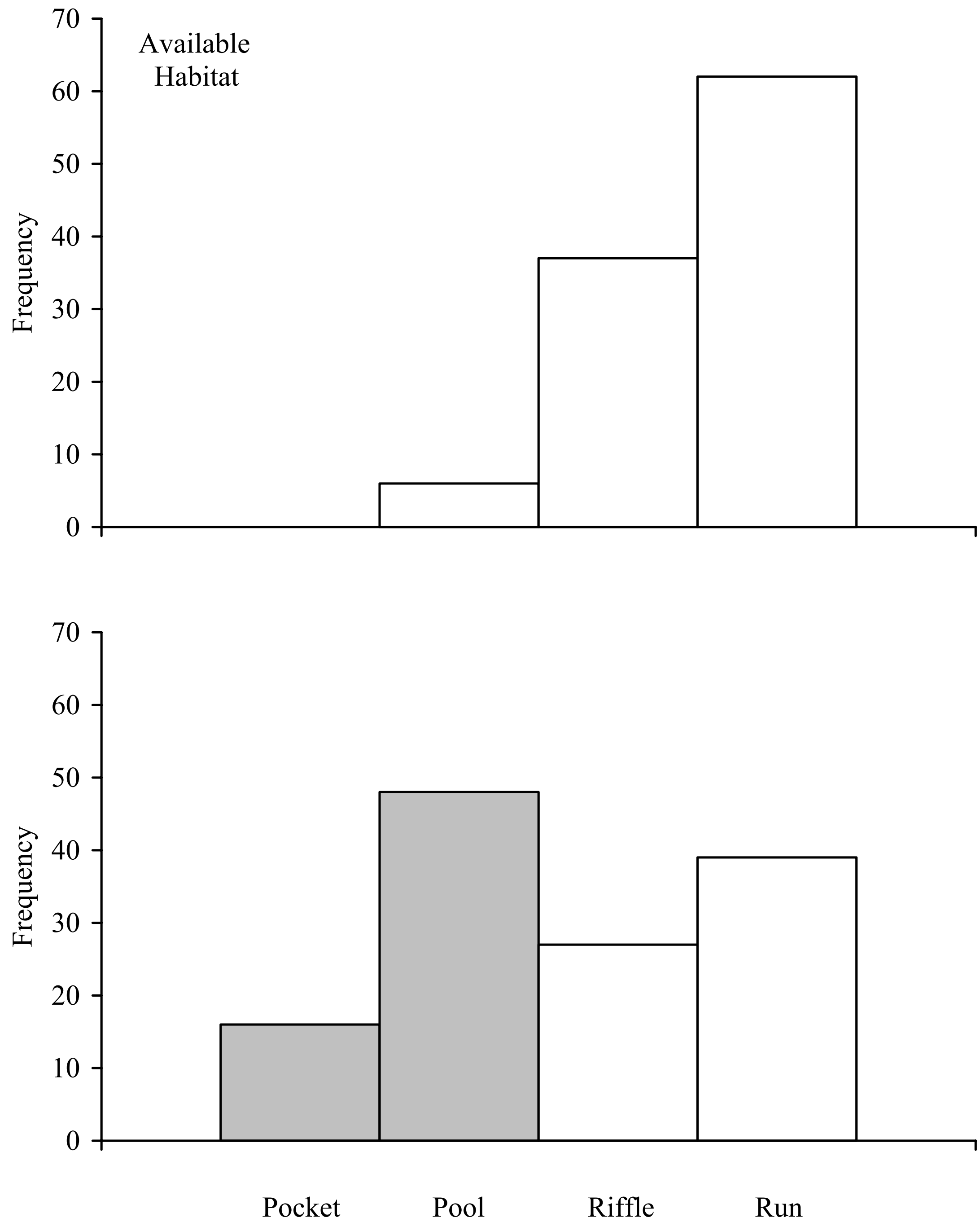

Figure 20. Mesohabitat availability (top) and use (bottom) by large bull trout at night in Eastern Cascades streams during the summers of 2001 and 2002. Histograms represent frequency of occurrences for available mesohabitat (top; N = 105) and mesohabitat use by large bull trout (bottom; N = 130). Shaded bars represent mesohabitat used by bull trout that differed significantly ($P \leq 0.05$) from available.

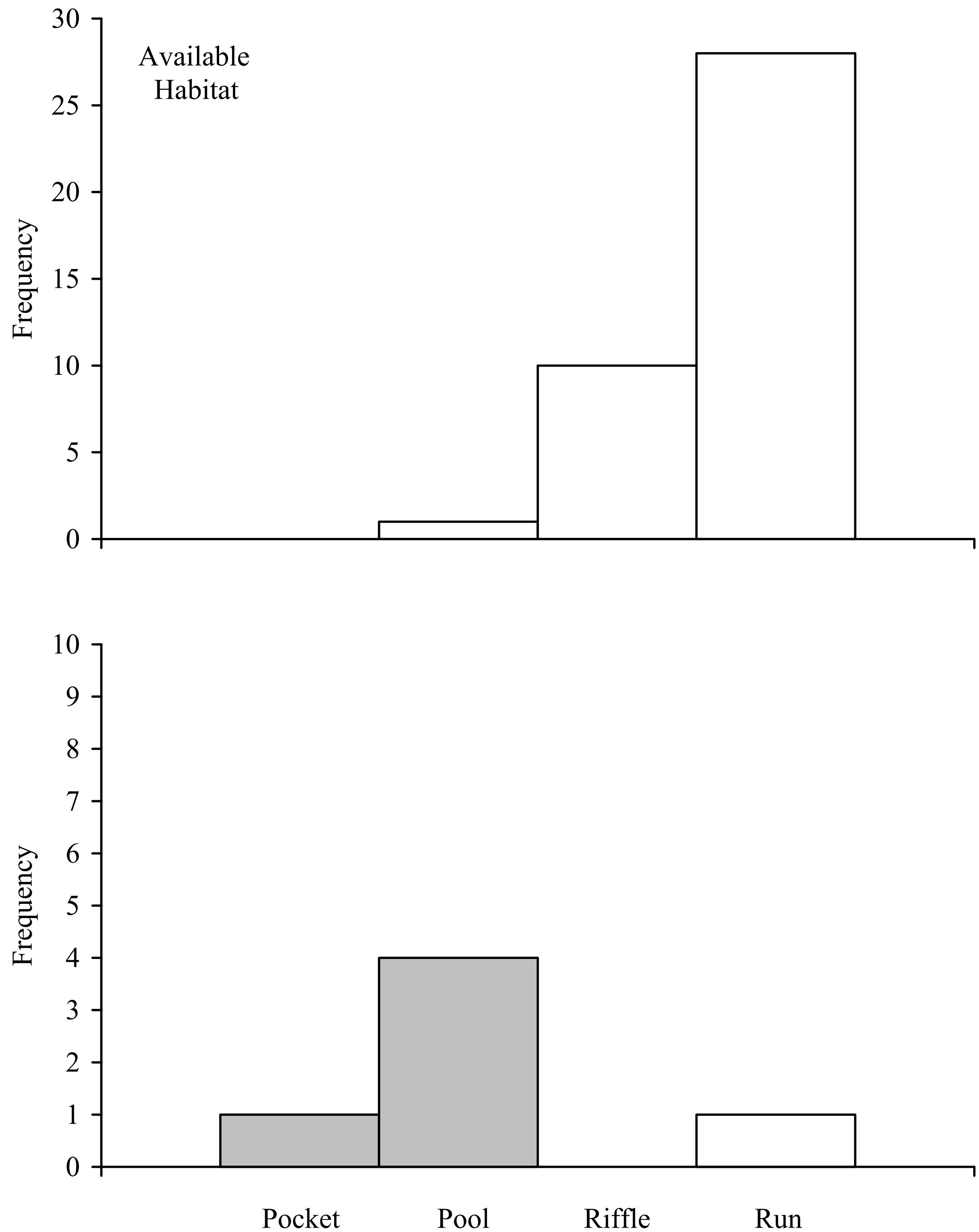

Figure 21. Mesohabitat availability (top) and use (bottom) by adult bull trout at night in Eastern Cascades streams during the summers of 2001 and 2002. Histograms represent frequency of occurrences for available mesohabitat (top; N = 39) and mesohabitat use by large bull trout (bottom; N = 6). Shaded bars represent mesohabitat used by bull trout that differed significantly ($P \leq 0.05$) from available.

Modeling Bull Trout Distributions

The global model predicting small bull trout distribution during the day adequately fit (Hosmer-Lemeshow GOF statistic = 9.21, 8 df, $P = 0.32$). The ANOVA of global model deviance residuals indicated no dependence among observation within streams (F = 0.29, 2 df, $P = 0.75$). Therefore, I assumed that the candidate set of models also fit adequately.

The best fitting model predicting small bull trout distribution during the day contained pool mesohabitat and was 1.30 (0.283/0.218) times more likely than the next best approximating model containing depth, pool mesohabitat, and percent fines (Table 5). The composite model contained these three predictors, riffle mesohabitat, percent gravel, and percent rubble (Table 6). Scaled odds ratios suggested small bull trout were 2.16 times more likely to be found for every 15% increase in fines (Table 6). Pool mesohabitats appeared to be strongly and positively related to the presence of small bull trout during the day (Table 6). However, the CI of the scaled OR was wide and contained one, so the precise nature of the relationship could not be determined.

Table 5. Model selection results based on logistic regression relating small bull trout distribution during the day to habitat characteristics in Eastern Cascades streams during the summers of 2001 and 2002.

Candidate Model	Log Likelihood	K	AIC_c	ΔAIC_c	w_i	Percent of Maximum ΔAIC_c Weight
Pool	-16.61	2	39.812	0.000	0.283	100.00
Depth, Pool, Fines	-14.38	4	40.340	0.529	0.218	76.78
Riffle	-17.01	2	40.610	0.798	0.190	67.09
Riffle, Rubble	-15.94	3	40.908	1.096	0.164	57.80
Depth	-17.32	2	41.244	1.432	0.139	48.87
Depth, Fines, Gravel, Rubble, Pool, Riffle	-13.62	7	47.350	7.539	0.007	2.31

Table 6. Model-averaged parameter estimates, scaled odds ratios (OR), OR confidence intervals (CI), and importance weights from models relating distribution of small bull trout during the day to multi-scale habitat characteristics.

Model Parameter	Estimated Coefficient	OR Unit Change	Scaled OR	90% CI	Importance Weight
Intercept	-2.061 (1.05)	-	-	-	-
Depth	2.377 (3.66)	0.2	1.609	0.49 - 5.34	0.36
Fines	0.051 (0.03)	15.0	2.155	1.04 - 4.46	0.22
Gravel	0.017 (0.03)	15.0	1.298	0.63 - 2.69	0.01
Rubble	-0.029 (0.02)	15.0	0.649	0.38 - 1.12	0.17
Pool	1.417 (1.06)	1.0	4.125	0.73 - 23.37	0.51
Riffle	-1.036 (1.16)	1.0	0.355	0.05 - 2.38	0.36

The global model predicting large bull trout distribution during the day adequately fit the data (Hosmer-Lemeshow GOF statistic = 12.87, 8 df, $P = 0.12$). The ANOVA of global model deviance residuals indicated no dependence among observations within streams (F = 1.01, 4 df, $P = 0.41$). Therefore, I assumed that the candidate set of models also fit adequately.

The most plausible model predicting large bull trout distribution during the day contained depth, percent gravel, and percent rubble and was 2.11 times more plausible as the next best approximating model that contained depth, percent rubble, and pool mesohabitat (Table 7). The composite model contained these four predictors, current velocity, and riffle mesohabitat (Table 8). Importance weights for depth, percent gravel, and percent rubble were at least two times greater than those of other predictors in the composite model suggesting strong evidence for these three predictors (Table 8). Scaled odds ratios indicated large bull trout were strongly and positively associated with stream depth. Large bull trout were 2.47 times more likely to occur for every 0.2 m increase in depth (Table 8). Large bull trout were negatively associated with percent rubble and percent gravel and were 2.00 (1/0.500) and 2.02 times less likely to occur with every 15% increase in rubble and gravel substratum, respectively (Table 8). Large bull trout were 4.59 times less likely to be found in riffle mesohabitats (Table 8). Distributions of large bull trout during the day appeared to be positively related to pool mesohabitats (Table 8). However, the CI of the scaled OR was wide and contained one, so the precise nature of the relationship could not be determined.

Table 7. Model selection results based on logistic regression relating large bull trout distribution during the day to habitat characteristics in Eastern Cascades streams during the summers of 2001 and 2002. Models shown are the 10% confidence set of models.

Candidate Model	Log Likelihood	K	AIC_c	ΔAIC_c	w_i	Percent of Maximum ΔAIC_c Weight
Depth, Gravel, Rubble	-27.35	4	65.633	0.000	0.438	100.00
Depth, Rubble, Pool	-28.09	4	67.125	1.491	0.208	47.45
Gravel, Rubble, Riffle	-28.45	4	67.845	2.212	0.145	33.09
Gravel, Rubble	-30.70	3	70.025	4.391	0.049	11.13

Table 8. Model-averaged parameter estimates, scaled odds ratios (OR), OR confidence intervals (CI), and importance weights from models relating distribution of large bull trout during the day to multi-scale habitat characteristics.

Model Parameter	Estimated Coefficient	OR Unit Change	Scaled OR	90% CI	Importance Weight
Intercept	-0.269 (1.27)	-	-	-	-
Depth	4.530 (1.91)	0.20	2.474	1.32 - 4.63	0.69
Velocity	0.057 (2.74)	0.15	1.009	0.51 - 1.98	0.08
Gravel	-0.047 (0.03)	15.00	0.496	0.26 - 0.95	0.71
Rubble	-0.046 (0.02)	15.00	0.500	0.32 - 0.79	0.96
Riffle	-1.524 (0.89)	1.00	0.218	0.05 - 0.93	0.24
Pool	1.350 (0.94)	1.00	3.858	0.82 - 18.06	0.29

The global model predicting adult bull trout distribution during the day adequately fit the data (Hosmer-Lemeshow GOF statistic = 8.59, 8 df, P = 0.38). The ANOVA of global model deviance residuals indicated no dependence among observations within streams (F = 0.68, 1 df, P = 0.42). Therefore, I assumed that the candidate set of models also fit adequately.

The best fitting model predicting adult bull trout distribution during the day contained depth and was 4.09 times more likely than the next best approximating model containing run mesohabitat (Table 9). The composite model contained these two predictors, current velocity, and percent rubble (Table 10). Scaled odds ratios suggested small bull trout were 2.25 times more likely to be found for every 0.20 m increase in depth (Table 10). The CI of the scaled OR for the remaining predictors were wide and contained one, so the precise nature of the relationship could not be determined.

Table 9. Model selection results based on logistic regression relating adult bull trout distribution during the day to habitat characteristics in Eastern Cascades streams during the summers of 2001 and 2002. Models shown are the 10% confidence set of models.

Candidate Model	Log Likelihood	K	AIC_c	ΔAIC_c	w_i	Percent of Maximum ΔAIC_c Weight
Depth	-9.67	2	26.835	0.000	0.659	100.00
Run	-11.08	2	29.658	2.823	0.161	24.37
Velocity	-11.23	2	29.950	3.115	0.139	21.06

Table 10. Model-averaged parameter estimates, scaled odds ratios (OR), OR confidence intervals (CI), and importance weights from models relating distribution of adult bull trout during the day to multi-scale habitat characteristics.

Model Parameter	Estimated Coefficient	OR Unit Change	Scaled OR	90% CI	Importance Weight
Intercept	-2.240 (1.24)	-	-	-	-
Depth	4.049 (2.43)	0.20	2.247	1.01 - 4.99	0.66
Velocity	0.979 (4.47)	0.15	1.158	0.39 - 3.48	0.14
Rubble	0.705 (1.25)	1.00	2.024	0.26 - 15.77	0.04
Run	-0.012 (0.02)	15.00	1.198	0.67 - 2.14	0.20

Initially, the global model predicting small bull trout distribution at night adequately fit the data (Hosmer-Lemeshow GOF statistic = 12.23, 8 df, $P = 0.14$). However, the ANOVA of global model deviance residuals suggested dependence among observations within streams (F = 3.31, 7 df, $P < 0.01$). To account for this dependence, I added brook trout presence and stream temperature into the global model. The ANOVA of the global model deviance residuals indicated no detectable dependence among observations within streams (F-value = 1.72, 7 df, $P = 0.11$) and the global model fit adequately (Hosmer-Lemeshow GOF statistic = 12.79, 8 df, P = 0.12). Therefore, I assumed that the candidate set of models also fit adequately.

The most plausible model predicting small bull trout distribution at night contained pool mesohabitat and stream temperature and was 1.44 times more plausible than the next best approximating model containing pool mesohabitat, temperature, and the presence of brook trout (Table 11). The composite model contained these three predictors, depth, current velocity, and riffle mesohabitat (Table 12). Pool mesohabitat and temperature had the largest importance weights indicating that there was strong evidence for these two predictors (Table 12). Scaled odds ratios suggested that small bull trout were strongly and positively associated with pool mesohabitats. Small bull trout were 9.99 times more likely to occur in pool mesohabitats (Table 12). Small bull trout were negatively influenced by temperature and were 3.12 times less likely to occur for every 4 °C increase in stream temperature (Table 12). The CI of the scaled OR for the remaining predictors were wide and contained one, so the precise nature of their relationships could not be determined.

Table 11. Model selection results based on logistic regression relating small bull trout distribution at night to habitat characteristics in Eastern Cascades streams during the summers of 2001 and 2002. Models shown are the 10% confidence set of models.

Candidate Model	Log Likelihood	K	AIC_c	ΔAIC_c	w_i	Percent of Maximum ΔAIC_c Weight
Pool, Temperature	-84.79	3	177.844	0.000	0.380	100.00
Pool, Temperature, Brook Trout	-84.08	4	178.575	0.732	0.263	69.36
Depth, Pool, Temperature	-84.77	4	179.950	2.106	0.132	34.89
Pool, Brook Trout	-86.03	3	180.331	2.488	0.109	28.83
Velocity, Pool, Brook Trout, Temperature	-83.95	5	180.480	2.637	0.102	26.76

Table 12. Model-averaged parameter estimates, scaled odds ratios (OR), OR confidence intervals (CI), and importance weights from models relating distribution of small bull trout at night to multi-scale habitat characteristics.

Model Parameter	Estimated Coefficient	OR Unit Change	Scaled OR	90% CI	Importance Weight
Intercept	1.098 (1.35)	-	-	-	-
Depth	-0.298 (1.72)	0.20	0.942	0.54 - 1.65	0.15
Velocity	-0.961 (1.92)	0.15	0.866	0.54 - 1.39	0.12
Pool	2.301 (0.54)	1.00	9.987	4.14 - 24.08	1.00
Riffle	0.248 (0.43)	1.00	1.281	0.63 - 2.60	0.01
Temperature	-0.284 (0.15)	4.00	0.321	0.12 - 0.87	0.89
Brook Trout	-0.481 (0.41)	1.00	0.618	0.31 - 1.21	0.49

The global model predicting large bull trout distributions at night adequately fit (Hosmer-Lemeshow GOF statistic = 5.48, 8 df, $P = 0.70$). However, the ANOVA of global model deviance residuals indicated dependence among observations within streams ($F = 2.62$, 8 df, $P < 0.01$). Hence, I added brook trout presence and stream temperature into the global model to account for dependence among observations within streams. The ANOVA of the global model deviance residuals indicated no detectable dependence among observations within streams ($F = 1.21$, 8 df, $P = 0.29$) and the global model fit adequately (Hosmer-Lemeshow GOF statistic = 9.42, 8 df, $P = 0.31$). Therefore, I assumed that the candidate set of models also fit adequately.

The most plausible model predicting large bull trout distribution at night was the global model and was 3.65 times more plausible than the next best approximating model containing stream depth, current velocity, percent rubble, pool mesohabitat, and stream temperature (Table 13). Scaled odds ratios suggested large bull trout were positively associated with stream depth and pool mesohabitats and were 2.46 times more likely to occur for every 0.20 m increase in depth and 5.22 times more likely to occur in pool mesohabitats (Table 14). Large bull trout were negatively related to current velocity, percent rubble, presence of brook trout, and stream temperature and were 2.07, 1.34, 2.11, and 2.79 times less likely to occur for every OR unit change, respectively (Table 14).

Table 13. Model selection results based on logistic regression relating large bull trout distribution at night to habitat characteristics in Eastern Cascades streams during the summers of 2001 and 2002. Models shown are the 10% confidence set of models.

Candidate Model	Log Likelihood	K	AIC_c	ΔAIC_c	w_i	Percent of Maximum ΔAIC_c Weight
Depth, Velocity, Rubble, Temperature, Pool, Brook Trout	-124.06	7	264.751	0.000	0.781	100.00
Depth, Velocity, Rubble, Temperature, Pool	-126.42	6	267.339	2.588	0.214	27.42

Table 14. Model-averaged parameter estimates, scaled odds ratios (OR), OR confidence intervals (CI), and importance weights from models relating distribution of large bull trout at night to multi-scale habitat characteristics.

Model Parameter	Estimated Coefficient (SE)	OR Unit Change	Scaled OR	90% CI	Importance Weight
Intercept	2.118 (0.96)	-	-	-	-
Depth	4.508 (1.53)	0.20	2.464	1.49 - 4.07	1.00
Velocity	-4.838 (1.97)	0.15	0.484	0.30 - 0.79	1.00
Rubble	-0.019 (0.01)	15.00	0.748	0.64 - 0.87	1.00
Pool	1.652 (0.51)	1.00	5.219	2.27 - 11.98	1.00
Brook Trout	-0.745 (0.35)	1.00	0.475	0.27 - 0.84	0.79
Temperature	-0.256 (0.11)	4.00	0.359	0.18 - 0.73	1.00

The global model predicting adult bull trout distribution at night adequately fit the data (Hosmer-Lemeshow GOF statistic = 0.24, 4 df, $P = 0.99$). The ANOVA of global model deviance residuals indicated no dependence among observations within streams ($F = 0.29$, 2 df, $P = 0.75$). Therefore, I assumed that the candidate set of models also fit adequately.

The most plausible model predicting adult bull trout distribution at night contained pool mesohabitat and percent rubble and was 2.16 times more plausible than the next best approximating model containing pool mesohabitat (Table 15). The composite model contained these two predictors, current velocity, and run mesohabitat (Table 16). Pool mesohabitat and percent rubble had the largest importance weights indicating that there was strong evidence for these two predictors (Table 16). Scaled odds ratios suggested that small bull trout were strongly and positively associated with pool mesohabitats. Bull trout were 565.27 times more likely to occur in pool mesohabitats (Table 16). The CI of the scaled OR for the remaining predictors were wide and contained one, so the precise nature of their relationships could not be determined.

Table 15. Model selection results based on logistic regression relating adult bull trout distribution at night to habitat characteristics in Eastern Cascades streams during the summers of 2001 and 2002. Models shown are the 10% confidence set of models.

Candidate Model	Log Likelihood	K	AIC_c	ΔAIC_c	w_i	Percent of Maximum ΔAIC_c Weight
Pool, Rubble	-8.46	3	25.929	0.000	0.633	100.00
Pool	-10.44	2	27.471	1.542	0.293	46.27

Table 16. Model-averaged parameter estimates, scaled odds ratios (OR), OR confidence intervals (CI), and importance weights from models relating distribution of adult bull trout at night to multi-scale habitat characteristics.

Model Parameter	Estimated Coefficient (SE)	OR Unit Change	Scaled OR	90% CI	Importance Weight
Intercept	-5.523 (3.04)	-	-	-	-
Run	-0.052 (1.84)	0.20	0.990	0.54 - 1.81	0.07
Velocity	-15.600 (24.58)	0.15	0.096	0.00 - 40.74	0.07
Rubble	0.061 (0.04)	15.00	2.478	0.95 - 6.44	0.70
Pool	6.337 (2.90)	1.00	565.268	4.89 - 65342.37	0.99

Available percent fine substratum from streams not containing brook trout was greater than in streams containing brook trout (Figure 22). However, the difference was of minimal biological importance (i.e., 5.19 %). The remainder of the microhabitat variables did not differ in their availability between streams containing brook trout and those where brook trout were absent (Figures 22, 23).

Temperature within non-brook trout streams (mean = 8.66 °C) was less than 1 °C higher than from streams containing brook trout (mean = 8.38 °C), which I did not consider to be a biologically meaningful difference. The 95% CI (-0.12, 0.69) of the difference between the two means contained zero indicating an imprecise estimate of the difference.

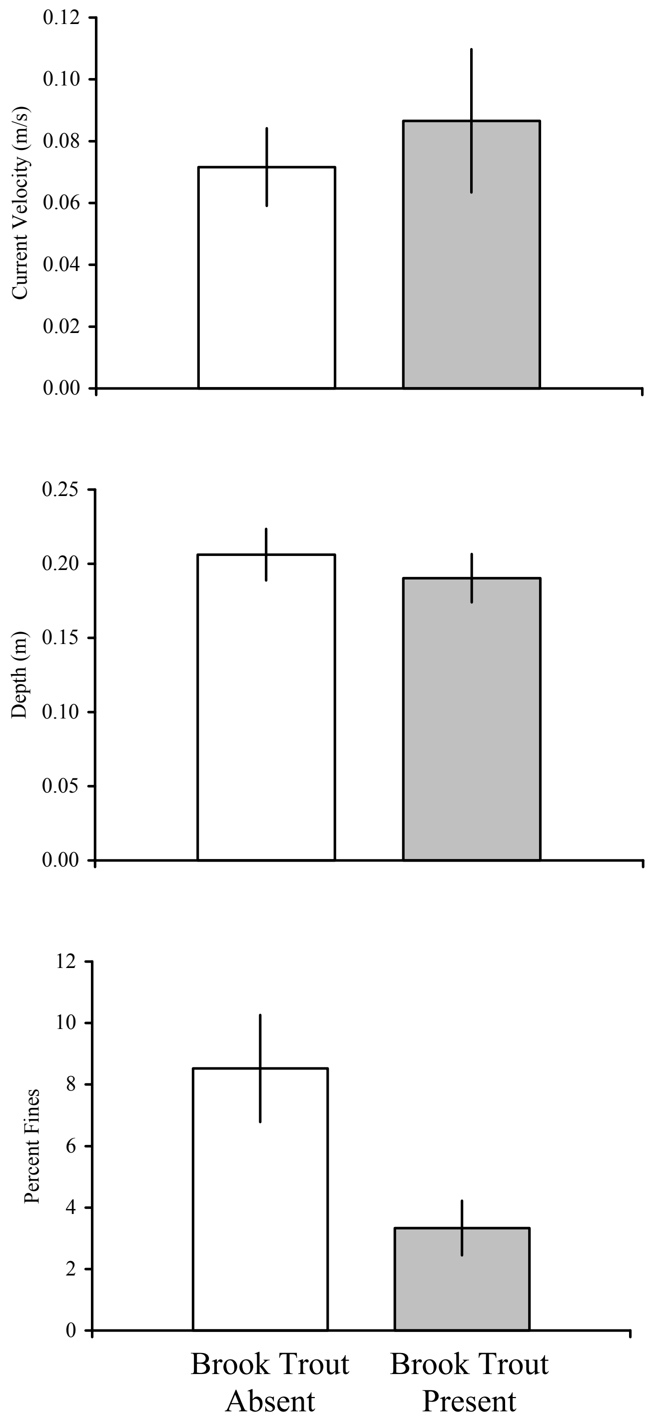

Figure 22. Mean available current velocity, depth, and percent fines from Eastern Cascades streams surveyed during the summers of 2001 and 2002 separated by presence of brook trout. Vertical lines represent $\pm$ 1 standard error.

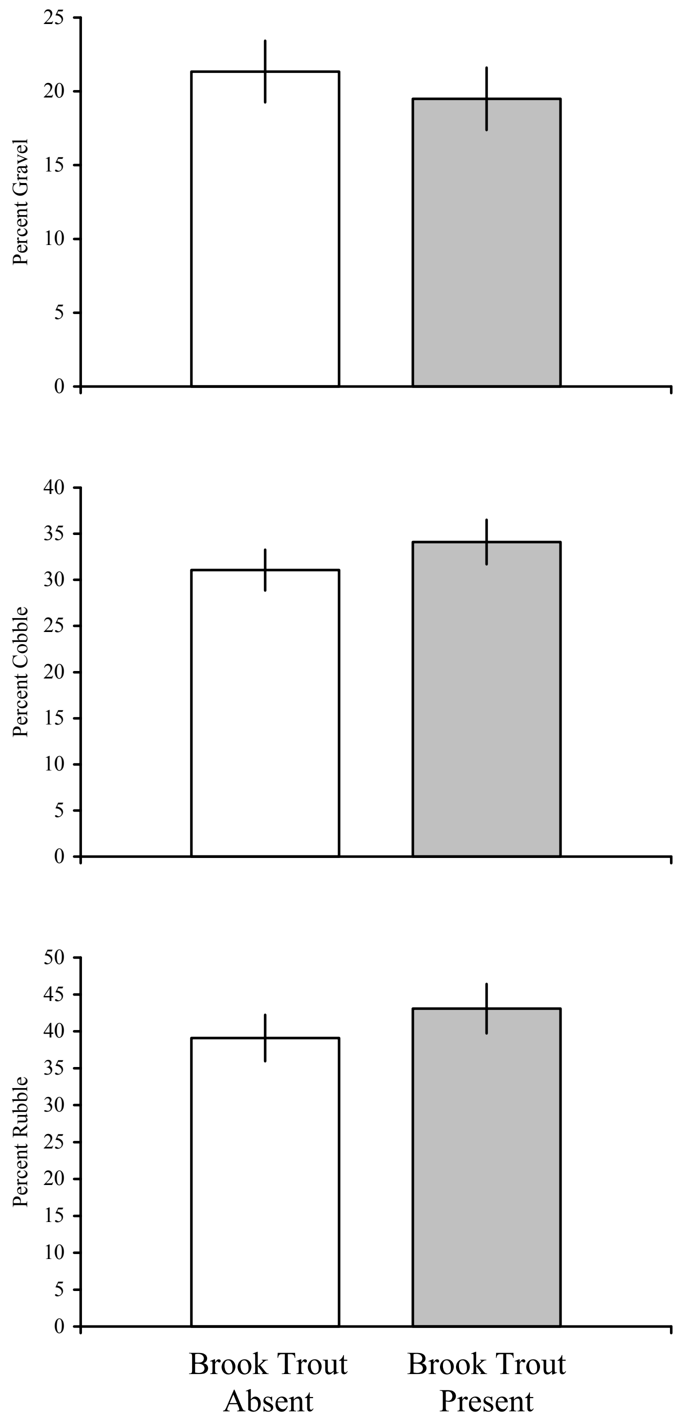

Figure 23. Mean available percent gravel, cobble, and rubble from Eastern Cascades streams surveyed during the summers of 2001 and 2002 separated by presence of brook trout. Vertical lines represent ± 1 standard error.

CHAPTER 5

DISCUSSION

The majority (88%) of my observations occurred at night, corroborating previous work documenting nocturnal behavior by bull trout (Thurow 1997; Jakober et al. 1998, 2000; Polacek and James 2003). Diel activity of fishes is governed by food availability and risk of predation (Metcalfe et al. 1999). Optimal activity of fish, therefore, should represent a time when food availability is greatest but when predation risk is minimal. The propensity for aquatic macroinvertebrates to drift at night is greater than during the day (Waters 1962), whereas risk of predation to fishes during the day is greater than at night (Metcalfe et al. 1999). Given that bull trout are adapted to forage in low light conditions (Schutz and Northcote 1972), nocturnal activity may represent a mechanism by which bull trout optimize foraging while reducing the risk of predation.

Bull trout always were observed < 10 cm from the streambed regardless of time of day or size class. Previous researchers also have shown that bull trout are closely associated with the streambed (Thurow 1997; Bonneau and Scarnecchia 1998; Spangler and Scarnecchia 2001; Polacek and James 2003). Current velocity adjacent to the streambed is lower than near the water surface (Hynes 1970), so fishes near the streambed expend less energy to maintain their position than those within the water column (Facey and Grossman 1990; 1992). Anatomical adaptations also have allowed fishes to cope with living in lotic environments (Bisson et al. 1988). Although generally fusiform, bull trout have a broader head and appear more dorso-ventrally compressed than their congener, Dolly Varden (Cavender 1978). These features create a streamlined shape that is well suited to reducing the effects of current velocity (Bisson et al. 1988). Hence, the morphological features and benthic nature of bull trout may allow them to minimize energy expenditure in higher velocity areas of streams.

Bull trout also may use the streambed areas for shelter (henceforth, concealment). Risk of predation during the day may lead to a diel shift in concealment (Metcalfe et al. 1999). Thurow (1997) reported all juvenile (50 – 250 mm) bull trout concealed within the substrata during the day and observed them only after turning over stones. Although I did not manipulate the substrata during observations, the few bull trout I observed during the day were concealed adjacent to or in contact with organic debris, vegetation, large substrata, or large woody debris. Additionally, I found that bull trout tended to be closer to cover during the day (mean = 0.18 m) than at night (mean = 0.25 m), which is similar to previous investigations of bull trout behavior in an artificial stream channel (Baxter and McPhail 1997) and in Idaho (Bonneau and Scarnecchia 1998) and Montana (Jakober et al. 2000) streams. The risk of predation is greater during the day than at night and can be minimized by maintaining close association with cover (Metcalfe et al. 1999). Thus, I hypothesize that bull trout exhibit concealment behavior during the day to avoid predators but stray from cover at night to feed.

Previous research suggested that large, unembedded substrata provide vital habitat (e.g., cover) for stream-dwelling bull trout (Thurow 1997; Bonneau and Scarnecchia 1998). In contrast, I found small and large bull trout primarily used microhabitats with small (i.e., fines, gravel) substrata and bull trout distribution within streams was negatively related to large (i.e., rubble) substratum during the day and night. Small substrata, such as fines and gravel, offer little value for fish cover whereas larger substrata, such as cobble and rubble, can be important cover components (Bjornn and Reiser 1991). However, fine substratum does provide important habitat for burrowing mayflies (e.g., Ephemeridae) and Chironomidae (Merritt and Cummins 1996). The depositional areas within my study sites accumulated organic debris that likely served as a food source for Plecoptera, Trichoptera, and Diptera (Merritt and Cummins 1996), which juvenile bull trout use during the summer months (Nakano et al. 1992; Rieman and McIntyre 1993 and references therein). As such, the relationship with small substrata may represent foraging areas for aquatic insects.

Alternatively, my observations of small and large bull trout using smaller substrata may be an artifact of sampling bias rather than a true habitat use pattern. Although percent rubble was negatively related to the distribution of small and large bull trout during the day and night, I cannot discredit the importance of larger substrata for cover. Indeed, Thurow (1997) reported juvenile (50 – 250 mm) bull trout conceal within substrata during the day, up to 32 cm below the streambed. I believe small and large bull trout may have been concealed within larger substrata during the day and were not visible during sampling, which lessened my ability to detect individuals. My results, however, did suggest adult bull trout had an affinity for rubble substratum, which corroborates previous work (Thurow 1997; Bonneau and Scarnecchia 1998). These larger individuals are more conspicuous and hence, easier to detect, than smaller individuals. Moreover, the adult bull trout were often too large to conceal themselves within the substrata, which may explain the pattern of affinity for larger substrata by adult bull trout.

My observations suggest that individual bull trout were relatively solitary. Rainbow trout (1% of observations) were the only other species observed within 20 cm of bull trout focal points, although my study sites contained populations of westslope cutthroat trout and nonnative brook trout. The solitary nature of bull trout may be due to several factors. First, the solitary nature of bull trout may be a mechanism for partitioning resources. Bull trout evolved in glacially dominated headwater stream systems (Haas and McPhail 2001) that are generally much less productive than similar surface or ground water fed systems (Fureder et al. 2001). Hence, food resources were presumably very scarce. Bull trout may have developed this solitary behavior as a means of minimizing the inter- and intraspecific competition for the scarce resources. Second, the solitary nature of bull trout may be due to its phylogenetic history of coexistence with native salmonids. Rainbow trout and westslope cutthroat trout, which are water column species, have coevolved with bull trout, a benthic species (Behnke 1992; Nakano et al. 1992, 1998). The phylogenetic history of coexistence with these species may have allowed each species to exploit different resources spatially (*sensu* Grossman and Freeman 1987), minimizing potential competition. Lastly, the solitary nature of bull trout may be a mechanism to reduce the risk of cannibalism. Indeed, bull trout are known to be piscivorous (Boag 1987; Donald and Alger 1993; Beauchamp and Van Tassell 2001) and cannibalistic (Cavender 1978; Beauchamp and Van Tassell 2001; Polacek and James 2003). Wilhelm et al. (1999) reported small ($\leq$ 250 mm fork length) bull trout avoided large ($>$ 250 mm fork length) bull trout in a small alpine lake because of the risk of cannibalism. Assuming this avoidance behavior is similar in streams, bull trout may segregate by size (see below) and remain solitary to evade the risk of cannibalism.

I observed all size classes of bull trout using deeper microhabitats during the day than at night. As well, I observed the largest (i.e., adult) bull trout using the deepest microhabitats during the day and night. My findings are consistent with those of previous studies documenting use of deeper areas by bull trout during the day than at night (Bonneau and Scarnecchia 1998; Jakober et al. 2000; Muhlfeld et al. 2003; Polacek and James 2003). Deeper water may provide greater safety from avian and terrestrial predators than shallower water (Power 1984). Smaller fish are susceptible to avian and terrestrial predators and are more vulnerable to predation by larger fish species (Harvey 1991). Larger, predatory fish can cause smaller fish to change habitat use from deeper stream areas to shallower stream margins (Power et al. 1985). Thus, larger bull trout may be using deep areas (e.g., pool mesohabitats) to avoid terrestrial predators, whereas smaller bull trout may be using shallower pocket water to avoid predation from larger, aquatic and terrestrial predators.

All size classes of bull trout had affinities for low velocity habitats during the day and night. Use of low velocity areas has previously been documented as an important microhabitat component for bull trout (Thurow 1997; Spangler and Scarnecchia 2001) and other salmonids (Everest and Chapman 1972; Bozek and Rahel 1991; Heggenes et al. 1991; Muhlfeld et al. 2001). Fish should occupy habitats that optimize the potential to increase their energy gain (Werner and Hall 1974). Occupying high current velocity positions within a stream requires high-energy expenditures (Facey and Grossman 1990; 1992). Stream fishes reduce energy expenditure and increase energy gain by selecting microhabitats with reduced velocity in areas adjacent to food supply (Fausch 1984). Thus, I hypothesize bull trout were attempting to minimize energy loss by maintaining positions in low velocity areas while maximizing potential for energy gain by remaining adjacent to food supply.

Distribution of bull trout was negatively related to increasing stream temperatures. For example, I found that for every 4.0 ºC increase in stream temperature, bull trout were 2.79 – 3.11 times less likely to be observed. Compared to other salmonids, bull trout require some of the coldest water to survive (Rieman and McIntyre 1993; Selong et al. 2001). Mean stream temperatures of my study sites ranged from 7.0 – 12.5 ºC. At temperatures above 12.0 ºC, few bull trout observations were made. Similar findings indicated bull trout densities increased below 13.9 ºC in several northern Idaho streams (Saffel and Scarnecchia 1995). Although mine was not a study of thermal tolerances of bull trout, my observations agree with previous studies suggesting that increased stream temperature has the potential to reduce bull trout populations (Fraley and Shepard 1989; Saffel and Scarnecchia 1995; Selong et al. 2001; Dunham et al. *in press*) and hence, the number of observations of habitat use within streams.

Distribution of bull trout also was negatively related to the presence of brook trout. My results suggest that bull trout at night were 1.62 – 2.11 times less likely to occur if brook trout were present in my study sites. This effect could not be attributed to differences in habitat availability or temperature because I found similar habitat availability and temperature between streams containing brook trout and non-brook trout streams. Brook trout compete for resources with bull trout, which may regulate densities of the latter (Nakano et al. 1998; B. Rieman *personal communication*). In sympatry, brook trout have been shown to achieve greater growth than bull trout (Gunckel et al. 2002) and the greater growth and hence, size of brook trout may lead to displacement of bull trout. Given that bull trout and brook trout overlap throughout much of the bull trout range (Rieman et al. 1997; Thurow et al. 1997), the potential exists for brook trout to displace bull trout from optimal habitat or foraging locations (B. Rieman *personal communication*), which may eventually cause declines in bull trout populations.

I found that all size classes of bull trout bull trout had an affinity for pool mesohabitats. In my study sites, large woody debris often was the dominant pool-forming feature and I often observed bull trout using large woody debris as cover. Large woody debris pieces, aggregates, and root wads often are important pool forming features (Beschta and Platts 1986; Frissell et al. 1986). Pools formed by large woody debris provide quality-rearing habitat and cover for stream-dwelling fish (Angermeier and Karr 1984; Benke et al. 1985; Beschta and Platts 1986; Meehan 1991). Large woody debris within streams also can function as a substratum and food source for aquatic macroinvertebrates (Benke et al. 1984). Consequently, I believe that bull trout were associated with pool mesohabitats formed by large woody debris because these habitats may have provided concealment during the day from predators, refuge from high velocities, and may have allowed limited foraging.

A potential limitation of my study is that I could only use data for bull trout I observed, not those missed during sampling, which may have biased my data. The ability to detect bull trout in streams is significantly influenced by capture (sighting) efficiency (Peterson et al. 2002). For example, bull trout are more difficult to observe during the day and in larger streams (Thurow et al. 2003). The lesser number of bull trout I observed during the day (N = 26) compared to night (N = 187) was consistent with previous research documenting lower sighting efficiency during the day (Bonneau et al.

1995; Thurow et al. 2003). However, my observations of bull trout preference for deeper microhabitats were not consistent with the stream size effects. Bull trout sighting efficiency also is positively related to stream temperatures (Thurow and Schill 1996). In contrast, my bull trout observations decreased with increasing stream temperatures. Thus, I believe that this pattern was not an artifact of sampling bias. Stream-dwelling bull trout and other salmonids also move significant distances (25 - 100 m) in response to snorkel sampling activities (Peterson et al. 2003), potentially biasing fish-habitat studies. Bull trout movement, however, was not significantly related to physical habitat characteristics; hence fish movement may not have biased my observations of habitat use. Nonetheless, I acknowledge that differential detectability and fish movement during my surveys may have confounded my estimates of bull trout habitat use. Future studies of bull trout may, therefore, require investigating the effects of incomplete detectability in fish-habitat use models.

Management Implications

The conservation and restoration of stream-dwelling bull trout populations will require the maintenance and restoration of critical juvenile rearing habitats. My study suggests that deep, low velocity microhabitats with depositional substrata are important to different size classes of bull trout during the day and at night within Eastern Cascades streams. These characteristics are indicative of pool and pocket water microhabitats, suggesting that management for bull trout may be applied at the mesohabitat level. Indeed, chi-square tests and logistic regression models indicated that bull trout exhibited an affinity for pool and pocket water mesohabitats. Moreover, pool mesohabitats generally had the largest importance weights compared to other microhabitat variables. These findings suggest that pool and pocket water mesohabitats may be important summer rearing habitats for juvenile bull trout. Additionally, mesohabitats are formed by interactions between the river and surrounding landscape (Frissell et al. 1986) and as such, they may form a convenient basis for estimating the effect of land management on stream habitats and ultimately, bull trout. Therefore, I believe that bull trout habitat conservation and management should be concentrated at the mesohabitat scale.

Pools within my study sites often were formed by large woody debris that also was used as cover by bull trout. Large woody debris can create pools, decrease current velocity, and increase retention of organic matter that supports aquatic invertebrates (Gregory et al. 1991). By providing suitable fish and invertebrate habitat, large woody debris in streams may, therefore, support higher densities of trout (e.g., Flebbe and Dolloff 1995). Large woody debris is generally recruited from trees in adjacent riparian zones (Gregory et al. 1991). These riparian trees also provide shade, reducing solar radiation and minimizing increases in stream temperature (Gregory et al. 1991) that can cause reduced growth and survival of bull trout (Selong et al. 2001). Consequently, preserving riparian zones from logging or grazing may serve as an effective management tool for ensuring formation of pools that provide cover and critical rearing habitat for bull trout populations.

As suggested by my results, bull trout may be less likely to be found in the presence of brook trout. Brook trout are thought to be partly responsible for the decline in native fish populations (Rieman et al. 1997; Thurow et al. 1997). Once introduced into a watershed, brook trout are capable of expansion throughout a river system (Adams et al.

2002) and it appears that brook trout may be capable of displacing populations of bull trout to unsuitable habitats (Gunckel et al. 2002; B. Rieman *personal communication*). Reducing the effect of brook trout may require population control (removal) or reducing the potential for their expansion within the range of bull trout. Alternatively, the installation of artificial barriers has been proposed as a mechanism to reduce the potential for brook trout expansion in rivers (Thompson and Rahel 1998; Kruse et al. 2001). However, these methods are not without limitations. First, removal via electrofishing or ichthyocides may fail to capture all brook trout within streams. As a result, remaining brook trout may experience less competition for resources that may result in higher growth and fecundity (Hunt 1969). Second, success of artificial barriers depends on the size of watershed in which they are installed. For example, fishes within a smaller watershed with less stream connectivity may be more susceptible to environmental perturbations (e.g., rain-on-snow events) than those within a larger watershed with higher stream connectivity. Moreover, artificial barriers may block migration of fluvial or adfluvial bull trout that may have the ability to refound populations after environmental disturbances (Rieman and McIntyre 1993). Hence, I believe that brook trout removal may be a waste of scarce resources (e.g., manpower) and the installation of barriers may be risky. Based on my findings, I believe that management efforts should be focused on conserving bull trout rearing habitat and restoring degraded habitats that will be necessary for the persistence of the species.

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APPENDIX

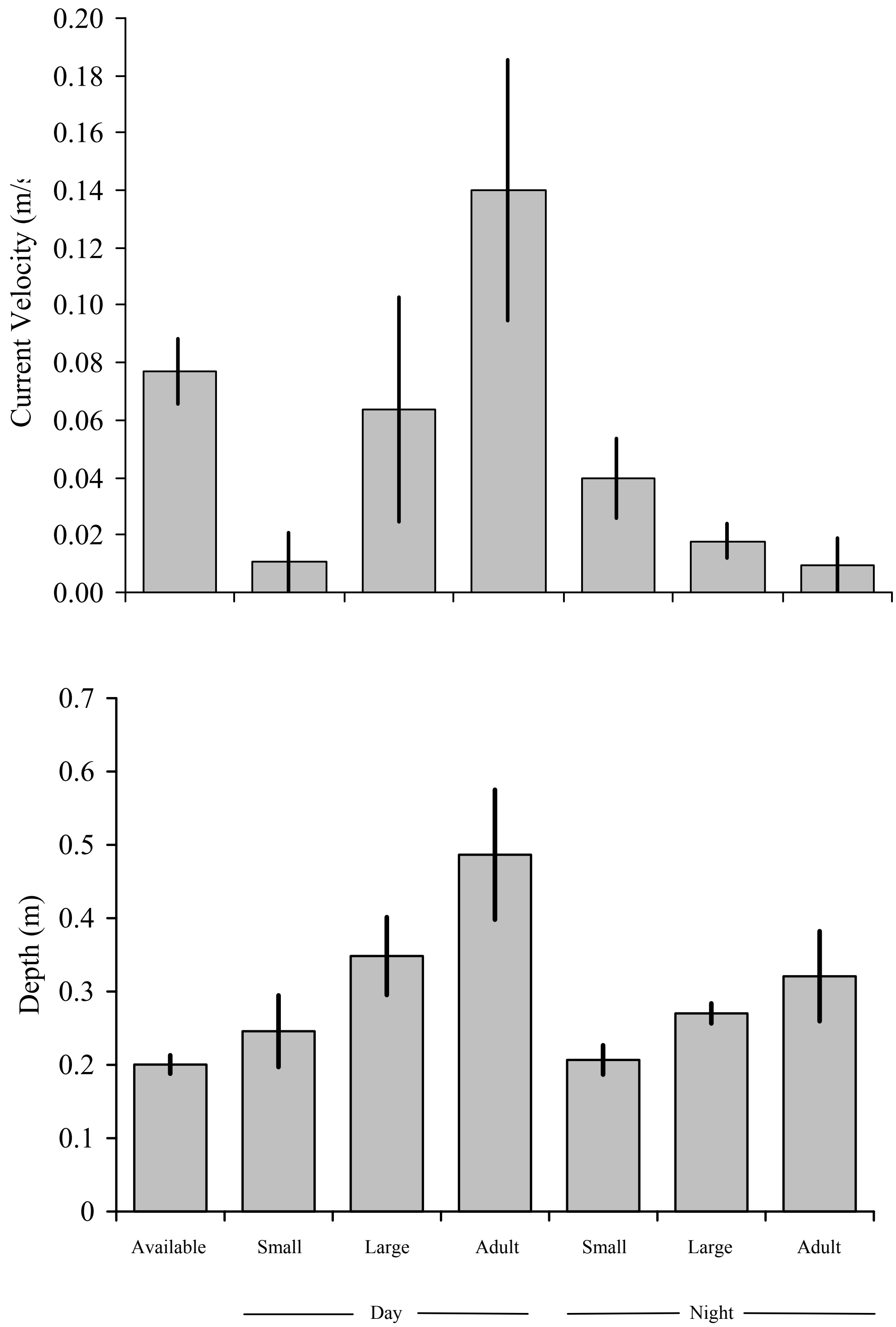

Figure A1. Mean available current velocity and depth and mean current velocity and depth used by small, large, and adult bull trout during the day and at night from Eastern Cascades streams during the summers of 2001 and 2002. Vertical lines represent $\pm$ 1 standard error.

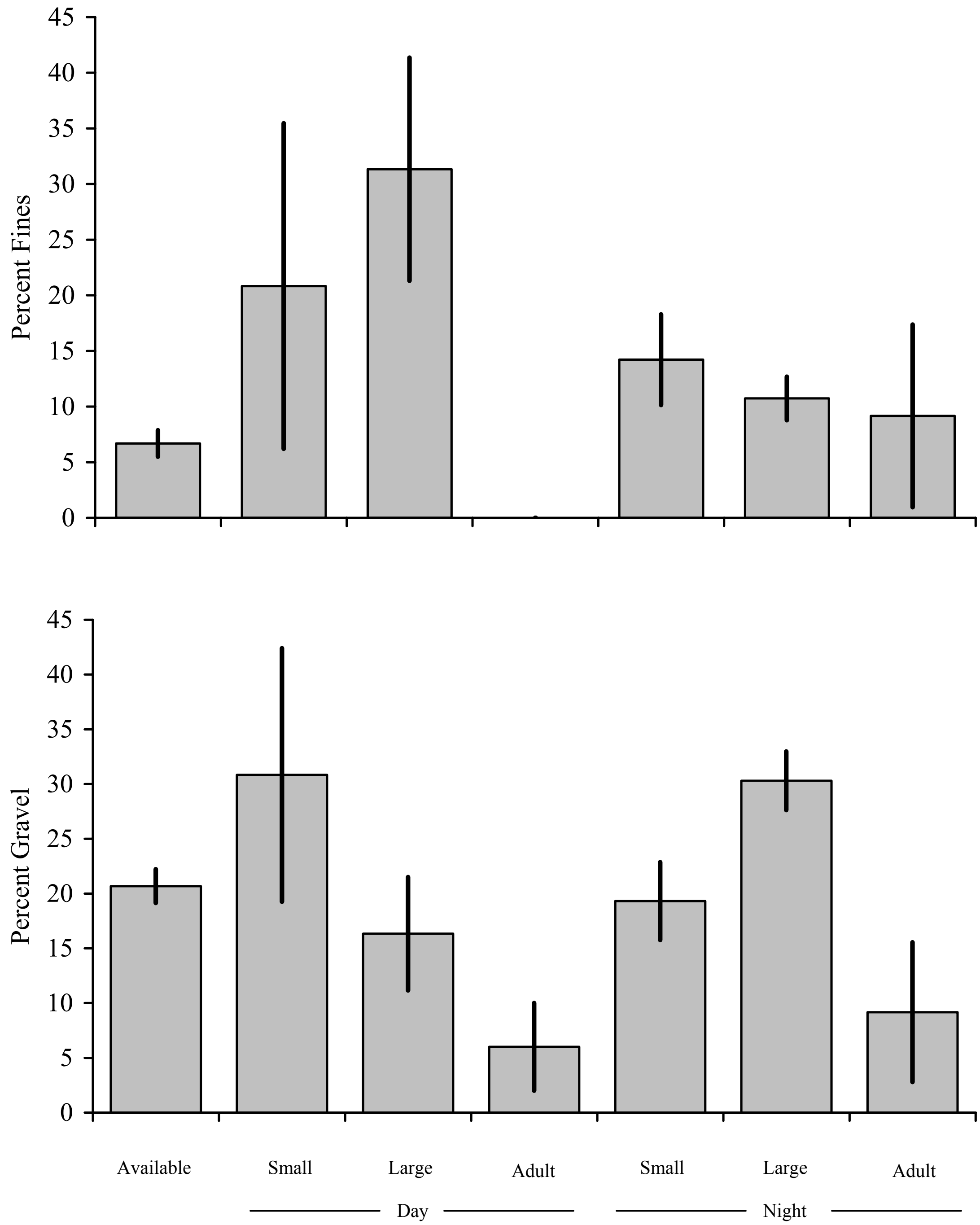

Figure A2. Mean available percent fines and percent gravel and mean percent fines and percent gravel used by small, large, and adult bull trout during the day and at night from Eastern Cascades streams during the summers of 2001 and 2002. Vertical lines represent ± 1 standard error.

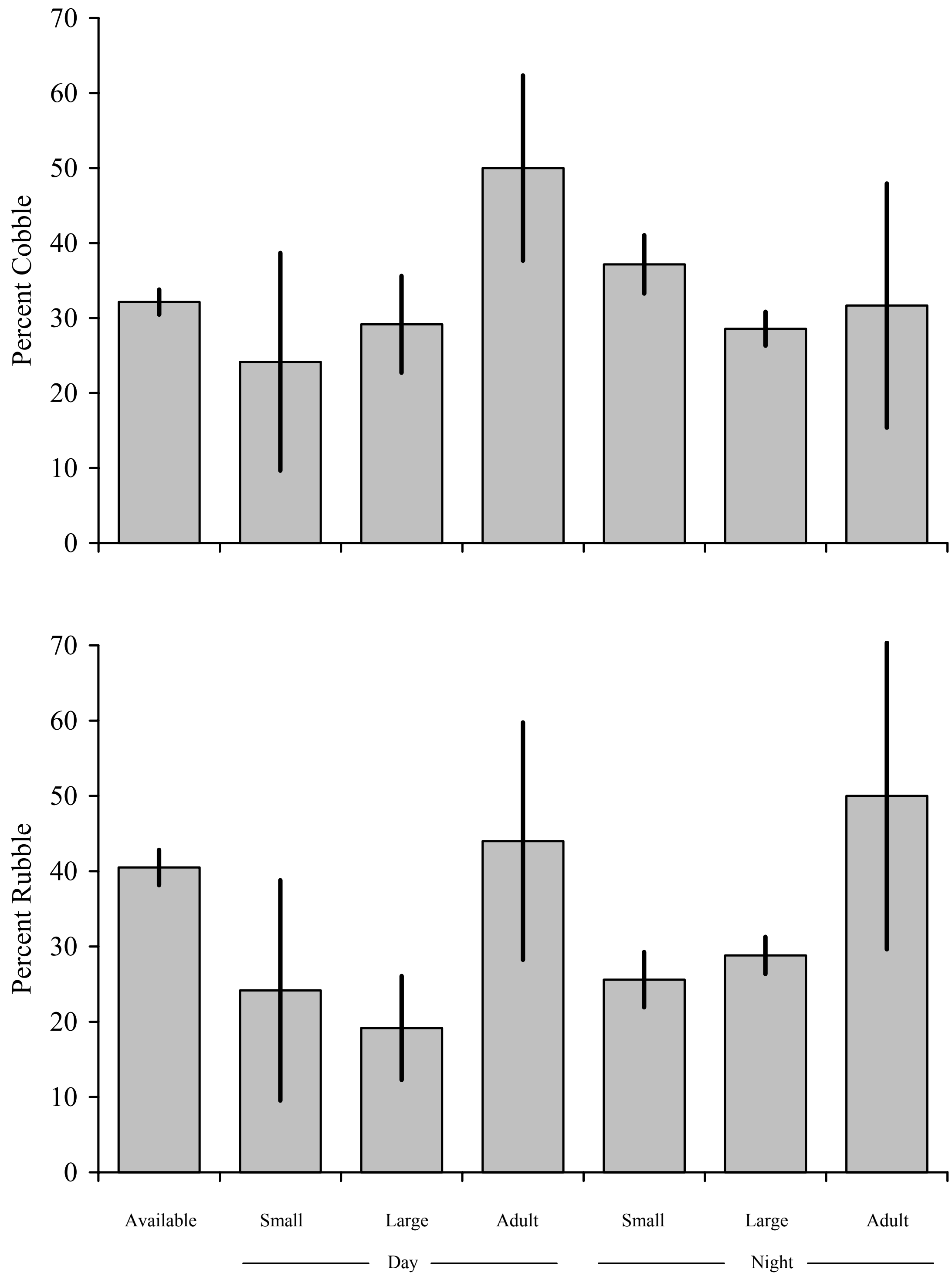

Figure A3. Mean available percent cobble and percent rubble and mean percent cobble and percent rubble used by small, large, and adult bull trout during the day and at night from Eastern Cascades streams during the summers of 2001 and 2002. Vertical lines represent $\pm$ 1 standard error.