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[Article]

Physical, Biotic, and Sampling Influences on Diel Habitat Use by Stream-Dwelling Bull Trout

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Abstract.—We used daytime and nighttime underwater observation to assess microhabitat use by bull trout *Salvelinus confluentus* ($N = 213$) in streams of the intermountain western USA during the summers of 2001 and 2002. We recorded fish focal points and measured a set of habitat characteristics as well as habitat availability via line transects. Bull trout were benthic and solitary; most (88%) were observed at night. We developed a conditional logistic regression model to account for the effect of fish movement in response to snorkeling, and we fitted 18 candidate models to evaluate the relative influences of biotic and abiotic factors on habitat use. The candidate models were also fitted with a naïve logistic regression (i.e., no movement) to evaluate the effects of movement on inferences of microhabitat use. The most plausible model describing bull trout habitat use was the same for the conditional and naïve regressions and included depth, velocity, percent rubble substratum, and the day × depth, body size × depth, and body size × day × depth interactions. The presence of brook trout *S. fontinalis* and the abundance of conspecifics did not strongly influence microhabitat use by bull trout. The relative rankings of the remaining models differed substantially between the conditional and naïve models. Relative to the conditional models, the naïve models overestimated the importance of diurnal differences in habitat use and overestimated the use of deepwater habitats, particularly during the day. Both model types suggested that all sizes of bull trout were generally found in deeper, low-velocity habitat at night, whereas small bull trout (70–90 mm total length) were found in shallower habitats during the day. We recommend that biologists account for fish movement in response to sampling to avoid biasing modeled habitat use patterns by bull trout.

Recognizing and understanding how stream-dwelling fishes interact with their environment is paramount for effective management (Lobb and Orth 1991; Kwak et al. 1992; Orth and White 1993; Grossman and Ratajczak 1998; Peterson and Rabeni 2001). Studying habitat use at a microhabitat scale provides spatially explicit information about fish affinities for characteristics such as water depth and substrate (LaCroix et al. 1995; Petty and Grossman 1996). Microhabitat studies also reveal size-related (Rosenberger and Angermeier 2003), seasonal (Baltz et al. 1991), and diel (Bonneau and Scarnecchia 1998) variations in habitat use, which are important for understanding fish life history requirements.

Resource managers strive to identify key habitats and the mechanisms responsible for habitat use patterns. Habitat use may be mediated by abiotic and biotic factors, including intra- and interspecific competition (Fausch and White 1986), predation (Power 1984; Harvey 1991), and environmental variables (Fausch et al. 1994; Grossman et al. 1998). Identifying the factors influencing habitat use can be crucial for developing effective conservation strategies, particularly for rare and sensitive species, such as the bull trout *Salvelinus confluentus*.

Bull trout are to be 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 one-half of the historical range,

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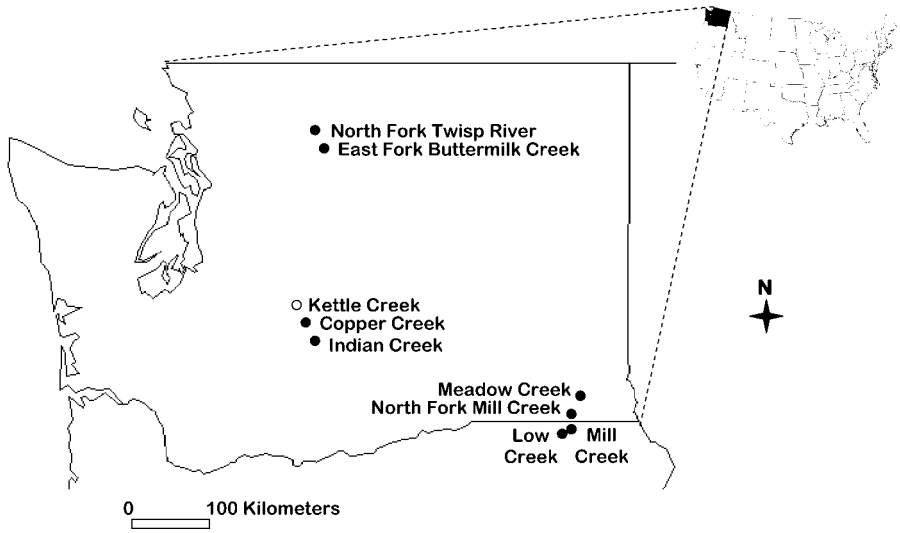

FIGURE 1.—Locations of the study sites at which bull trout diel habitat use was examined during summer 2001 and 2002 (filled circles represent single sample sites, the open circle for Kettle Creek two proximate sites).

and much of that loss has occurred throughout the southern extent (Rieman et al. 1997). Anthropogenic activities have apparently caused much of the decline in bull trout (Rieman and McIntyre 1993; Rieman et al. 1997). Logging, 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). The subsequent decline in distribution and abundance led to the listing of the bull trout as a threatened species under the U.S. Endangered Species Act (USFWS 1998).

An expanding body of literature suggests that the introduction and invasion of brook trout *Salvelinus fontinalis* has also adversely affected bull trout. Brook trout are known to hybridize with bull trout (Leary et al. 1983; Kitano et al. 1994), which may lead to a reduction in the genetic diversity and integrity of bull trout. Further, brook trout mature at a younger age than bull trout (Scott and Crossman 1973) and may outcompete bull trout for essential resources (Nakano et al. 1998; Gunckel et al. 2002). Interspecific competition can result in the displacement of bull trout populations at larger scales (Rieman et al. 2006), potentially increasing the populations' risk of extirpation from environmental perturbation (Rieman and McIntyre 1993; Dunham and Rieman 1999).

The behavior of stream-dwelling fishes is commonly assessed via snorkeling (Dolloff et al. 1996). A fundamental assumption of snorkeling is that the presence of a snorkeler does not substantially influence fish behavior. Recent research, however, suggests that bull trout do respond to the presence of snorkelers and that the response can be influenced by factors such as time of day and habitat characteristics (Peterson et al. 2005). Observed habitat use patterns derived from snorkeling can thus be confounded by fish response and may result in biased evaluations of bull trout habitat use. Consequently, failure to address the influence of snorkelers on fish behavior may result in an erroneous determination of bull trout habitat use and poor management decisions.

For successful conservation and restoration of imperiled bull trout, the identification and management of habitats essential for the species' persistence are needed. Protection of key habitats can only be accomplished if managers understand bull trout resource use, which in turn requires an understanding of factors influencing habitat use and an evaluation of the influence of sampling method on observed fish behavior. Therefore, the objectives of our study were to (1) describe daytime and nighttime microhabitat use by stream-dwelling bull trout, (2) identify the biotic and abiotic factors that influence habitat use, and (3) examine the influence of fish's response to sampling on inferences about habitat use patterns.

Study Area

We studied the diel microhabitat use of stream-dwelling bull trout in 10 streams east of the Cascade Range in Washington and Oregon (Figure 1). Our goal was to evaluate diel habitat use in streams covering a broad range of physical habitat conditions within the range of bull trout. We therefore randomly selected

study sites using stream-habitat-based strata. Each stratum represented typical physical and chemical conditions encountered in Washington streams supporting bull trout (Peterson and Banish 2002). The strata ($N = 7$) represented relatively large ranges in physical and chemical conditions, including stream width, gradient, percent of undercut banks, density of large woody debris (defined below), and conductivity. For instance, one stratum consisted of large (mean wetted width > 7.5 m), low-gradient ($<2.6\%$) streams with few undercut banks ($<20\%$), moderate wood density (between 0.05 and 0.10 pieces/m^2), and low conductivity (<50 μS/cm). In contrast, another stratum consisted of moderately sized (mean wetted width between 5.0 and 7.5 m), moderate-gradient (between 2.6% and 4.0%) streams with few undercut banks, low wood density (≤ 0.05 pieces/m^2), and low conductivity.

Eight of the study streams also were used to evaluate the movement of salmonids in response to snorkeling (Peterson et al. 2005). We evaluated diel bull trout habitat use from July to September 2001–2002, when water levels had receded after snowmelt and when underwater visibility was optimal. All study sites contained a variety of habitats, and upstream and downstream site boundaries were marked with flagging prior to fish and habitat sampling.

Methods

Habitat use.—We assessed bull trout habitat use via snorkeling. We completed both daytime and nighttime snorkeling at 10 study sites, only daytime snorkeling at Mill Creek, and only nighttime snorkeling at the North Fork Twisp River. Prior to snorkeling, crews estimated underwater visibility. Horizontal visibility was estimated by averaging readings at three locations using a salmonid silhouette and the Secchi disk-like approach described by Thurow et al. (2006). Each study site was randomly assigned either day or night snorkeling as the first sampling method. Day snorkeling was completed between 1000 and 1500 hours, and night snorkeling occurred between 2230 and 0430 hours. We used identical techniques for evaluating habitat use during the day and night except that night snorkeling was completed with the aid of an underwater halogen light. All snorkeling began at the downstream boundary of the study site and proceeded upstream. During sampling, the snorkeler moved slowly and deliberately upstream to minimize disturbance and displacement of bull trout. An assistant on the streambank followed the snorkeler at all times and provided a light for viewing undercut banks or other poorly lit areas during the day. When a bull trout was located, the snorkeler visually estimated total length (TL) to the nearest size-class (70–99, 100–199, 200–300 mm), the distance of the fish from the streambed, and the presence and species of other fish within 20 cm of the bull trout's focal point (the point beneath the anterior portion of the fish: Grossman and Freeman 1987); data were recorded on a wrist slate. The focal point was marked with a labeled washer to facilitate microhabitat measurements after snorkeling was completed. The snorkeler also recorded the presence of all fish species observed in the study site. This process was continued until the upstream boundary of the study site was reached.

Habitat measurements.—After snorkeling, we measured the microhabitat characteristics at the locations where bull trout were detected (henceforth, habitat use) and of the study sites as a whole (henceforth, habitat availability). Habitat use and availability data were collected during daylight hours after day and night snorkel surveys were completed. Similar to previous studies, we defined microhabitat as a 20-cm × 20-cm square below a bull trout's focal point (Grossman and Freeman 1987). Microhabitat measurements included focal point velocity, mean column velocity, depth, distance from the streambed, distance to cover, and substrate composition. Focal point and average velocities were measured with a calibrated Geopacks basic flowmeter (Geopacks, Hatherleigh, Devon, UK). When water column depth was less than 75 cm, we measured average velocity at 0.6 × depth. For depths greater than 75 cm, average velocity was estimated as the average of readings taken at 0.2 and 0.8 × depth. Substrate composition was visually estimated and categorized as rubble (>150 mm), cobble (75–150 mm), gravel (6–75 mm), and fines (≤ 6 mm).

We measured habitat availability using a line transect method. Beginning at the lower end of each study site, a minimum of 13 transects (mean = 15) were established perpendicular to the flow at 10-m intervals. For consistency, we recorded habitat measurements in an upstream direction, starting on the left bank and proceeding to the right. At each transect, we measured microhabitat availability at locations equal to 0.25, 0.50, and 0.75 of wetted width using the procedures detailed above. In each site, we counted the number of pieces of woody debris, which we defined as wood pieces of at least 3 m in length and 10 cm in diameter lying within the wetted channel. Wood density was estimated as the total number of wood pieces divided by the wetted width. We also recorded the number and lengths of pools. We only counted pools with lengths greater than or equal to the wetted channel width. Percentage of pool habitat was calculated as total pool length divided by study site length.

Statistical analysis.—Bull trout habitat use may be influenced by intraspecific interactions. Therefore, we estimated bull trout abundance for each size-class prior

to statistical analysis. For each study site, we estimated abundance by summing the total number of bull trout detected and adjusting that value with snorkel efficiency models, that is,

$$A_i = \frac{N_i}{\hat{\pi}_i} \quad (1)$$

where A_i is the adjusted number of individuals, $\hat{\pi}_i$ is predicted snorkel efficiency expressed as a fraction, and N_i is the number individuals of size-class i counted during snorkeling. We estimated $\hat{\pi}_i$ using snorkeling efficiency models described by Thurow et al. (2006) and site-specific habitat data. Detection data from our study streams were used to develop the snorkeling efficiency models in Thurow et al. (2006).

We were unable to measure available distance to cover for comparison with observed distance to cover. Therefore, we 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, we computed mean differences and 95% confidence intervals that provided information of the magnitude and precision of estimated differences (Johnson 1999).

We examined bull trout microhabitat use by means of logistic regression in which observed bull trout presence was coded as 1 and habitat availability within a stream was coded as 0. Thus, a positive relationship with a microhabitat variable indicated that bull trout used that microhabitat disproportionately to its availability.

Fish movements in response to sampling activities may confound attempts to assess fish habitat use (Peterson et al. 2005). For example, Peterson et al. (2005) assessed bull trout movement in response to common sampling techniques and found that the proportion of fish (mean TL = 148 mm) moving upstream from a 50-m reach averaged 28% and 25% for day and night snorkeling, respectively. Movement also was negatively related to the amount of fine substrate and water depth and positively related to the depth of the adjacent upstream habitat unit. To account for fish movement in this study, we jointly modeled species presence and movement following Peterson et al. (2005) as follows:

$$P(d) = P(\mathrm{Oc}) \times P(s|\mathrm{Oc}), \quad (2)$$

where $P(d)$ is the probability of observed presence (detection); $P(\mathrm{Oc})$ is the probability of actual presence, modeled using a logistic regression model; and $P(s|\mathrm{Oc})$ is the probability that a species remained at a location during sampling. The probability of fish remaining at a location was estimated for both the habitat use and habitat availability locations based on existing day and night snorkeling models (Peterson et al. 2005). These models illustrated that bull trout moved upstream more often than downstream and that movement rates were related to sampling method and habitat complexity. The joint estimation of species nonmovement and presence precluded the use of traditional maximum likelihood methods. An appropriate method for jointly modeling species presence and movement is the Markov chain–Monte Carlo (MCMC) method (Fonnesbeck and Conroy 2004; Peterson et al. 2005). We used the MCMC method as implemented in PyMC version 2.3 (Fonnesbeck 2005) to fit models relating bull trout presence to microhabitat characteristics. All models were fit using 100,000 iterations, a 25,000-iteration burn-in (i.e., the first 25,000 MCMC iterations were dropped), and diffuse priors. Models also included a random effect to account for statistical dependence among observations taken within a stream study site.

To examine the possible influence of fish body size, time of day, and the presence of brook trout on bull trout microhabitat use, observations were coded as binary indicators (0 or 1) prior to model fitting. Three size-classes were so coded, namely, 100–199 mm, 200–300 mm, and 70–99 mm, the last serving as the baseline. Observations of bull trout presence during day snorkeling events received a coding of 1, whereas observations at night were coded as 0. Streams containing brook trout were coded as 1, and study sites without brook trout were coded as 0. Pearson's product-moment correlations were run on all pairs of continuous predictor variables (i.e., physical and chemical measurements) prior to analyses. To avoid multicollinearity, predictor variables that were strongly correlated ($r^2 > 0.5$) were not used together in the modeling procedure.

We were primarily interested in evaluating the relative influence of biotic interactions, body size, and time of day on bull trout microhabitat use. We first developed a global logistic regression model that contained all of the uncorrelated microhabitat variables (Table 1) that we believed could influence bull trout distributions. We then constructed a subset of 18 ecologically meaningful candidate models. The relative influence of depth and current velocity on microhabitat use was evaluated using nine models for each variable (Table 2). We were secondarily interested in evaluating the effect of fish movement on inferences of bull trout microhabitat use. Consequently, we fit the global model and 18 candidate models using the conditional logistic regression model (equation 1) that incorporated estimates of fish movement and a naïve logistic

TABLE 1.—Means, SD, and ranges of abiotic and biotic factors in western U.S. streams (with and without nonnative brook trout) during evaluation of bull trout microhabitat use. Asterisks indicate predictors used in candidate microhabitat use models.

Variable	Brook trout absent			Brook trout present		
	Mean	SD	Range	Mean	SD	Range
Site length (m)	200.7	18	193–227	204.5	22.1	201–234
Mean wetted width (m)	5.08	1.53	2.9–8.4	4.87	0.47	4.0–5.3
Bull trout abundance*	205.0	178.8	17–494	77.4	38.4	29–117
Brook trout abundance				15.9	8.3	9–31
Mean visibility (m)	2.25	0.62	1.6–3.9	2.01	0.73	1.1–3.0
Wood density (pieces/m^2)	0.02	0.01	0.00–0.04	0.03	0.00	0.02–0.03
Percent pool	17.91	10.48	4–34	19.36	3.16	16–21
Probability of remaining[a]						
Day	0.70	0.17	0.4–1.0	0.64	0.15	0.4–1.0
Night	0.80	0.11	0.6–1.0	0.78	0.12	0.6–1.0
Microhabitat availability						
Current velocity (m/s)*	0.05	0.09	0–0.56	0.06	0.13	0–0.58
Depth (m)*	0.24	0.16	0.02–0.81	0.22	0.14	0.02–0.97
Substrate composition (%)						
Rubble*	31.56	27.62	0–100	36.34	26.57	0–90
Cobble	31.24	23.64	0–100	33.71	22.72	0–100
Gravel	25.35	25.67	0–100	20.34	18.79	0–90
Fines	10.54	21.12	0–100	8.97	20.39	0–100

[a] Probability of a fish remaining at a location during daytime or nighttime snorkeling observations.

regression that assumed no fish movement in response to sampling.

We used Akaike's information criterion (Akaike 1973) with the small sample bias adjustment (AIC_c; Hurvich and Tsai 1989) to evaluate the fit of each candidate model. Because MCMC methods produce a distribution of AIC values, we used the mean AIC from 100,000 iterations for all inferences (Fonnesbeck and Conroy 2004; Peterson et al. 2005). After all AIC_c values were calculated, the relative plausibility of each candidate model was assessed using Akaike weights (Burnham and Anderson 1998). The Akaike weights vary from 0 to 1, and the best-fitting candidate model has the highest weight. 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, we constructed a confidence set of 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.

We based all inferences on the confidence model set. To facilitate interpretation of parameter estimates, we also calculated scaled odds ratios (ORs) for each predictor variables as

$$\mathrm{OR} = \exp(\beta u), \tag{3}$$

where β is the parameter estimate and u is the unit scalar (Hosmer and Lemeshow 2000). The scaled OR allowed for biologically meaningful interpretation

TABLE 2.—Biological interpretations of predictors used in candidate models of bull trout habitat use within intermountain western U.S. streams during summer 2001 and 2002.

Predictor variables	Biological inference (hypothesis)
Velocity, depth, rubble substrate	Microhabitat characteristics influence the distribution of bull trout within a stream
Abundance × depth, abundance × velocity	Intraspecific interactions influence microhabitat habitat use by all sizes of bull trout
Body size × depth, body size × velocity	Microhabitat use patterns of bull trout vary with body size
Day × depth, day × velocity	Microhabitat use varies with time of day
Brook trout × depth, brook trout × velocity	Presence of brook trout influences microhabitat use by all sizes of bull trout
Abundance × day × depth, abundance × day × velocity	The influence of intraspecific interactions on microhabitat habitat use varies with time of day
Body size × day × depth, body size × day × velocity	Size-specific microhabitat use patterns vary with time of day
Brook trout × day × depth, brook trout × day × velocity	The influence of brook trout presence on microhabitat use patterns varies with time of day
Brook trout × body size × depth, brook trout × body size × velocity,	The influence of brook trout presence on microhabitat use patterns varies with bull trout body size
Abundance × body size × depth, abundance × body size × velocity	The influence of large bull trout on microhabitat habitat use varies with time of day

TABLE 3.—Predictor variables (vel = current velocity; BS = body size; brook trout = presence of nonnative brook trout), number of parameters (K), log likelihood (LL), differences in Akaike's information criterion corrected for small-sample bias (ΔAIC_c), Akaike weights (w), and model ranks for two sets of candidate models (i) used to predict bull trout presence within streams. The conditional model incorporated estimates of fish movement; the naïve model did not.

Candidate model	K	Conditional model				Naïve model			
		LL	ΔAIC_c	w_i	Rank	LL	ΔAIC_c	w_i	Rank
Vel, depth, rubble, day × depth, BS × depth, BS × day × depth	8	−301.3	0.00	0.93	1	−288.5	0.00	0.99	1
Vel, depth, rubble, abundance × depth, BS × depth, abundance × BS × depth	8	−304.4	6.25	0.04	2	−297.4	17.97	0.00	4
Vel, depth, rubble, brook trout × depth, BS × depth, brook trout × BS × depth	8	−305.3	8.14	0.02	3	−300.5	24.03	0.00	7
Vel, depth, rubble, brook trout × depth, day × depth, brook trout × day × depth	8	−306.6	10.69	0.00	4	−294.6	12.31	0.00	3
Vel, depth, rubble, BS × depth	6	−309.0	11.38	0.00	5	−302.4	23.83	0.00	6
Vel, depth, rubble, day × depth, abundance × depth, day × abundance × depth	8	−307.7	12.95	0.00	6	−294.3	11.71	0.00	2
Vel, depth, rubble, day × depth	6	−312.0	17.34	0.00	7	−300.0	18.90	0.00	5
Vel, depth, rubble, abundance × depth	6	−313.4	20.08	0.00	8	−305.8	30.57	0.00	8
Vel, depth, rubble, brook trout × depth	6	−315.6	24.57	0.00	9	−310.1	39.08	0.00	9
Vel, depth, rubble, brook trout × vel	6	−318.6	30.44	0.00	10	−311.5	41.92	0.00	10
Vel, depth, rubble, abundance × vel	6	−318.9	31.06	0.00	11	−311.6	42.04	0.00	11
Vel, depth, rubble, BS × vel	6	−319.0	31.29	0.00	12	−312.0	42.87	0.00	13
Vel, depth, rubble, day × vel	6	−319.2	31.68	0.00	13	−311.6	42.15	0.00	12
Vel, depth, rubble, brook trout × vel, day × vel, brook trout × day × vel	8	−318.3	34.03	0.00	14	−310.4	43.98	0.00	14
Vel, depth, rubble, brook trout × vel, BS × vel, brook trout × BS × vel	8	−318.3	34.04	0.00	15	−311.2	45.41	0.00	18
Vel, depth, rubble, abundance × vel, BS × vel, abundance × BS × vel	8	−318.5	34.55	0.00	16	−311.2	45.55	0.00	19
Vel, depth, rubble, day × vel, BS × vel, BS × day × vel	8	−318.7	34.92	0.00	17	−311.0	45.17	0.00	17
Vel, depth, rubble, day × vel, abundance × vel, day × abundance × vel	8	−318.8	35.03	0.00	18	−311.0	45.00	0.00	16
Global model	24	−305.9	44.11	0.00	19	−293.8	45.55	0.00	15

rather than the single-unit-of-change interpretation. For example, we scaled percent rubble using 15% because we believed that a 15% change in percent rubble was biologically more meaningful than a single unit of change (i.e., 1%). The precision of each predictor was estimated by computing a 90% credibility interval (CI; Congdon 2001) for each scaled OR; 90% CIs are analogous to 90% confidence intervals. A 90% CI that contained values with magnitudes that were considered meaningful implied a biologically important relationship between the predictor variable and bull trout presence. Conversely, a 90% CI containing 1.0 indicated that results were imprecise (following Thompson and Lee 2000).

Goodness of fit (GOF) was assessed for the global and best-fitting models by means of a simple discrepancy measure and 1,000 simulated data points (Gelman et al. 1996). This method compares deviances of simulated and observed data. Fit is considered adequate when the GOF statistic is close to 0.5 (Gelman et al. 1996).

Results

All sites contained bull trout, and underwater visibility averaged 2.2 m (Table 1). Brook trout were detected at three sample sites, westslope cutthroat trout *Oncorhynchus clarkii lewisi* were detected at four sites, and rainbow trout *O. mykiss* were detected at five sites. We measured microhabitat use for 26 bull trout observed during the day and 187 observed at night. We observed only five fish in the 200–300-mm size-class, so we combined the data for the 100–199- and 200–300-mm size-classes into a 100–300-mm class.

All bull trout were observed less than 10 cm from the substrate; hence, no analyses were necessary to test for differences in distance from the streambed, because we believed differences within the range of 10 cm were not biologically important (Johnson 1999). Similarly, few fish of other species (three rainbow trout; 1% of observations) were observed within 20 cm of bull trout focal points; thus, evaluation of direct interactions between bull trout and other fishes was not possible.

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% confidence interval (−0.20 to +0.05) of the difference between the two means contained zero, indicating an imprecise estimate of the difference.

The best-fitting model of bull trout presence within streams was identical for the conditional and naïve logistic regression models (Table 3) and included current velocity, depth, rubble substratum, and the day × depth, body size × depth, and body size × day × depth interactions. The overall GOF statistic for the global and best-fitting conditional and naïve logistic regression models varied from 0.28 to 0.41, indicating that model fit was adequate. The best conditional and naïve logistic models had Akaike weights that were 22 times greater than those of the next-best models. Thus, both confidence model sets contained only the best-fitting model. In contrast, the relative rankings for the remaining candidate models differed between the

TABLE 4.—Mean (SD) parameter estimates, scaled odds ratios (OR), and associated 90% credibility intervals (CIs) for best-fitting conditional and naïve logistic regression models of bull trout presence within western U.S. streams.

Parameter	Estimate (SD)	OR unit scalar	Scaled OR	90% CI
Conditional model				
Intercept	−0.522 (0.287)			
Current velocity	−3.722 (1.263)	0.05	0.83	0.75–0.92
Depth	3.227 (1.127)	0.2	1.91	1.31–2.76
Rubble	−0.017 (0.005)	15.0	1.00	1.00–1.00
Day × depth	−4.317 (1.955)	0.2	0.42	0.22–0.80
Body size × depth	6.049 (1.476)	0.2	3.35	2.06–5.45
Day × body size × depth	−2.311 (1.967)	0.2	0.63	0.33–1.21
Random effect	0.471 (0.382)			
Naïve model				
Intercept	−0.581 (0.233)			
Current velocity	−3.722 (1.135)	0.05	0.83	0.76–0.91
Depth	3.833 (1.418)	0.2	2.15	1.35–3.43
Rubble	−0.021 (0.004)	15.0	1.00	1.00–1.00
Day × depth	−3.819 (2.091)	0.2	0.47	0.23–0.93
Body size × depth	4.399 (1.032)	0.2	2.41	1.71–3.39
Day × body size × depth	−0.603 (2.235)	0.2	0.89	0.42–1.86
Random effect	0.333 (0.290)			

conditional and naïve logistic regression models (Table 3). In general, models containing diurnal changes in habitat use (i.e., day effect) were ranked higher among naïve models than among conditional models. The results also indicated that conditional models containing intra- and interspecific interactions were ranked higher than naïve models containing those variables.

Of the microhabitat variables considered, the scaled OR of the best-fitting conditional logistic regression model suggested that depth had a greater influence on bull trout distribution within a stream than did current velocity and rubble substratum (Table 4). The likelihood of observing small bull trout (70–99 mm) at night increased (on average) 1.9 times for every 0.2-m increase in depth. The likelihood of observing large bull trout (100–300 mm) at night was 3.4 times greater than that of observing small bull trout for every 0.2-m increase in water depth. Observations of small bull trout increased in likelihood by 1.2 times (1.00/0.83) with each 0.05-m/s decrease in current velocity. The influence of water depth on bull trout observations also varied with body size and time of day. The scaled OR suggested that the likelihood of observing small bull trout at a given depth during the day was 2.4 times lower than the likelihood of nighttime observations at the same depth (Table 4).

The parameter estimates and scaled ORs were similar between the best-fitting naïve and conditional logistic regression models. The most notable exceptions included estimates of the effect of time of day (Table 4). The results of the conditional logistic regression suggested that small bull trout at a given depth were 2.4 (1.00/0.42) times less likely to be observed during the day than at night, whereas the naïve logistic regression suggested that daytime observations were 2.1 (1.00/0.47) times less likely, indicating that failure to account for fish movement may result in biased habitat use assessments. Similarly, the scaled ORs of the conditional model indicated that the likelihood of daytime observations of large bull trout decreased 3.4 times with each 0.2-m increase in depth, while the naïve model estimated a likelihood decrease of 2.7 times; this result may also imply fewer observations at the same depth when movement is not accounted for. Estimates of the naïve model also were much more imprecise.

Discussion

The majority (88%) of our microhabitat 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 may be governed by food availability and risk of predation (Metcalfe et al. 1999). Optimal activity of fish, therefore, may represent times when food availability is greatest and predation risk is minimized. The propensity for aquatic macroinvertebrates to drift is greater at night than during the day (Waters 1962), whereas risk of predation to fishes is greater during the day 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 opportunity while reducing the risk of predation.

All observed bull trout were less than 10 cm from the streambed regardless of the time of day or size-class. Previous researchers have documented the close association of bull trout 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 that near the water surface (Hynes 1970), so fish near the streambed expend less energy to maintain their positions (Facey and Grossman 1990, 1992). Anatomical adaptations also have allowed fishes to cope with living in lotic environments (Bisson et al. 1988). Although it is generally fusiform, the bull trout has a broader head, has eyes located closer to the dorsum, and is more dorsoventrally compressed than its congener, the Dolly Varden *Salvelinus malma* (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 and enhance foraging in higher velocity areas of streams.

Bull trout also may use streambed areas for shelter (henceforth, concealment). Risk of predation during the day may lead to a diel shift in concealment, since the greater risk of predation during the day can be minimized by maintaining close association with cover (Metcalfe et al. 1999). For example, Heggenes et al. (1993) documented that small (<250-mm) brown trout *Salmo trutta* were concealed during the day in the winter to avoid predation. Fraser et al. (1993) noted that Atlantic salmon *Salmo salar* (mean TL = 88 mm) remained concealed during the day as temperatures dropped below 10°C. Thurow (1997) reported that all juvenile (50–250-mm) bull trout were concealed within the substrate during the day at cold (0.8–1.4°C) water temperatures and observed them only after turning over stones. Although we did not manipulate the substrate during observations, the few bull trout we observed during the day were concealed near or in contact with organic debris, vegetation, large substrata, or large woody debris. We hypothesize that bull trout exhibit concealment behavior during the day to avoid predators and stray from cover at night to forage.

Our 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 study sites contained populations of westslope cutthroat trout and brook trout. The solitary nature of bull trout may be attributable to several factors. First, solitary behavior 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 groundwater-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 intra- and interspecific competition for scarce resources. Second, solitary behavior may be related to a phylogenetic history of coexistence with native salmonids. Rainbow trout and westslope cutthroat trout tend to occupy the water column and have coevolved with bull trout, a benthic species (Behnke 1992; Nakano et al. 1992, 1998). The phylogenetic history of coexistence among these species may have enabled each to partition resources spatially (sensu Grossman and Freeman 1987), thereby minimizing competition. Lastly, solitary behavior may be a mechanism for reducing the risk of cannibalism. 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 that small bull trout (≤250 mm fork length [FL]) avoided large conspecifics (>250 mm FL) in a small alpine lake because of the risk of cannibalism. Although untested in streams, bull trout may evade cannibalism by engaging in size segregation and solitary behavior.

Depth was an important microhabitat characteristic describing the distribution of bull trout within streams. We found that bull trout inhabited greater depths at night and shallower depths during the day. Our observations are consistent with the results from an experimental stream channel containing juvenile bull trout (mean FL = 62.4 mm; Baxter and McPhail 1997) but differ from those of several field studies (Saffel and Scarnecchia 1995; Thurow 1997; Bonneau and Scarnecchia 1998; Jakober et al. 2000; Polacek and James 2003). These discrepancies may be related to the influences of water depth and time of day on fish movement. Fish movement in response to snorkelers is negatively related to water depth of the sampled area and is greater during day snorkeling (Peterson et al. 2005). If more fish move out of shallower habitats than deeper areas before being observed, particularly during the daytime, then habitat use in deeper water will be overestimated. Therefore, failure to account for fish movement might lead biologists to falsely conclude that shallow areas are not essential habitat and may diminish the importance of shallow rearing areas used by bull trout (Saffel and Scarnecchia 1995; Spangler and Scarnecchia 2001) and other salmonids (Moore and Gregory 1988) during the summer.

Large bull trout were more likely to use deeper microhabitats than were small bull trout during both day and night. Deeper water may provide more concealment from avian and terrestrial predators than shallower water (Power 1984; Angermeier 1992). Small fish, however, are vulnerable to predation by large fish (Harvey 1991), and the presence of large predatory fish may cause small individuals to seek shallower stream margins (Power et al. 1985). Therefore, our observed pattern of habitat use may indicate a mechanism by which large bull trout avoid predators in deeper areas and small bull trout use shallower water to avoid predation by large fish.

Both the conditional and naïve logistic regression models suggested that small bull trout had affinities for low-velocity microhabitats. 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

occupy habitats that optimize the potential for increases in energy gain (Werner and Hall 1974). Occupying high-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 supplies (Fausch 1984). We theorize that bull trout attempt to minimize energy loss by distributing themselves in low-velocity areas while maximizing the potential for energy gain by remaining adjacent to food supplies.

At the three sites containing brook trout, the presence of this species did not strongly influence the distribution of bull trout. Gunckel et al. (2002) similarly found no evidence that brook trout influenced microhabitat use by bull trout in eastern Oregon streams, but they reasoned that bull trout may displace brook trout when resources are scarce. Other researchers, however, have demonstrated brook trout negatively influence bull trout distributions. Nakano et al. (1998) revealed that brook trout engaged in interference competition with bull trout during a manipulative experiment; when brook trout were removed, bull trout increased their foraging rate and distance. Rieman et al. (2006) provided evidence of upstream displacement of bull trout by brook trout and suggested that bull trout populations in small streams (<2 m wide) are more vulnerable than those in larger streams (see also Rieman and McIntyre 1995). The streams containing brook trout in our study had complex habitats; they were generally deeper, had a higher percentage of pools, and had greater amounts of large woody debris than did streams without brook trout (Table 1). Our results are consistent with those of Rich et al. (2003), who surmised that bull trout are better able to withstand invasion by brook trout in streams with increased habitat complexity.

The best-fitting conditional and naïve models of bull trout microhabitat use were similar and included the same variables. This may be related to the fact that fish habitat use and fish movement were strongly influenced by the same factor, depth. Habitat use by larger bull trout during the day and by all sizes during the night was positively related to depth, and movement was negatively related to depth. Thus, fish using deeper habitats were unlikely to leave them in response to snorkeling. However, there were notable differences between depth parameter estimates of the two models when the time-of-day effect was considered. When the effect of snorkelers on fish movement was ignored (i.e., the naïve model), the models suggested that bull trout were more likely to be in deeper areas of streams during the day. We therefore advocate two approaches: (1) biologists who complete daytime snorkel surveys to assess bull trout habitat use must account for fish movement and (2) separate efficiency models for day and night snorkeling are required to assess abundance (see Thurow et al. 2006). Fish movement out of shallow sample sites in response to sampling may lead biologists to inaccurately estimate bull trout habitat use patterns or to underestimate abundance based on fish counts.

Similarly, naïve models that represented diurnal differences in habitat use were ranked higher (i.e., fit better) than the corresponding conditional models. This suggests that biases associated with snorkeler disturbances are minimal when a habitat relationship is strong or when biases are consistent with habitat use patterns, such as the depth effects. We caution, however, that this may be the exception rather than the rule for most fish species, and we encourage biologists to evaluate the influence of fish movement on observed habitat use by their species of interest.

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