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A Review of Bull Trout Habitat Associations and Exploratory Analyses of Patterns across the Interior Columbia River Basin

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Abstract.—An understanding of habitat relationships for bull trout *Salvelinus confluentus* remains an important component for identifying future restoration, management, and recovery efforts. We examined past efforts through a comprehensive synthesis of peer-reviewed articles evaluating bull trout habitat relationships, and we used field data within classification tree analysis (CTA) to improve our understanding of the consistency of bull trout habitat use patterns. We performed CTA using reach-level habitat data collected from currently occupied stream networks (i.e., those within the current distribution of bull trout) and unoccupied stream networks where hierarchical filters (i.e., area and temperature) were met and from occupied areas where temperature criteria were exceeded. Results from the literature review demonstrated consistent results at the microhabitat and channel unit scales; indicated the importance of slow-velocity, deeper habitats; and, together with observed diel shifts, highlighted the importance of complex habitat regardless of scale or season. At the reach scale, however, our results indicated substantially less consistency in bull trout habitat relationships. Including maximum stream temperature into the CTA did not result in changes to the overall structure of the CTA; results from the CTA indicated that bull trout were found in reaches with larger substrate, deeper pools, and more cover, but the specific criteria differed along a gradient of stream depth. Our results indicated (1) important gaps in our knowledge regarding the role of substrate size in juvenile bull trout habitat use, (2) the need for elucidation of habitat use patterns in downstream reaches, which may act as critical overwintering habitat or migratory corridors, and (3) the need to incorporate sampling efficiencies in future bull trout habitat evaluations.

Understanding the relationship between fish and their aquatic habitat requires a comprehensive assessment of habitat use patterns across a variety of spatial scales and across the array of habitat types that occur within each species' native range (Fausch et al. 2002). This task can be extremely challenging because species requirements and use patterns can vary across environmental and biotic gradients (Dunham et al. 1999; Rosenfeld and Boss 2001). In light of these difficulties, coarser, broad-scale assessments are essential for evaluating the consistency of habitat use across spatial scales that are relevant to the biology and management of the species of interest (e.g., Waples 1991).

The bull trout *Salvelinus confluentus* is a freshwater fish species that occurs across a relatively broad range of environmental conditions, from the high deserts of northern Nevada to the temperate rainforests of western British Columbia and north to the Yukon Territory (Dunham et al. 2008). Despite their broad range, bull trout are known to have very specific habitat requirements, including cold water temperatures (references herein). Across much of their historical range, habitat degradation and fragmentation (Rieman and McIntyre 1993; Rieman et al. 1997), introduction of nonnative species (Rieman et al. 2006), and angling pressure (Post et al. 2003; Parker et al. 2007) have been identified as primary factors contributing to the decline in distribution and abundance of bull trout and the species' subsequent listing as threatened under the Endangered Species Act (ESA). The current recovery documents organize bull trout populations into multiple small core areas (USFWS 2004), which are further organized into six recovery units within one distinct population segment under the ESA (i.e., at the species level). As such, identifying the factors affecting bull trout distribution and abundance across this large spatial scale is critical to effectively direct and prioritize management decisions aimed at bull trout recovery.

Prior to the 1990s, there was little information describing the basic habitat needs, life history strategies, and behavior of bull trout. In the last decade, however, there has been a substantial effort from the fisheries community to identify factors limiting the distribution and abundance of bull trout populations at a variety of spatial scales (Dunham and Rieman 1999; Rieman et al. 2006; Johnston et al. 2007); such efforts are a direct effect of the ESA (Al-Chokhachy et al. 2008). Through watershed assessments, researchers

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have demonstrated that the distribution of bull trout is largely governed by water temperature (e.g., Dunham et al. 2003) and watershed size (e.g., patch; Dunham and Rieman 1999). Although these factors help describe the distribution of bull trout at large spatial scales, there is a growing body of literature describing bull trout habitat relationships at smaller spatial scales, including microhabitat (1 m^2), channel unit (i.e., pool, riffle, and run; 1–20 m), and reach-level (100–300 m) assessments. Synthesizing previous bull trout habitat assessments is a necessary step in understanding the consistency of bull trout habitat relationships throughout their distribution, particularly where criteria for hierarchical watershed filters, such as area and temperature, are met. To address this need, we used a combination of methods to evaluate bull trout habitat use patterns within their current range. First, we performed a comprehensive review of peer-reviewed literature evaluating bull trout habitat relationships at multiple spatial scales, including microhabitat, channel unit, and reach scales. Next, we compared our findings from the literature review with the results from exploratory analyses using a large sample of field data to ask the simple but important question: "How does the physical instream habitat differ between reaches currently occupied and unoccupied by bull trout?" The combination of these approaches will help identify the consistency in patterns of bull trout habitat use, provide insight into which factors may be limiting bull trout populations, and ultimately help guide future research and management actions.

Methods

Literature Review

We used the Web of Science (http://apps.isiknowledge.com) and BIOSIS (www.biosis.org) as search engines for manuscripts containing the terms "bull trout" and "habitat" and that specifically evaluated bull trout habitat relationships. While we acknowledge that additional information does exist as unpublished "gray" literature, we limited our efforts to peer-reviewed literature for quality control and to minimize bias against those studies that were not publicly available. Once the list was compiled, we reviewed each manuscript and reported the following information: sampling methods, study design (i.e., random or nonrandom selection of study sites), data used in analyses (i.e., habitat use versus use and availability), life stage evaluated, diel period in which study occurred, season of study, and the specific habitat attributes that each study found to be significantly correlated with bull trout habitat use. Unfortunately, we were unable to conduct a formal meta-analysis of observed patterns of bull trout habitat use (e.g., it was not possible to calculate effect size) because studies were conducted using a variety of statistical techniques and methods and across different seasons, scales, and diel periods. Therefore, we summarized the results descriptively and reported which attributes were included in the analyses and which attributes were found to be significant or not significant in describing bull trout habitat use (where applicable). Since our goal was to synthesize as much information as available in the peer-reviewed literature, we also incorporated the results from studies that did not include formal test statistics (particularly earlier works) by reporting the authors' interpretation of their results; however, we identify such studies accordingly in our results tables.

Habitat Data Collection

Study site and design.—As part of the PACFISH/INFISH Biological Opinion (PIBO) Effectiveness Monitoring Program (Kershner et al. 2004), we collected stream habitat data from 2001 to 2007 to monitor the status and trends of stream and riparian habitat within the interior Columbia River basin. Within our study area, we collected stream habitat data at the reach scale (160–500 m) as an indicator of instream habitat in watersheds that were primarily (>50%) under federal management (Bureau of Land Management or U.S. Forest Service), and we selected sample reaches based on a spatially balanced random sample design (Stevens and Olsen 1999; see Kershner et al. 2004 for specific study site selection details). Within each watershed, we primarily selected the lowermost low-gradient reach (<3% based on visual observation); however, if reaches with gradients less than 3% were not available, higher-gradient reaches were sampled. We selected low-gradient reaches for monitoring as these areas are generally thought to be the most sensitive to change under variable sediment and flow regimes (Montgomery and MacDonald 2002).

Beginning in 2001, we began a 5-year, rotating-panel sampling schedule wherein 20% of all candidate reaches were randomly selected and sampled within a given year and each reach was resampled every 5 years. Under this approach, approximately 40% of our reaches were sampled twice during this period; for such reaches, we randomly selected the sample year to be used in the ensuing analyses. We sampled all reaches between June and September, which generally resulted in base flow sampling conditions, and at each reach we measured a number of stream attributes. For this analysis, we considered habitat attributes collected through the PIBO monitoring project that were previously demonstrated to have significant effects on the distribution and abundance of bull trout, including percent pool, residual pool depth, percent pool tail fines, median particle size (d_{50}), percent undercut banks, large woody debris (LWD) frequency, and channel sinuosity (for detailed data collection methods, see Kershner et al. 2004; Heitke et al. 2007).

Water temperature has been found to have a significant effect on the distribution of bull trout within and across stream networks (Selong et al. 2001; Dunham et al. 2003). While much of the spawning and summer rearing of bull trout are restricted to cold headwater reaches (Rieman and McIntyre 1993), the distribution of bull trout during the fall and winter months includes downstream portions of stream networks that exceed the thermal criteria during the summer months (Howell et al., in press). We included measures of summer water temperature in our analyses to investigate whether habitat factors that best explained the occupancy of stream reaches differed across thermal gradients. At each reach, we collected hourly temperature readings (between July 15 and August 31) by placing temperature loggers (Madge-Tech, Inc.) in deep pool habitat. For consistency with interagency bull trout recovery efforts in the Columbia River basin (i.e., Bull Trout Monitoring and Recovery Group; M. Hudson, U.S. Fish and Wildlife Service, personal communication), we used the maximum daily temperature observed at a given reach for these analyses.

Classification tree analyses of habitat.—For classification tree analysis (CTA), we selected reaches from our study area that occurred within the current range of bull trout in the interior Columbia River basin. From this initial list of reaches, we first limited our analysis to streams with wetted widths greater than 2 m because bull trout are less likely to occupy streams less than 2 m wide (Dunham and Rieman 1999). We also limited our analysis to watersheds with areas greater than 400 ha, since bull trout are more likely to be present in these larger watersheds (Dunham and Rieman 1999). Next, we used the most recent bull trout distribution data taken from state agencies within the region and reported in StreamNet (www.streamnet.org/online-data/GISData.html) to identify which of our study reaches occurred within the current distribution of bull trout (hereafter, "occupied reaches"; Figure 1). Under this criterion, only reaches that were located in the portion of the stream network occurring within the current distribution were considered occupied; reaches that were located on streams containing bull trout but that were outside of the current bull trout distribution were considered unoccupied. Lastly, we selected reaches that occurred on streams currently unoccupied by bull trout (or not within the current distribution) but that were within a proximate distance (25-km Euclidean distance) of an occupied stream for high colonization potential or historical occupation (Dunham and Rieman 1999).

We used CTA to help distinguish differences in the physical stream habitat between currently occupied and unoccupied streams. The CTA is a nonparametric method for exploring ecological relationships (Breiman et al. 1984; De'ath and Fabricius 2000). With a CTA, explanatory variables are initially rank-transformed, and the CTA algorithm iteratively partitions the data into the classes of the response variable. Under this recursive approach, the CTA selects the partition value and hierarchically selects the explanatory variable, which categorizes the response variable into the two classes with the smallest error (McCune and Grace 2002). A benefit of tree analyses such as CTA is the ease of interpretation (Cross and McInerny 2005), which can be critical in exploratory analyses such as these.

We used two exploratory analyses to evaluate factors associated with bull trout distribution patterns within the range of streams assessed in our study site. First, we evaluated differences in the physical habitat attributes between all streams currently occupied by bull trout and all unoccupied streams. Second, we incorporated maximum summer water temperature into the CTA to evaluate whether the physical habitat of occupied and unoccupied streams differed along thermal gradients. Research has illustrated that areas used for bull trout spawning and rearing are often limited by water temperatures (Rieman and McIntyre 1995), and in general bull trout are less likely to occur at temperatures exceeding 16°C (Howell et al., in press). However, prior to and after the spawning season, many bull trout migrate downstream to reaches where water temperatures can exceed the optimal thermal regimes during the summer months. Despite their high summer temperatures, these areas may provide important rearing and overwintering habitat for juveniles and adults (Swanberg 1997; Nelson et al. 2002; Homel and Budy 2008). Identifying potential differences between occupied and unoccupied habitat in these areas may be critical for understanding the role of connectivity in determining population persistence and viability and may provide insight into factors affecting bull trout migratory patterns. Within each of these analyses, we included the following attributes (Figure 2) measured at each of the PIBO reaches: (1) a measure of stream depth through residual pool depth; (2) the amount of pool habitat; (3) measures of cover and complexity, including percent undercut banks, channel sinuosity, and the amount and volume of LWD; and (4) substrate characteristics, including percent fine sediment in pool tails and median size of surface substrate (i.e., d_{50}).

For each CTA, we used the rpart procedure in R (R

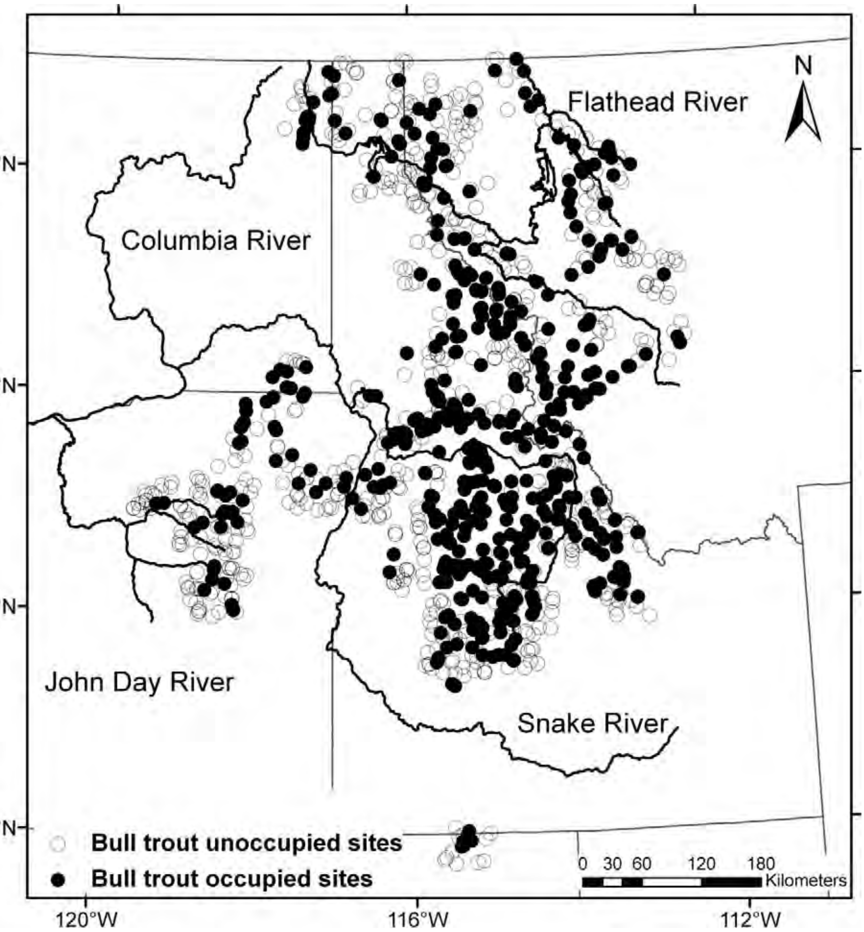

FIGURE 1.—Map of sample reaches that are currently occupied by bull trout (solid black circles) or are unoccupied (within 25 km of occupied reaches, see Methods; open circles) in the interior Columbia River basin.

Development Core Team 2004). We built each classification tree with the presence or absence of bull trout as a class variable, and all other variables were used as explanatory variables. To minimize overfitting of the data, the minimum number of observations prior to splitting each node was set at 20, and the minimum number of observations at the end of each node was set at 10. With our analyses, we were not interested in developing a predictive model but rather in exploring differences in habitat between bull trout occupied and unoccupied streams. Therefore, we included all of our data in the analyses and performed 10-fold cross validations ($n = 50$) to identify the most frequent tree structure (i.e., number of branches) that simultaneously minimized the relative error (De'ath and Fabricius 2000). We assessed the accuracy of each tree by predicting the occupancy of each reach and comparing these results with the actual occupancy for an estimate of the correct classification rate.

Results

Literature Review

Sampling methodologies and sample design.— Based on our search criteria and search engines, we located and reviewed 24 articles that evaluated bull trout habitat relationships. The majority of the studies (65%) did not include a random component in the study design as reaches were purposively selected for sampling (e.g., Edwards et al. 2006). Where applicable, we found that only one-third of the studies included both habitat use and availability when determining bull trout habitat use patterns. Snorkeling (day or night) was the most common methodology (54.2%) used to quantify the presence–absence or density of bull trout in relation to habitat attributes, while 20.8% of the

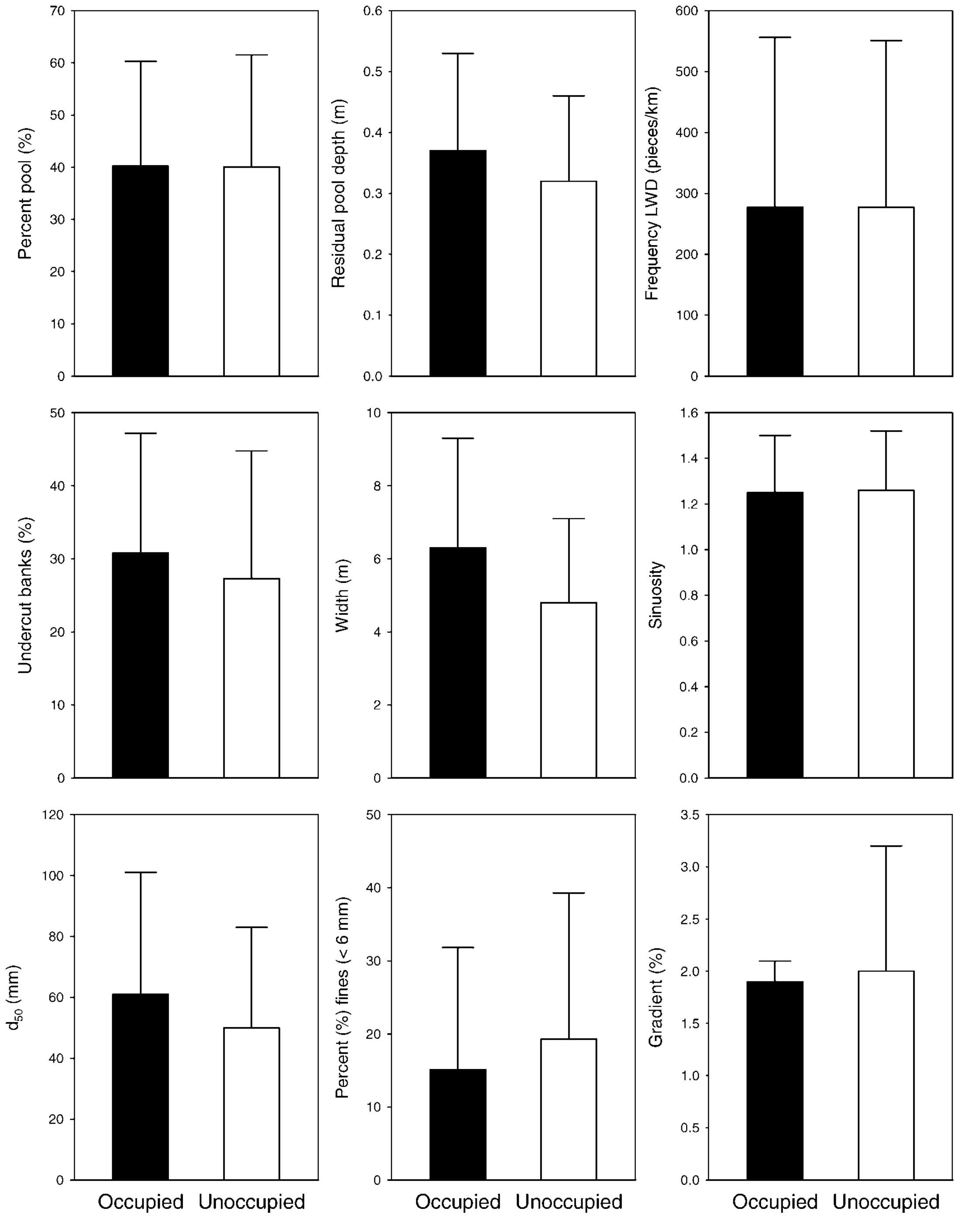

FIGURE 2.—Estimates of mean (+SD) percent pool habitat, residual pool depth, frequency of large woody debris (LWD), percent of undercut banks, stream width, channel sinuosity, median substrate particle size (d_{50}), percent fine sediment (<6 mm), and gradient within interior Columbia River basin reaches (sampled by the PACFISH/INFISH Biological Opinion Effectiveness Monitoring Program) that are currently occupied by bull trout (solid black bars) or are unoccupied (open bars).

TABLE 1.—Individual studies (all were conducted in summer and fall) and sampling methods (E = electrofishing; S = snorkeling) used to evaluate reach-scale assessments of bull trout habitat relationships across diel periods with measures of channel type, amount of overhead cover, stream depth, amount of large woody debris (LWD), stream size, substrate, and other instream attributes (temp = temperature, grad = gradient, vel = velocity; na = attribute not evaluated, ns = no significant relationship found, + = positive relationship, − = negative relationship).

Study	Method	Channel type	Cover[c]	Depth	LWD	Size	Substrate	Other
Daytime studies								
Dambacher and Jones 1997[a]	E	ns	+	ns	+	ns	+	Bank erosion (−)
Watson and Hillman 1997[b]	E, S	ns	+	+	+	+	+	Temp (ns), grad (−)
Dunham and Rieman 1999[b]	E, S	na	na	na	na	+	na	Grad (ns)
Earle and McKenzie 2001[a]	E	Pools and runs (+)	+	na	na	na	ns	na
Rich et al. 2003[b]	E	ns	ns	ns	+	ns	ns	Grad (−)
Ripley et al. 2005[b]	E	na	na	ns	na	+	+ (− to fines)	Grad (−)
Nighttime studies								
Saffel and Scarnecchia 1995[a]	S	Pocket pools (+)	na	ns	ns	na	ns	Temp (−), vel (ns)
Dunham et al. 2003[a]	S	na	ns	ns	ns	ns	ns	Temp (−), grad (ns)

[a] Juvenile stage was evaluated.
[b] Juvenile and adult stages were evaluated.
[c] Cover varied across individual studies.

studies used electrofishing methods, 8.3% included both snorkeling and electrofishing, and 8.3% used radiotelemetry methods.

The majority (65%) of the current and historical bull trout habitat studies focused on the juvenile age-classes; an additional 26% considered both juveniles and adults. Surprisingly, there were few efforts that quantified only adult bull trout habitat relationships (9%). Many (48%) of the studies compared diel habitat use, while 39% performed only daytime habitat studies and 13% performed only nighttime studies. The majority of the studies (53%) evaluated bull trout microhabitat relationships, 44% evaluated channel unit relationships, and 36% evaluated reach-level relationships. Within each scale, diel period, or season, not all studies evaluated the same habitat attributes; therefore, we present the total number of studies summarized by scale, diel period, and season and the total number of studies that evaluated each specific attribute in each of the following syntheses.

Summer–fall habitat relationships.—All eight of the reach-scale bull trout habitat studies occurred during the summer, with six daytime studies and two nighttime studies (Table 1). At this scale, there was limited evidence indicating consistent, positive relationships with reaches exhibiting more cover (3 of the 5 studies that evaluated this attribute), higher amounts of LWD (3/5), lower gradients (3/5), and colder water temperatures (2/3). Only one of the six studies that measured depth at this scale found that bull trout were positively associated with increasing stream depth. Similarly, at the reach scale, we did not find consistent results in the relationship between bull trout use and specific channel types as only two of the five studies found positive relationships with the amount of available pool and run habitat.

Six studies evaluated bull trout habitat relationships during the summer–fall at the channel unit scale; of these, four were daytime studies and two were nighttime studies (Table 2). Daytime evaluations demonstrated that bull trout consistently used channel units with cover (2/2), deeper channel units (2/2), and pool habitat (3/4). The results of these daytime studies were less conclusive for the negative relationship with riffle habitat (1/3) and the importance of large substrate (1/2), abundance of LWD (1/2), and other channel types. This pattern was consistent with the results from the two nighttime studies, which indicated use of pool habitat (2/2) and deeper channel units (1/1) and provided limited evidence of a relationship with riffle habitat (0/2) or substrate (0/1).

At the microhabitat scale, we found 10 individual studies that occurred during the summer–fall. At this scale (Table 3), daytime studies generally indicated that bull trout used deeper (5/8), slow-velocity (8/8) microhabitats with cover (5/6). However, both Baxter and McPhail (1997) and Banish et al. (2008) observed that bull trout used shallower microhabitat during daytime summer periods. During the nighttime, bull trout again consistently used slower-velocity microhabitat (9/10). However, there was little consistency in the use or nonuse of microhabitat with cover or depth during the nighttime. Similarly, there was no consistency in bull trout use of specific substrate types during either diel period at the microhabitat scale.

Winter–spring habitat relationships.—Six individual studies investigated bull trout habitat relationships at the channel unit scale during the winter–spring period; all six studies investigated daytime and nighttime use of

TABLE 2.—Individual summer–early fall studies and sampling methodologies (S = snorkeling, R = radiotelemetry) used to evaluate bull trout habitat relationships at the channel unit scale (i.e., pool, riffle) across diel periods, and the results reported in relation to measures of cover, channel unit depth, pool habitat, riffle habitat, substrate, large woody debris (LWD), and other instream attributes (sidech = sidechannels, vel = velocity; na = attribute not evaluated, ns = no significant relationship found, + = positive relationship, − = negative relationship).

Study	Method	Cover[e]	Depth	Pools	Riffles	Substrate	LWD	Other
Daytime studies								
Fraley and Shepard 1989[a,b]	na	+	na	+	na	na	na	na
Goetz 1997[c]	S	na	na	+	−	na	na	Sidech (+)
Swanberg 1997[d]	S	+	+	−	ns	na	ns	Area (ns)
Muhlfeld and Marotz 2005[b,c]	R	na	+	+	ns	+	+	Runs (ns)
Nighttime studies								
Saffel and Scarnecchia 1995[c]	S	na	+	+	ns	ns	na	Vel (ns)
Bonneau and Scarnecchia 1998[c]	S	na	na	+	ns	na	na	Area (ns)

[a] Juvenile and adult stages were evaluated.
[b] Indicates formal statistics not used in the study.
[c] Juvenile stage was evaluated.
[d] Adult stage was evaluated.
[e] Cover varied across individual studies.

channel units (Table 4). Daytime studies found that bull trout associated with channel units with cover (2/2), deeper channel units (2/2), pool habitat (5/6), and run habitat (4/4). Similar to the summer period, there was little consistency in the use or nonuse of riffle habitat as three of six studies found a negative relationship with riffle habitat. There were limited results regarding use of larger substrate (1/1) or abundance of LWD (1/1) during the winter–spring period. During the nighttime, bull trout were typically found in channel units without cover (2/2). Three of four nighttime studies found that bull trout continued to use pool and run channel units during this period, whereas Muhlfeld et al. (2003) found a shift to shallower channel units; however, the depth of the shallower habitat observed during that study averaged 1 m.

TABLE 3.—Individual summer–fall studies and sampling methods (E = electrofishing; S = snorkeling, O = experimental observation) used to evaluate bull trout habitat relationships at the microhabitat scale across diel periods, and the results reported in relation to measures of cover, depth, substrate, velocity, and other instream attributes (embed = embeddedness, chan = channel unit type; na = attribute not evaluated, ns = no significant relationship found, + = positive relationship, − = negative relationship).

Study	Method	Cover	Depth	Substrate	Velocity	Other
Daytime studies						
Baxter and McPhail 1997[a,b]	O	+	−	−	−	na
Goetz 1997[a]	S	+	+	−	−	Embed (+)
Bonneau and Scarnecchia 1998[a,b]	S	+	+	na	−	na
Earle and McKenzie 2001[a]	E	+	ns	ns	−	na
Hagen and Taylor 2001[b,c]	S	na	+	na	−	Chan
Polacek and James 2003[a,b]	S	na	+	ns	−	Embed (ns)
Al-Chokhachy and Budy 2007[c]	S	+	+	ns	−	na
Banish et al. 2008[c]	S	ns	−	ns	−	na
Nighttime studies						
Baxter and McPhail 1997[a,b]	O	−	−	−	+	na
Goetz 1997[a]	S	+	+	−	−	Embed (ns)
Sexauer and James 1997[a,b]	S	ns	ns	ns	−	na
Bonneau and Scarnecchia 1998[a,b]	S	−	+	na	−	na
Hagen and Taylor 2001[b,c]	S	na	−	na	−	Chan (ns)
Spangler and Scarnecchia 2001[a]	S	+	−	+	−	na
Spangler and Scarnecchia 2001[d]	S	ns	+	ns	−	na
Polacek and James 2003[a,b]	S	ns	−	ns	−	Embed (ns)
Al-Chokhachy and Budy 2007[c]	S	+	+	ns	−	na
Banish et al. 2008[c]	S	ns	+	ns	−	na

[a] Juvenile stage was evaluated.
[b] Formal statistics were not used in this study.
[c] Juvenile and adult stages were evaluated.
[d] Adult stage was evaluated.

TABLE 4.—Individual winter–spring studies and sampling methods (E = electrofishing; S = snorkeling, R = radiotelemetry) used to evaluate bull trout habitat relationships at the channel unit scale (i.e., pool, riffle) across diel periods, and the results reported in relation to measures of cover, channel unit depth, pool habitat, riffle habitat, substrate, and other instream attributes (LWD = large woody debris; na = attribute not evaluated, ns = no significant relationship found, + = positive relationship, − = negative relationship).

Study	Method	Cover	Depth	Pools	Riffles	Substrate	Other
Daytime studies							
Goetz 1997[a]	S	na	na	+	−	na	Runs (+)
Thurow 1997[a]	S	na	na	ns	−	na	Runs (+)
Jakober et al. 1998[b,c,d]	S	+	na	+	−	na	Beaver ponds (+)
Jakober et al. 2000[d,e]	S	+	na	+	ns	na	na
Muhlfeld et al. 2003[a,d]	R	na	+	+	ns	na	Runs (+)
Muhlfeld and Marotz 2005[a,d]	R	na	+	+	ns	+	Runs (+), LWD (+)
Nighttime studies							
Thurow 1997[a]	S	na	na	ns	+	na	Runs (+)
Jakober et al. 1998[c,d]	S	ns	na	+	ns	na	na
Jakober et al. 2000[d,e]	E, S	ns	na	+	ns	na	na
Muhlfeld et al. 2003[a,d]	R	na	−	ns	ns	na	Shoals and runs (+)

[a] Juvenile stage was evaluated.
[b] Cover varied across individual studies.
[c] Adult stage was evaluated.
[d] Formal statistics were not used in this study.
[e] Juvenile and adult stages were evaluated.

Six studies evaluated bull trout winter–spring habitat relationships at the microhabitat scale (Table 5). At this scale, bull trout were consistently found in deeper (5/5), slow-velocity (4/5) microhabitat with cover (5/5) and larger substrate (3/4) during the daytime. Despite the positive relationship with substrate size reported in three of the studies considered here, the fourth study (Goetz 1997) found that bull trout negatively associated with substrate size and exhibited a positive association with embedded substrate. In nighttime studies, bull trout continued the use of deep (4/5), slow-velocity (5/5) microhabitat. However, we found mixed results for use of microhabitat with cover: two studies reported no apparent pattern in use of covered microhabitat, two studies reported that bull trout used microhabitat without overhead cover, and one study found a positive relationship with cover. Most studies found no consistent patterns of substrate use during the nighttime.

Diel shifts in habitat use.—Ten studies evaluated diel shifts in bull trout habitat use (Table 6). The majority of these studies evaluated juveniles only (6/10) or juveniles and adults (3/10), and only one study focused solely on adult diel shifts in habitat use. The

TABLE 5.—Individual winter–spring studies and sampling methods (E = electrofishing; S = snorkeling; R = radiotelemetry) used to evaluate bull trout habitat relationships at the microhabitat scale across diel periods, and the results reported in relation to measures of cover, depth, substrate, velocity, and other instream attributes (embed = embeddedness; na = attribute not evaluated, ns = no significant relationship found, + = positive relationship, − = negative relationship).

Study	Method	Cover	Depth	Substrate	Velocity	Other
Daytime studies						
Goetz 1997[a]	S	+	+	−	−[d]	Embed (+)
Thurow 1997[a,b]	S	+	+	+	−	na
Bonneau and Scarnecchia 1998[a,b]	S	+	+	+	−	na
Jakober et al. 2000[b,c]	E, S	+	+	na	−	na
Muhlfeld et al. 2003[a,b]	R	+	+	+	ns	na
Nighttime studies						
Goetz 1997[a]	S	ns	+	−	−	Embed (+)
Sexauer and James 1997[a,b]	S	+	ns	ns	−	na
Bonneau and Scarnecchia 1998[a,b]	S	−	+	+	−	na
Jakober et al. 2000[b,c]	E, S	ns	+	na	−	na
Muhlfeld et al. 2003[a,b]	R	−	+	ns	−	na

[a] Juvenile stage was evaluated.
[b] Formal statistics were not used in this study.
[c] Juvenile and adult stages were evaluated.
[d] Velocity in spring was significantly higher than velocity in winter.

TABLE 6.—Individual studies that have evaluated diel shifts in bull trout habitat use, the scale of each study (M = microhabitat scale; CU = channel unit scale), the season, and the results reported in relation to measures of cover, depth, substrate, velocity, and other instream attributes (na = attribute not evaluated, ns = no significant relationship found, + = positive relationship, − = negative relationship).

Study	Scale	Cover	Depth	Substrate	Velocity	Other
Summer and fall studies						
Baxter and McPhail 1997[a]	M	−	+	−	+	na
Goetz 1997[a]	M	−	−	−	−	na
Bonneau and Scarnecchia 1998[a]	M	−	−	na	−	na
Hagen and Taylor 2001[a]	M	na	−	na	−	na
Polacek and James 2003[a]	M	na	−	ns	ns	na
Al-Chokhachy and Budy 2007[b]	M	ns	ns	ns	−	na
Banish et al. 2008[b]	M	ns	+	ns	ns	na
Winter and spring studies						
Goetz 1997[a]	M	−	−	ns	−	na
Goetz 1997[a]	M	−	ns	−	ns	na
Bonneau and Scarnecchia 1998[a]	M	−	ns	na	+	na
Jakober et al. 2000[b]	M	na	−	na	−	na
Muhlfeld et al. 2003[a]	M	−	−	−	−	na
Jakober et al. 1998[c,d]	CU	−	na	na	na	na
Jakober et al. 2000[b,d]	CU	−	na	na	na	Riffles and glides (+)
Muhlfeld et al. 2003[a]	CU	na	na	na	na	Shallower channel units (+)

[a] Juvenile stage was evaluated.
[b] Juvenile and adult stages were evaluated.
[c] Adult stage was evaluated.
[d] Formal statistics were not used in this study.

three studies that evaluated diel shifts at the channel unit scale all occurred during winter and spring periods. Two of these studies found shifts to shallower channel units at night, but Jakober et al. (1998) observed continued use of pools and glides during both diel periods. Two of these studies evaluated diel use of cover, and both reported shifts to channel units without cover during nighttime periods.

Studies at the microhabitat scale occurred across all seasons; for studies that included separate diel comparisons for each season, we report the results as independent and season specific ($n = 12$). Most studies (7/9) found that bull trout used microhabitats without cover during the nighttime period, but two studies demonstrated no significant shift in use of cover between diel periods. Bull trout were generally reported to shift to shallower microhabitats during the nighttime (7/12); however, in two studies, bull trout shifted to deeper microhabitat during the nighttime, and three studies observed no change in depth across diel periods. Similar to the seasonal results, there was little consistency in diel shifts with respect to substrate use as four of the eight studies reported shifts to smaller substrate sizes during the nighttime period. The majority of studies reported that bull trout shifted to slower-velocity microhabitats during the nighttime (7/12), but three studies observed no diel change, and two studies documented a shift to higher-velocity microhabitats during the night.

Classification Tree Analyses of Habitat

During the period of this study, we sampled 660 reaches where the watershed area upstream of the reach was greater than 400 ha, the wetted width exceeded 2 m, and the reach was identified as either (1) occupied by bull trout or (2) unoccupied but located within 25 km of occupied reaches. Of this total number of reaches, 310 reaches occurred in streams currently occupied by bull trout and 350 reaches occurred in proximal but unoccupied portions of stream networks (Figure 1). Watersheds above reaches in streams occupied by bull trout averaged 4,801 ha (SD = 2,732 ha) in size, and occupied reaches had an average maximum temperature of 17.0°C (SD = 3.1°C). Watersheds above unoccupied reaches averaged 3,477 ha (SD = 2,356 ha), and the average maximum summer temperature in unoccupied reaches was 18.0°C (SD = 4.0°C).

Including maximum stream temperature in the CTA did not result in changes to the overall CTA structure, and thus we report only one CTA for our data set. The CTA cross validation demonstrated that four splits minimized error rates in classifying the presence–absence of bull trout, and the model resulted in an overall correct classification rate of 60%.

Results from CTA suggested that reaches currently occupied by bull trout contained larger substrate, deeper pools, and more cover than unoccupied reaches; however, our results also indicated that occupied

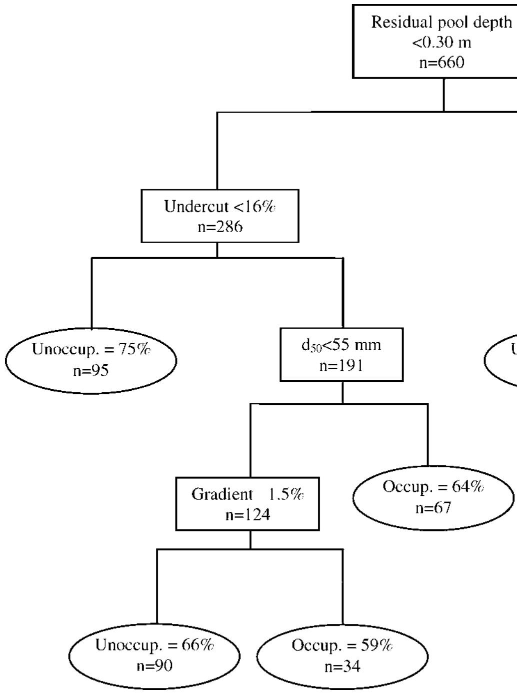

FIGURE 3.—Results from classification tree analysis exploring differences in physical habitat between interior Columbia River basin stream reaches that are occupied by bull trout (occup.) and those that are unoccupied (unoccup.). Rectangles represent the splitting criteria for branches of the tree (n = sample size; response to criteria consistently moves left at the branch), and the ellipses (terminal nodes) show the percent of reaches at each terminal node that were either occupied or unoccupied.

reaches contained smaller substrate in low-gradient areas than did unoccupied reaches. Specifically, we found that bull trout were generally absent from reaches where reach-level estimates of residual pool depth were less than 0.30 m and where the percent of undercut banks was less than 16% (i.e., 75% of such reaches were unoccupied; Figure 3). Within reaches where the percent of undercut banks exceeded 15%, bull trout were present in 64% of streams with a d_{50} greater than 55 mm; when d_{50} values were less than 55 mm, bull trout were absent from 66% of the reaches where gradient exceeded 1.5% and were present in 54% of the reaches where gradient was less than 1.5%. Where the residual pool depth exceeded 0.30 m, bull trout were present in 68% of the reaches with a d_{50} greater than 25 mm and were absent from 58% of reaches with a d_{50} of 25 mm or less.

Discussion

Quantifying the factors determining the distribution and abundance of bull trout across different spatial scales within systems (e.g., microhabitat versus reach) and across the geographic regions relevant to recovery continues to be an important component in the conservation and management of bull trout throughout the Pacific Northwest (Al-Chokhachy et al. 2008). The hierarchical nature of fluvial-geomorphic properties (Frissell et al. 1986; Imhof et al. 1996) and factors affecting the distribution and abundance of fishes (Fausch et al. 2002) suggests that robust assessments of habitat use within and across spatial scales (e.g., microhabitat, channel unit, watershed) are needed for thorough evaluations of bull trout habitat relationships. Biotic and density-dependent effects (Rosenfeld 2003), nonlinear relationships (Olden and Jackson 2001), and interactions between these and other factors (e.g., differential habitat use across life history strategies) all have the potential to complicate our assessments of fish habitat relationships. Here, we used multiple approaches to (1) help synthesize our current understanding of bull trout habitat use patterns, (2) explore differences in the physical habitat of streams where the presence–absence of bull trout was previously known, and (3) identify areas of research that warrant further investigation.

Consistency of Bull Trout Habitat Relationships

Since the late 1990s, there has been a substantial effort to improve our understanding of bull trout ecology, including habitat associations. Previous studies have demonstrated that the distribution of bull trout at the watershed scale is largely influenced by water temperatures (Dunham et al. 2003), patch size (Rieman and McIntyre 1995; Dunham and Rieman 1999; Rich et al. 2003), and levels of forest management practices (Ripley et al. 2005). Our CTA and our review of previous studies both indicated a general consistency of results at the microhabitat and channel unit scales, but this consistency diminished in our review of studies conducted at the larger, reach level. These results demonstrate the importance of understanding habitat relationships at the various spatial scales that bull trout can utilize throughout different life stages. Below, we discuss the relevance of our findings and illustrate important gaps in our current understanding of bull trout habitat relationships.

Microhabitat and channel unit assessments have consistently found bull trout to be associated with slow-velocity, deeper habitats regardless of season or diel period. The affinity of bull trout for slow-velocity, deeper habitat is probably a function of their basic physiology and swimming abilities (Mesa et al. 2004) and piscivorous feeding habits (Rieman and McIntyre 1993). This positive association of bull trout with slow-velocity habitat was observed both in microhabitat studies, where velocity is commonly measured directly, and in channel unit evaluations, where the presence of slow-velocity habitats is usually measured indirectly by considering the relative importance of different channel units (i.e., riffle versus pool). While our CTA did not include specific measurements of stream velocity, our results indicated the importance of deep pools, which are commonly slow-velocity habitats, as a factor influencing the distribution of bull trout. At the reach scale and in our CTA (which was conducted at the reach scale), however, there is little evidence supporting the importance of the amount of pool habitat as it relates to the distribution of bull trout, indicating that the quality of pool habitat (e.g., deeper versus shallower) may be important in the relationship between bull trout and pool habitat. Furthermore, the consistent use of slow-velocity microhabitats in previous studies may also indicate the importance of nondiscrete slow-velocity habitats (i.e., pocket pools, small eddies, etc.), which may be difficult to quantify using typical channel unit classifications (e.g., Roper and Scarnecchia 1995) in larger, reach-scale assessments.

Both our CTA results and previous research at the microhabitat and channel unit scales also suggest that the availability of deeper-water habitat is an important factor affecting the distribution of bull trout (references reviewed herein). Although diel and nighttime evaluations indicate use of shallower habitat during the nighttime period, most studies still observed bull trout using relatively deepwater habitat at night in comparison with the depths available. Deeper-water habitat, measured explicitly in microhabitat and channel unit studies, is probably used as a source of cover (Gibson and Power 1975; Spalding et al. 1995). The importance of deeper-water habitat, however, was not indicated in reach-level assessments. This inconsistency was likely due to different methodologies for quantifying depth since depth at the reach scale is often measured to estimate average reach depth, which may minimize the importance of smaller-scale, deeper channel units or microhabitats within these reaches. In addition, reach-level efforts that include both juvenile and adult bull trout may mask potential ontogenetic shifts in use of water depth (Al-Chokhachy and Budy 2007; Banish et al. 2008) and thus may add to the inconsistency of results at the reach scale.

Most studies observed that bull trout were positively associated with cover during daytime periods regardless of habitat scale and season and appeared to use a variety of other cover types, including LWD, vegetation, undercut banks, and turbulence. In contrast to daytime periods, most nighttime evaluations indicated a diel shift to habitats without cover, which probably explains the improved detection efficiency of snorkeling methods during nighttime sampling events relative to daytime snorkeling (Thurow et al. 2006). Similar to the results from the literature review, our CTA indicated the importance of cover, particularly in reaches with shallower pool depths, a pattern consistent with habitat selection experiments for other salmonids (Spalding et al. 1995; Rosenfeld and Boss 2001).

Substrate size was the one habitat variable for which there appears to be little agreement across bull trout habitat evaluations. Some studies found that bull trout associated with large substrate sizes, while others failed to demonstrate use of any particular substrate size regardless of size-class. Part of the difficulty in identifying the importance of substrate size in bull trout habitat selection may be due to the confounding issue of water velocity and substrate size. For example, slow-velocity habitat, which is consistently used by bull trout, is also an area where fine sediment can be deposited at the microhabitat scale (Knighton 1998). Nevertheless, large substrate may be particularly important for juvenile bull trout due to their use of interstitial spaces between substrate particles (Dambacher and Jones 1997; Thurow 1997; Banish et al. 2008). However, at the same time, the concealment of bull trout within interstitial spaces of large substrate may indicate why juvenile bull trout are more difficult to detect in observational studies (Jakober et al. 2000; Thurow et al. 2006); therefore, observational studies may be biased against detecting juvenile bull trout in habitats with large substrate. This confounding issue may explain, in part, why more studies do not consistently report the use of interstitial spaces. Banish et al. (2008) hypothesized that juvenile bull trout may utilize gravel interstices to avoid predation; it is also likely these interstitial spaces provide low-velocity refugia during high flow events (e.g., as has been observed for coastal cutthroat trout *Oncorhynchus clarkii clarkii*; Anderson 2008) or overwinter refugia (Power et al. 1999). Our CTA supported these hypotheses as bull trout were positively associated with larger substrate sizes and were generally absent from higher-gradient reaches with smaller substrate (i.e., $d_{50} < 55$ mm). The negative association with high levels of fine sediment in spawning and rearing habitat may also be due to the negative effect of fine sediment on egg-to-fry survival (Tappel and Bjorn 1983) and growth (Suttle et al. 2004). Overall, these findings warrant additional research that specifically investigates juvenile bull trout use of substrate as a source of refugia from predation and flow events and how increasing levels of fine sediment, which fills these interstitial spaces, may negatively impact juvenile bull trout growth and survival.

Our literature review also showed an inconsistency in the strength of bull trout habitat relationships at the reach scale, which may be a result of different attributes of the sampling designs and methodologies used to evaluate bull trout relationships. First, the majority of the studies at the reach (and all) scales used nonrandom study designs to select areas for evaluating bull trout habitat relationships. Nonrandom sampling can substantially affect the results of species-habitat models, particularly when comparing the results from random and nonrandom study designs (Edwards et al. 2006). Additionally, half of the reach-level studies used snorkeling methods in their evaluations of bull trout habitat relationships, and the low sampling efficiencies of snorkeling methods (both daytime and nighttime; Thurow et al. 2006) may have affected the consistency of the results across studies. The inconsistencies in the results at the reach scale may also be due to the natural low densities and clumped distribution patterns of bull trout within streams (Al-Chokhachy et al. 2009), which may moderate the strength of bull trout habitat relationships at this scale. In addition, our understanding of the complexity of factors affecting fish habitat relationships coupled with the simple approaches used to evaluate these relationships (e.g., linear regression) may also have contributed to the inconsistency at the reach scale. Our results from the CTA, which clearly indicate nonlinear patterns of occurrence (e.g., importance of cover in shallower systems), support this concept and indicate the need for alternative approaches, such as the exploratory approach used here, to improve our understanding of the factors affecting bull trout habitat use at these larger, reach scales. Finally, while the use of the reach scale has been and continues to be consistent in fisheries research and monitoring, the application of such arbitrarily selected units may not be appropriate in considering bull trout habitat relationships. Our review of studies conducted at the microhabitat and channel unit scales clearly indicate bull trout use of specific habitat qualities, yet whether and how these smaller spatial scales fit into larger, reach-level scales or are organized across the landscape warrant additional research with robust sampling designs and methods.

Temperature and Bull Trout Habitat Use

The well-documented sensitivity of bull trout to elevated water temperatures (Selong et al. 2001) has led to a body of research focused on evaluating bull trout habitat relationships in cold headwater systems. However, in our analysis, temperature did not help to explain patterns of occupancy within our study site. The difference between this result and the results of previous efforts is probably due to the difference in distribution data used in our analysis versus other analyses. For example, Dunham et al. (2003) generally focused on the presence–absence of juvenile bull trout during the summer months, whereas our occupancy data relied on known bull trout distribution across seasons. We considered this approach to be appropriate for our analyses as we looked for differences in instream habitat between occupied and unoccupied streams over a substantially larger portion of bull trout range in the interior Columbia River basin. In many systems, bull trout have been found to express both resident and migratory life histories within a single local population (Nelson et al. 2002; Al-Chokhachy and Budy 2008); thus, habitat requirements may differ depending on the life history strategies. Large downstream migrations to reaches that exceed the optimal thermal criteria for bull trout during the summer months but that are thermally suitable during months other than summer are common among bull trout populations (Homel and Budy 2008; Howell et al., in press). For bull trout, these reaches downstream of spawning locations act as key rearing habitat for juveniles (Homel and Budy 2008) and overwinter habitat for all life stages during the fall through spring (Jakober et al. 1998; Watry and Scarnecchia 2008; Howell et al., in press).

Clearly, more research is needed to quantify bull trout habitat use patterns in migratory corridors and stream reaches at and above the upper bounds of bull trout thermal tolerance. In our review, we found only one study (e.g., Jakober et al. 1998) that explicitly evaluated bull trout habitat associations in the lowermost reaches of the species' distribution. This deficiency is probably due to the challenges of working in large-river environments and the difficulties of quantifying fish habitat relationships in areas where densities are generally low and where a large percentage of suitable habitat remains unused (Rosenfeld 2003), thus reducing the explanatory power and effectiveness of predictive models (Al-Chokhachy and Budy 2007). Despite these difficulties, large-river, lower-elevation stream reaches may serve as migratory corridors and as overwinter habitat for bull trout and may be critical for maintaining a suite of diverse life history strategies within populations and connectivity among populations.

Limitations of Synthesis and Analyses

Despite the consistency of our literature review and CTA results, we acknowledge limitations in our approach and the information that was available for inclusion in our CTA. First, we were unable to perform a formal meta-analysis because of (1) small sample sizes for available literature, particularly studies conducted at the reach scale, (2) the diversity of analytical techniques used to evaluate bull trout habitat relationships, (3) the lack of statistical information provided, and (4) the lack of control in many instances (e.g., habitat availability data). We hope this study will encourage future efforts to consider these issues and that future analyses will incorporate robust sampling designs and report measures of habitat use, habitat availability, variance estimates, and sample sizes to allow for formal meta-analyses of bull trout habitat relationships. Secondly, we acknowledge that we did not incorporate the effects of current or historical barriers in our analyses. Barriers have been identified as a major factor affecting the abundance and distribution of bull trout (Al-Chokhachy et al. 2008). However, understanding how and when these barriers have contributed to the current distribution of bull trout can be problematic. Although many historical barriers have been removed through recent programs (e.g., Allen 2002), the presence of barriers may have led to bull trout absences that were unrelated to instream habitat.

Finally, our CTA relied on available bull trout distribution data within the interior Columbia River basin, which may have limited the clarity of our results. In particular, we were not able to distinguish between juvenile and adult bull trout distributions, and the importance of different habitat qualities probably differs across size-classes of bull trout. Next, the accuracy of this distribution data, however, may be clouded by the bull trout's low detection rates and elusive behavior, which can lead to a high proportion of false absences if not properly accounted for in presence–absence surveys (Stauffer et al. 2002). The accuracy of expert opinions and the use of historical spawning surveys to describe the distribution of bull trout in systems containing nonnative brook trout *S. fontinalis*, a species with similar appearance and spawn timing, may further limit the reliability of the distribution data used herein, thus illustrating the need for field efforts to continue to update information about bull trout distribution. Nevertheless, by using data collected across 660 streams in the interior Columbia River basin, we identified patterns of habitat use that were consistent with the results from our literature review and our understanding of bull trout biology.

Management Implications and Future Research

The importance of physical habitat as a template for biological processes highlights the need for continued investigations of the factors governing bull trout habitat use. While we acknowledge that physical habitat is not the sole factor determining the distribution and abundance of bull trout (e.g., Rieman et al. 2006, 2007), identification and restoration of suitable habitat conditions may ensure the persistence of bull trout populations in areas where other limiting factors are absent or minimized (e.g., nonnative species; Quist and Hubert 2005) and may limit the invasion success of nonnative source populations (Benjamin et al. 2007). While watershed-level attributes can have effects that may override the importance of local habitat attributes for bull trout distribution (Dunham et al. 2003), understanding the consistency of bull trout habitat use patterns at these smaller spatial scales is an important step toward guiding feasible restoration and management actions.

The current distribution of bull trout encompasses a wide range of ecosystems, and understanding the consistency of habitat use patterns is an important component in the conservation and management of this species. Using exploratory CTAs for streams within the interior Columbia River basin and reviews of studies conducted at the microhabitat and channel unit scales and scattered across much of the species' current range, we found general consistencies in factors affecting the distribution of bull trout. Based on our analyses, we found water depth and velocity to be two factors that were consistently associated with patterns of bull trout distribution. The diel shifts in habitat use observed by most studies, particularly with respect to cover and depth, also highlight the importance of complex habitat for bull trout (references herein).

In addition to the information gaps already discussed, our analysis revealed additional gaps in our current knowledge of bull trout habitat use, indicating the need for additional research to help direct future restoration and management. First, there continues to be a need for more research evaluating bull trout habitat use patterns, particularly within regions such as the Klamath River basin, the northern latitudes of bull trout distribution, and the coastal areas, where differences in life history strategies (Brenkman and Corbett 2005) and resource limitations may result in different habitat use patterns than were observed here. Next, additional analyses are needed to better understand the consistency of the relationships between landscape attributes (e.g., catchment size) and bull trout distribution. Much of our current knowledge is based on data from central Idaho (i.e., Dunham and Rieman 1999), and additional efforts are needed to investigate the consistency of such patterns across the range of bull trout. Next, where possible, experimental studies should be considered to help identify how bull trout habitat use differs as habitat qualities interact (e.g., cover and pool depth; Spalding et al. 1995) and how these patterns change across bull trout life stages; such studies would help to elucidate where and when bull trout habitat use may change based on the availability of specific habitat attributes. Finally, additional research is needed to understand the importance of biotic factors as they relate to bull trout habitat use. Despite clear evidence of the longitudinal displacement of bull trout by brook trout within stream networks (Rieman et al. 2006), changes in bull trout habitat use when in sympatry with brook trout have not been as apparent (Nakano et al. 1998; Gunckel et al. 2002) and further efforts are needed. Additionally, more research is needed to quantify how changes in the abundance and distribution of native fishes have affected bull trout habitat use and distribution (e.g., Nakano et al. 1998). In many systems, bull trout have coevolved with other salmonids, and their position as a top predator in these systems (Rieman and McIntyre 1993) would indicate that declines in native fishes (e.g., Chinook salmon *O. tshawytscha*; Nehlsen et al. 1991) may have significant effects on bull trout habitat use within and across systems.

As our efforts to quantify bull trout habitat relationships progress, explicit consideration must be given to the use of robust sampling designs and methodologies. The bull trout is associated with cold headwater streams that are difficult to access and to sample. The use of complex habitat often results in relatively low sampling efficiencies regardless of technique (Thurow et al. 2006; Dunham et al. 2009). However, much of our current understanding of bull trout habitat relationships is built upon data collected without a firm understanding of how well we sample. As habitat complexity increases, our sampling efficiency decreases (Rosenberger and Dunham 2005), which suggests that we have a considerable amount to learn about how habitat shapes the distribution and abundance of bull trout.

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