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Evaluating the Utility of Beaver Reintroduction Programs for Enhancing Habitat for Rainbow Trout and Steelhead

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EVALUATING THE UTILITY OF BEAVER REINTRODUCTION PROGRAMS FOR ENHANCING HABITAT FOR RAINBOW TROUT AND STEELHEAD

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Jonathan Rodger Hegna

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ABSTRACT

EVALUATING THE UTILITY OF BEAVER REINTRODUCTION PROGRAMS FOR ENHANCING HABITAT FOR RAINBOW TROUT AND STEELHEAD

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Beaver reintroduction programs are increasingly being viewed as a way to enhance salmonid habitat and production. However, the actual effectiveness of using beavers as a habitat enhancement tool for ESA listed steelhead *Oncorhynchus mykiss* populations is unknown. We examined the type of habitat, at both the microhabitat and mesohabitat levels, preferred by steelhead in three small streams in the upper Yakima Basin, WA through standard snorkel surveys and habitat measurements. Our results suggest that steelhead in small streams strongly prefer (relative to availability) microhabitats that have deeper water (> 30 cm), slow stream velocities (< 0 .05 m/s), and complex cover types. Habitat partitioning among the size-classes (small < 50 mm, medium 50-90 mm, large > 90 mm total length, TL) principally operated around water depth and to a lesser extent around stream velocity, with larger steelhead (> 90 mm TL) occupying slower and deeper water than smaller steelhead (< 90 mm TL). Mesohabitat analyses indicate that all size-classes of steelhead avoid riffles and strongly prefer pool habitat, while only large steelhead (> 90 mm TL) strongly prefer beaver pond habitat and small steelhead (< 50 mm TL) prefer glides. Consequently, in small streams the creation of deep pool habitat, either through artificial means or through beaver reintroduction programs, will be beneficial for increasing the amount of highly preferred habitat for steelhead populations.

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CHAPTER I

INTRODUCTION

Steelhead Ecology

Steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) is an important salmonid species throughout the Pacific Northwest for commercial and recreational fishing. This species displays two different life-history strategies that includes a resident type (i.e., rainbow trout) and an anadromous type (i.e., steelhead). Steelhead generally reside in freshwater for 2-3 years and typically occupy riffles and feed on a variety of drifting and benthic aquatic invertebrates (e.g., dipterans, daphniids, mayflies, stoneflies, beetle larvae, aquatic worms, amphipods) (Bisson et al. 1988; Scott and Gill 2008; Wydoski and Whitney 2003). Steelhead may also eat smaller fish and fish eggs. After undergoing smoltification and migrating to the ocean, the more abundant supply of food in the ocean allows steelhead to substantially increase their growth. In the ocean, steelhead may spend 1-3 years feeding upon a variety of crustaceans (e.g., amphipods), polychaetes, squid, herring, mackerel, and other fish (Atcheson et al. 2012; Light 1985; Wydoski and Whitney 2003). Upon returning from the ocean, steelhead can weigh between 2.2-4.5 kilograms and can be 45-63 centimeters in length (Wydoski and Whitney 2003). The most common life history pattern for steelhead in Washington is 2 years in freshwater and 2 years in the ocean (Conely et al. 2009; Scott and Gill 2008; Wydoski and Whitney 2003).

Steelhead stocks are designated as winter-run or summer-run based on the timing of return to freshwater and sexual maturity (Conely et al. 2009; Scott and Gill 2008). Winter-run steelhead enter freshwater between November and May, are sexually mature, and usually spawn between mid-April and mid-May. Summer-run steelhead enter freshwater between April and October, take several months to sexually mature, and generally spawn between March and May.

In western Washington both life history types exist, while in the interior Columbia River Basin only the summer-run life history type exists.

Currently, 11 distinct population segments (DPS) of steelhead are listed as threatened and 1 population is listed as endangered under the Endangered Species Act (Conely et al. 2009; ESA 1973). Habitat degradation from agricultural development, hydroelectric dams, habitat fragmentation, and continued development along rivers and streams has been largely responsible for population declines of steelhead in the Pacific Northwest (Scott and Gill 2008; Williams et al. 1991). The steelhead population residing in the upper Yakima Basin in Washington State where this study took place is currently listed as threatened as part of the Middle-Columbia DPS and has a mixed population of anadromous steelhead and resident rainbow trout (Conely et al. 2009; Scott and Gill 2008). Consequently, federal regulations require the improvement of stream habitat and increased numbers of steelhead for delisting to occur. Hereafter, we will refer to individuals from this mixed population as steelhead.

Beaver Ecology

The Eurasian beaver (*Castor fiber*) and the North American beaver (*Castor canadensis)* are both semi-aquatic herbivores (Collen and Gibson 2000). Beavers live in small family units or colonies that generally consist of two parents, the young of the year, and the yearlings (Collen and Gibson 2000; Müller-Schwarze and Sun 2003). A beaver colony may build one or more lodges and may or may not actually build a dam (Collen and Gibson 2000; Müller-Schwarze and Sun 2003; Naiman et al. 1988; Rosell et al. 2005). In general, beavers tend to colonize small, low-gradient, first- to fourth-order streams (Collen and Gibson 2000; Müller-Schwarze and Sun 2003; Rosell et al. 2005). Alternatively, beavers can also colonize lakes and large streams. In order to survive the long winter months, a food cache is constructed to supply the colony with food throughout the winter (Collen and Gibson 2000; Müller-Schwarze and Sun 2003). The diet of a beaver varies considerably among the seasons. In the fall and winter, beavers typically tend to eat more woody vegetation, while in the spring and summer they eat more herbaceous vegetation (Collen and Gibson 2000; Müller-Schwarze and Sun 2003; Rosell et al. 2005). Consequently, tree-cutting activity is usually highest in the fall when beavers are preparing for winter.

Relatively deep, lentic ponds are required by beavers for a number of important reasons (Collen and Gibson 2000; Müller-Schwarze and Sun 2003; Naiman et al. 1988; Rosell et al. 2005). Firstly, deep water is needed to keep the entrance to the lodge underwater for protective purposes. A deep pond also allows the floating of cut logs, which can be cumbersome for beavers to move. The quiet, slow-moving waters of a deep pond are also ideal for building a food cache. The water must be slow enough to prevent the food cache from drifting away, and the pond must be deep enough to allow the wood to sink to the bottom. A deep pond also prevents the water from freezing completely through, which allows a beaver colony to access its food cache during winter. Lastly, a deep pond allows a beaver to swiftly escape from predators. To this effect beavers will relentlessly build dams to get the water levels that they desire. Interestingly, the North American beaver has been found to have a much greater dam-building propensity than the Eurasian beaver (Müller-Schwarze and Sun 2003).

Stream Habitat

The quality of stream habitat is one of the strongest factors that directly determines the number of salmon and trout that a stream can produce (Cramer and Ackerman 2009, 2009b; Williams et al. 1991). Stream habitat is composed of a myriad of intrinsic factors that include stream depth, velocity, substrate, cover, woody debris, temperature, and water-quality measures. This multitude of factors directly determines the carrying capacity of a stream for salmonids.

Stream habitat use is best analyzed at more than one spatial scale to allow for a more thorough understanding of a species' biological requirements (Frissell et al. 1986). The mesohabitat scale divides the habitat within a stream reach into discrete habitat or channel units (Cramer and Ackerman 2009; Frissell et al. 1986; Hankin and Reeves 1988; Hawkins et al. 1993). Different mesohabitat units like riffles, glides, and pools are differentiated based on differences in stream velocity, depth, slope, and bed topography (Frissell et al. 1986). On a smaller spatial scale, microhabitat analyses involve recording the depth, velocity, cover, and substrate that a specific fish is using at a specific point within a habitat unit. Examining both of these habitat levels provides the most effective information for determining which factors influence fish (Holecek et al. 2009; Muhlfeld et al. 2001).

Steelhead and Beaver Reintroduction Programs

Due to many years of over-exploitation, many beaver populations were exterminated in North America and Europe (Collen and Gibson 2000; Müller-Schwarze and Sun 2003; Naiman et al. 1988; Rosell et al. 2005). Today beavers are slowly recolonizing their past range both naturally and with the help of reintroduction programs (Collen and Gibson 2000; Halley and Rosell 2003; Macdonald et al. 1995; Macdonald et al. 2000; McKinstry and Anderson 2002; Müller-Schwarze and Sun 2003; Pollock et al. 2003; Pollock et al. 2004; South et al. 2000). One analysis estimates that prior to the arrival of Europeans an estimated 25 million beaver dams crossed rivers and restricted flow in North America (Pollock et al. 2003). In pristine areas, the number of beaver dams ranges from 7.5 to more than 74 per kilometer (Warren 1932; Scheffer 1938). Thus, the impact of reintroducing beavers on the hydrology and habitat of streams could be considerable on the landscape level. Nevertheless, beaver reintroduction programs can be controversial due to the potential or perceived negative impacts of beavers on road infrastructure, farmland, private property, habitat, and fish production (Collen and Gibson 2000; Kemp et al. 2012).

Beaver (*Castor canadensis*) reintroduction programs have recently been proposed and are underway in several different locations in Washington State for the purpose of enhancing stream habitat for salmonids. Beavers are considered ecosystem engineers and are valued for their ability to increase the amount of stream habitat, stabilize stream flow, decrease stream incision, increase riparian habitat, store water, increase fish production, and create heterogeneity in the environment through their dam building activities (Kemp et al. 2012; Müller-Schwarze and Sun 2003; Pollock et al. 2007; Pollock et al. 2003; Pollock et al. 2004; Rosell et al. 2005). Beavers can have both positive and negative impacts on stream temperature and water quality that are largely dependent upon location (Collen and Gibson 2000; Kemp et al. 2012; Rosell et al. 2005). In the interior Columbia River Basin beaver dams have been found to greatly accelerate stream restoration through the rapid aggradation of sediment, which can reconnect an incised channel with the surrounding flood plain and increase riparian vegetation (Pollock et al. 2007). However, beaver reintroduction programs are controversial, and there are genuine knowledge gaps about their ability to enhance habitat for rainbow trout and steelhead (Collen and Gibson 2000; Kemp et al. 2012; Rosell et al. 2005).

Most research to date on beaver-fish interactions has focused primarily on coho salmon (*Oncorhynchus kisutch*), brook trout (*Salvelinus fontinalis*), and Atlantic salmon (*Salmo salar*) (Kemp et al. 2012). A number of previous studies suggest that coho salmon greatly benefit from beaver pond habitat (Beechie et al. 1994; Bisson et al. 1988; Bramblett et al. 2002; Bustard and

Narver 1975a, 1975b; Dolloff 1987; Everest et al. 1986; Leidholt-Bruner et al. 1992; Murphy et al. 1989; Nickelson et al. 1992; Pollock et al. 2004; Sanner 1987; Swales and Levings 1989). The National Oceanic and Atmospheric Administration determined that coho salmon production in the Stillaguamish Watershed in Washington is greatly limited by the amount of beaver pond habitat (Pollock et al. 2004). Researchers in New Brunswick found that juvenile Atlantic salmon living in beaver pond habitat exhibited higher growth rates and were healthier than those living in non-beaver pond habitat (Sigourney et al. 2006). Similarly, several studies show that brook trout populations benefit from beaver pond habitat (Allen 1956; Huey and Wolfrum 1956; Johnson et al. 1992; Rupp 1955). The main benefits cited by these studies were increased growth of fish and production of stream invertebrates.

Research on the use of beaver ponds by steelhead and rainbow trout is very limited (Kemp et al. 2012). Gard (1961) conducted primitive research that suggested that "trout" in beaver ponds were about five times as large as fish residing in other stream habitats. Although no species-specific analyses were conducted, this study did demonstrate that rainbow trout have the ability to use beaver ponds. Conversely, researchers examining a large fifth-order stream in Oregon over four years found that steelhead greatly avoided beaver pond habitat (Everest et al. 1986). In the upper Yakima Basin, however, beavers are being reintroduced primarily into smaller-order streams with drastically different habitat conditions that may greatly influence habitat use by steelhead (Cramer and Ackerman 2009, 2009b; Hartman 1965; Harvey and Nakamoto 1996).

The controversy surrounding beaver reintroduction programs, the economic importance of productive fisheries, and the need to improve habitat for steelhead populations under the ESA were the motivating factors to study microhabitat and mesohabitat use and preference by steelhead in the upper Yakima Basin (ESA 1973). Quantitatively evaluating habitat factors that are essential to steelhead populations will be paramount for the effective conservation and management of the species. We specifically set out to assess three different objectives in small streams within the upper Yakima Basin: (1) determine the level of use of and preference for important microhabitat features in the environment, (2) evaluate the level of use of and preference for mesohabitats with an emphasis on beaver pond habitat, and (3) assess differences in habitat use and preference among size-classes of steelhead to investigate habitat partitioning.

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CHAPTER II

EVALUATING THE UTILITY OF BEAVER REINTRODUCTION PROGRAMS FOR ENHANCING HABITAT FOR RAINBOW TROUT AND STEELHEAD

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Introduction

The quality of stream habitat is one of the strongest factors that directly determines the number of salmon and trout that a stream can produce (Cramer and Ackerman 2009, 2009b; Williams et al. 1991). Stream habitat is composed of a myriad of intrinsic factors, such as stream depth, velocity, substrate, cover, woody debris, temperature, and water-quality measures. This multitude of factors directly determines the carrying capacity of a stream for salmonids.

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The controversy surrounding beaver reintroduction programs, the economic importance of productive fisheries, and the need to improve habitat for steelhead populations under the ESA were the motivating factors to study microhabitat and mesohabitat use and preference by steelhead in the upper Yakima Basin (ESA 1973). Quantitatively evaluating habitat factors that are essential to steelhead populations will be paramount for the effective conservation and management of the species. We specifically set out to assess three different objectives in small streams within the upper Yakima Basin: (1) determine the level of use of and preference for important microhabitat features in the environment, (2) evaluate the level of use of and preference for mesohabitats with an emphasis on beaver pond habitat, and (3) assess differences in habitat use and preference among size-classes of steelhead to investigate habitat partitioning.

Methods

Study sites

We chose three small streams north of the town of Cle Elum, Washington within the upper Yakima Basin to examine microhabitat and mesohabitat availability, use, and preference by steelhead (Figure 1). Jack Creek, Jungle Creek, and Iron Creek were specifically selected because they are all recognized as critical habitat areas for steelhead under the Yakima Basin Steelhead Recovery Plan (Conely et al. 2009). The upper Yakima Basin is located along the eastern slopes of the Cascade Mountain Range and is characterized by warm, dry summers, with extreme low flows occurring between August and September. Two of the streams, Jack Creek and Jungle Creek, are small second- to third-order tributaries along the North Fork of the Teanaway River. The third stream, Iron Creek, is a second- to third-order tributary of Swauk Creek. Beavers were reintroduced to Jack Creek in 2009 but not into the other streams. The beaver population has greatly expanded since reintroduction and has built numerous dams along the stream.

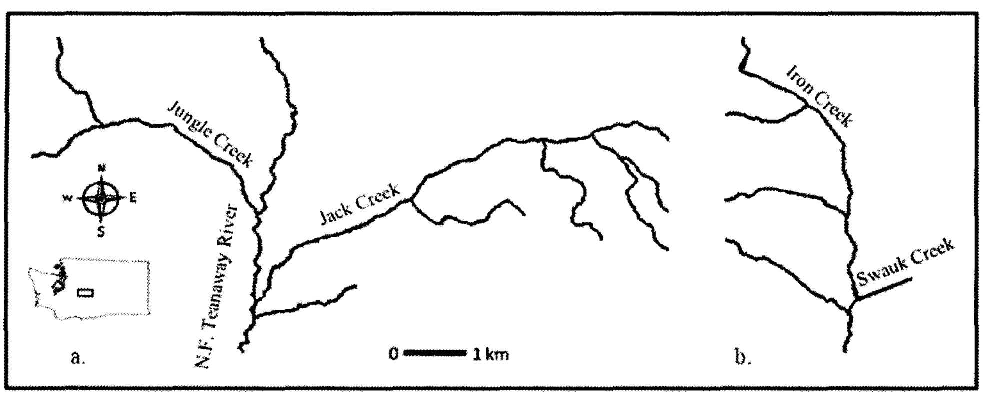

Figure 1. Map of stream field sites along the North Fork Teanaway River (a) and Swauk Creek (b) in the Upper Yakima Basin of central Washington.

Beavers were not present at Iron Creek or Jungle Creek. Steelhead were the dominant fish species observed within each stream. Cutthroat trout were also observed, but were much less abundant. Several species of sculpin (*Cottus* spp.) were also observed to be abundant throughout all the streams. In Jack Creek, brook trout (*Salvelinus fontinalis*) were observed and were largely isolated to deep pools and beaver ponds.

Microhabitat and mesohabitat use and availability

We quantified habitat use and availability through the use of spatially-stratified transects. Each designated stream field site was segmented into appropriate stream reaches. At each stream reach, a starting point for a transect was determined randomly, except for two transects at Jack Creek where non-random starting points were chosen in order to obtain enough data on beaver pond habitat. In general, at least 300 meters of stream habitat were needed to obtain adequate data on the use of mesohabitats. We used four 75-meter transects at Jungle Creek, three 100-meter transects at Iron Creek, and four 200-meter transects at Jack Creek. The longer transects at Jack Creek were needed to sample enough beaver ponds. Transects were separated by a minimum of 300 meters.

We used snorkel surveys along each stream transect between August and September of 2012 to quantify microhabitat and mesohabitat use (O'Neal 2007). The summer low-flow period is when stream habitat is at its lowest supply, and it is considered the most limiting time period for steelhead in terms of stream carrying capacity (Cramer and Ackerman 2009, 2009b). The snorkel surveys involved one diver that slowly snorkeled up the stream transect and used a waterproof diving notebook to record microhabitat and mesohabitat data on all fish observed between 1000 and 1730 hours. Fish were classified into a size-class with the aid of a ruler. The three designated size-classes were small (< 50 mm total length, TL), medium (50 - 90 mm TL), and large (> 90 mm TL). Steelhead and cutthroat trout can be hard to distinguish when they are less than 90 mm (TL). Therefore, it is possible that our visual counts of steelhead (< 90 mm TL) may have included some cutthroat trout.

Stream depth and focal depth were measured directly by the diver with the use of a ruler. Focal depth refers to the actual vertical position of a fish in the water column. To determine focal velocity we marked the location of each fish with a readily identifiable marker, recorded the focal depth of each fish, and then measured the exact focal velocity used by each fish with a flow meter (Geopacks: Advanced FlowMeter) after the snorkel survey was complete. Substrate was visually classified into five different categories using a modified Wentworth scale: sand-silt (< 0.5 cm), gravel (0.5 cm – 7.5 cm), cobble (7.5 cm – 30 cm), boulder (> 30 cm), and bedrock. Eight different microhabitat cover categories were used: woody debris, cobble, boulder, overhanging vegetation, roots, undercuts, underwater algae / vegetation, and turbulence. Cover had to be within 40 cm of a fish to be considered "used."

We determined microhabitat availability for each stream transect. A random starting location at the beginning of each transect was chosen. At pre-specified intervals, three equidistant points perpendicular to the stream transect were measured for the same microhabitat characteristics as previously described (i.e., depth, velocity, cover, and substrate). Velocity was measured in the water column at approximately half the total stream depth to mimic the height in the water column that steelhead often use (Bugert et al. 1991; Johnson and Johnson 1981; Johnson and Ringler 1980). During the stream surveys, if water depth and velocity were too low to allow for the effective use of the flow meter, we used manual object displacement to estimate stream velocity. At Iron and Jungle Creeks we used 3-m intervals, while at Jack Creek we used 5-m intervals because the transects were longer. Thus, the relative frequency of occurrence of different types of microhabitat (i.e., availability) could be determined for microhabitat preference analyses.

Mesohabitat data were also collected to characterize each mesohabitat unit (e.g., riffle, glide, pool, beaver pond) surveyed along each transect and to quantify mesohabitat availability. We took depth and velocity measurements haphazardly every 1-2 meters down the active channel. A minimum of three measurements was required to characterize a habitat unit. In pools and beaver ponds, the maximum depth was measured and used as the major descriptor (Cramer and Ackerman 2009, 2009b). The length and average wetted width of each habitat unit was directly measured. Width measurements were taken at least every three meters, with a minimum of three required. Surface area and, thus, the availability of mesohabitat could then be estimated for mesohabitat preference analyses. Fish density was estimated by dividing the total number of steelhead observed within a habitat unit by the surface area of the habitat unit. We quantified habitat complexity through the use of a categorical scale that ranged from 1 (lowest complexity) to 4 (highest complexity), based on the number of different types of habitat available in a habitat unit (Table 1; modified from Holecek et al. 2009). The

Table 1. Rating scale for evaluating the structural complexity of mesohabitat units. Structural cover types include woody debris, boulder, cobble, undercuts, roots, underwater algae / vegetation, and overhanging vegetation. –Modified from Holecek et al. (2009).

Complexity Rating	Rating Description
1	The lowest complexity. Habitat unit generally contains only one dominant, homogeneous, structural cover type.
2	Low complexity. Habitat unit contains no more than two dominant, structural cover types.
3	Moderate complexity. Habitat unit contains up to three different dominant, structural cover types.
4	Highest complexity. Three or more complex structural cover types are abundantly available in the habitat unit. Snorkeler generally has difficulty maneuvering around the habitat unit because of the high complexity.

Table 2. Rating scale for evaluating the amount of cover that woody debris provides fish within mesohabitat units.

Woody Debris Rating	Rating Description
1	Woody debris is absent to minimal, structural complexity is lacking.
2	Woody debris provides cover for 10-20 % of the habitat unit.
3	Woody debris provides noticeable complexity and cover for 20-50 % of the habitat unit.
4	Woody debris is abundant, making snorkeling difficult. Woody debris provides cover for more than 50 % of the habitat unit.

availability of woody debris cover was evaluated with a rating scale that estimated the amount of surface area within a habitat unit that had woody debris cover (Table 2).

Data analysis

To determine mesohabitat and microhabitat preference, we employed G-tests that compared the observed level of habitat use with an expected level based on habitat availability (Holecek et al. 2009; Muhlfeld et al. 2001). Each stream was evaluated both separately by fish size-class and with all size-classes combined. If a G-test was significant, we used Jacobs electivity index (D) to evaluate the degree of preference (Jacobs 1974):

$$D = (r - p) / (r + p - 2rp),$$

where r represents the proportion of fish using a particular habitat category and p is the proportion of that habitat category available in the environment. The electivity index ranges from -1 (complete avoidance) to 1 (complete preference); a value of 0 represents use in proportion to availability (i.e., neutral use). In Jack Creek only three of the four transects were used to assess microhabitat preference because wildfires in the summer of 2012 prevented us from accessing the site. By the time the area had been re-opened, beavers had built several new dams that drastically changed the availability of habitat along the transect.

We examined differences in fish density (all size-classes combined and large fish) among mesohabitat types with Welch's ANOVA. ANOVA was used to examine differences in the use of stream depth among the size-classes, while Welch's ANOVA was used to assess differences in the use of stream velocity among the size-classes. We also compared the mean depth and velocity used by each size-class against the respective stream means with T-tests. The Kruskal-Wallis Test was used to evaluate physical differences in habitat complexity and woody debris among mesohabitat types. Differences in depth and velocity among mesohabitat units were evaluated with Welch's ANOVA. The Pearson's chi-square test was used to examine direct associations between fish size-class and the usage of mesohabitat types. Jack Creek was evaluated separately because it contained beaver ponds, while Jungle Creek and Iron Creek were evaluated together. Odds ratios were then used to quantify effect size and significance.

We used multiple regression to examine which mesohabitat factors were associated with fish density. Fish density was the response variable, while the predictor variables used in the model were velocity, depth, surface area, and woody debris rating of the habitat unit. Variance inflation factors were used as indicators for problems with multicollinearity in the analysis.

We used Tukey's post-hoc test to evaluate the results of all ANOVA tests, while the Games-Howell post-hoc test was used to evaluate the results of all Welch's ANOVA tests. Leven's test was used to test for unequal variance among groups. We used Mann-Whitney tests to evaluate the results from all Kruskal-Wallis tests conducted. The Bonferroni correction was applied to all applicable tests to control for multiple comparisons and to lower the risk of type I error. We used Minitab to perform all ANOVA, Kruskal-Wallis, and T-tests analyses; SPSS for Welch's ANOVA and Pearson's chi-square tests; Excel for all G-tests; and MedCalc statistical software to calculate odds ratios.

Results

Microhabitat

During the summer of 2012, we took observations on 781 steelhead in three streams. Sample sizes varied among streams and size-classes: 193 small, 160 medium, and 123 large individuals were observed in Jack Creek; 53 small, 37 medium, and 27 large individuals were observed in Jungle Creek; and 77 small, 72 medium, and 43 large individuals were ôbserved in Iron Creek.

All three size-classes of steelhead showed distinct preferences for certain stream depths (Table 3; Figure 2). Furthermore, each size-class used deeper water than the respective stream means (all T-tests, $P < 0.001$). In all streams, Jacob's electivity index indicated that small individuals most strongly preferred water depths between 10 cm and 30 cm and generally avoided water deeper than 30 cm. Medium-sized individuals generally had a weak to neutral preference for stream depths between 10 cm and 15 cm, while they generally had a strong preference for stream depths greater than 15 cm. Large individuals showed a progressively stronger preference for stream depths greater than 20 cm. All three size-classes strongly avoided shallow water less than 11 cm deep. Direct comparisons among the size-classes showed significant size-related differences in depth use (Jack Creek, ANOVA: $F_{2, 474} = 191.66$, $P < 0.001$; Jungle Creek, ANOVA: $F_{2, 112} = 51.45$, $P < 0.001$; Iron Creek, ANOVA: $F_{2, 189} = 26.35$, $P < 0.001$). Large steelhead occupied significantly deeper water than small steelhead (Tukey post-hoc tests, $P < 0.001$).

Table 3. G-test results comparing the observed level of stream depth and focal velocity use with the expected level of use based on habitat availability for steelhead *Oncorhynchus mykiss* by size-class (small, medium, large) for Jack, Jungle, and Iron Creeks in central Washington during August-September 2012.

	Depth Use			**Velocity Use**		
	G	d.f.	*P*	G	d.f.	*P*
Jack Creek						
Small	154.99	7	<0.001	108.89	5	<0.001
Medium	152.32	7	<0.001	103.98	5	<0.001
Large	237.4	7	<0.001	111.53	5	<0.001
Iron Creek						
Small	113.66	6	<0.001	43.45	5	<0.001
Medium	147.82	6	<0.001	25.44	5	<0.001
Large	151.66	6	<0.001	67.4	5	<0.001
Jungle Creek						
Small	48.9	6	<0.001	52.04	5	<0.001
Medium	75.62	6	<0.001	25.98	5	<0.001
Large	64.17	6	<0.001	41.39	5	<0.001

Each size-class of steelhead also showed distinct preferences for certain focal velocities (Table 3; Figure 3). All size-classes used stream velocities lower than the respective stream means (all T-tests, $P < 0.001$). Jacob's electivity index indicated that all size-classes in Jack and Iron Creeks along with medium and large fish in Jungle Creek strongly preferred water velocities less than 0.02 m/s; small individuals in Jungle Creek preferred velocities between 0.02 and 0.05 m/s. Stream velocities greater than 0.10 m/s were strongly avoided by all size-classes in all three streams. Direct comparisons among the size-classes showed some significant size-related differences in the use of stream velocity (Jack Creek, Welch's ANOVA: $W_{2, 474} = 2.42$, $P = 0.09$; Jungle Creek, Welch's ANOVA: $W_{2, 112} = 14.59$, $P < 0.001$; Iron Creek, Welch's ANOVA: $W_{2, 189} =$

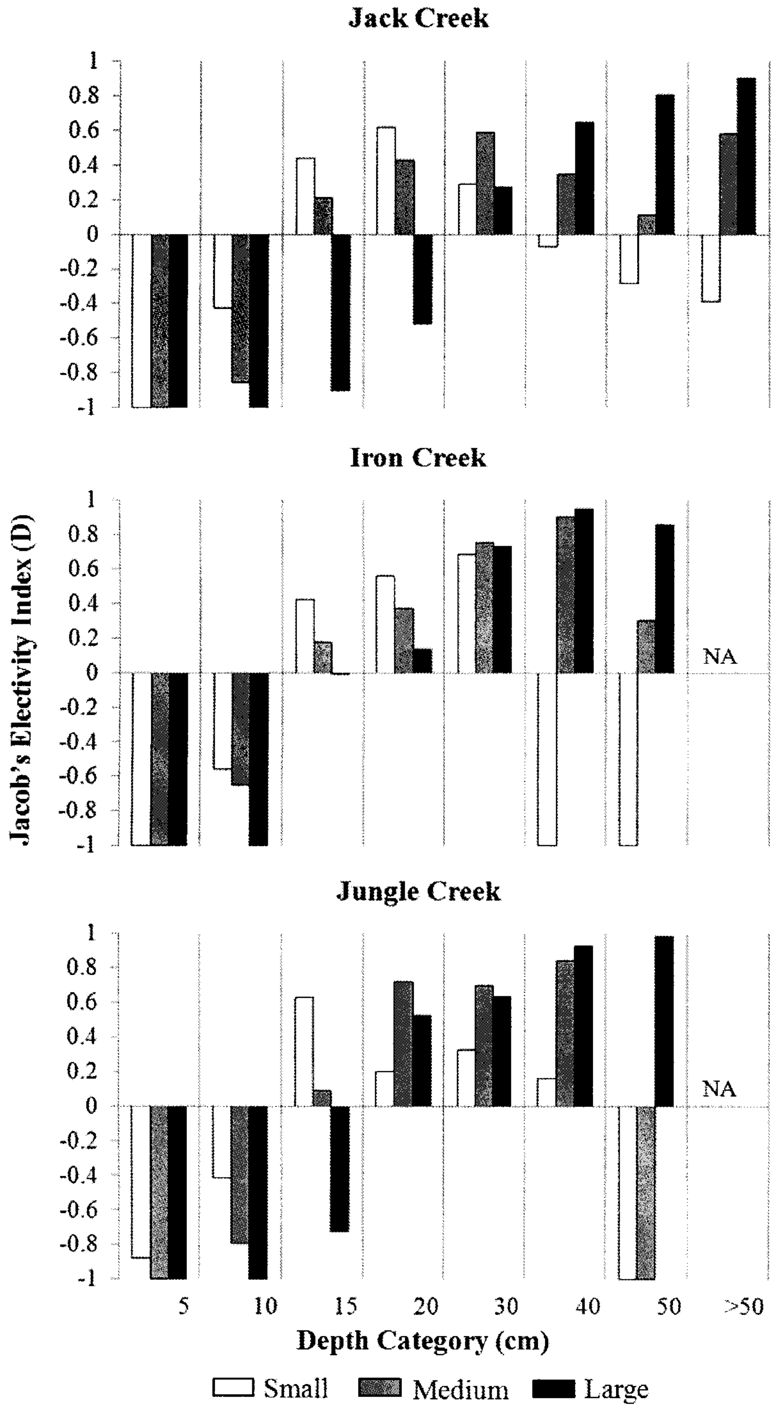

Figure 2. Water depth preference values (Jacob's electivity index) for each size-class (small, medium, large) of steelhead *Oncorhynchus mykiss* in Jack, Iron, and Jungle Creeks in central Washington during August-September 2012.

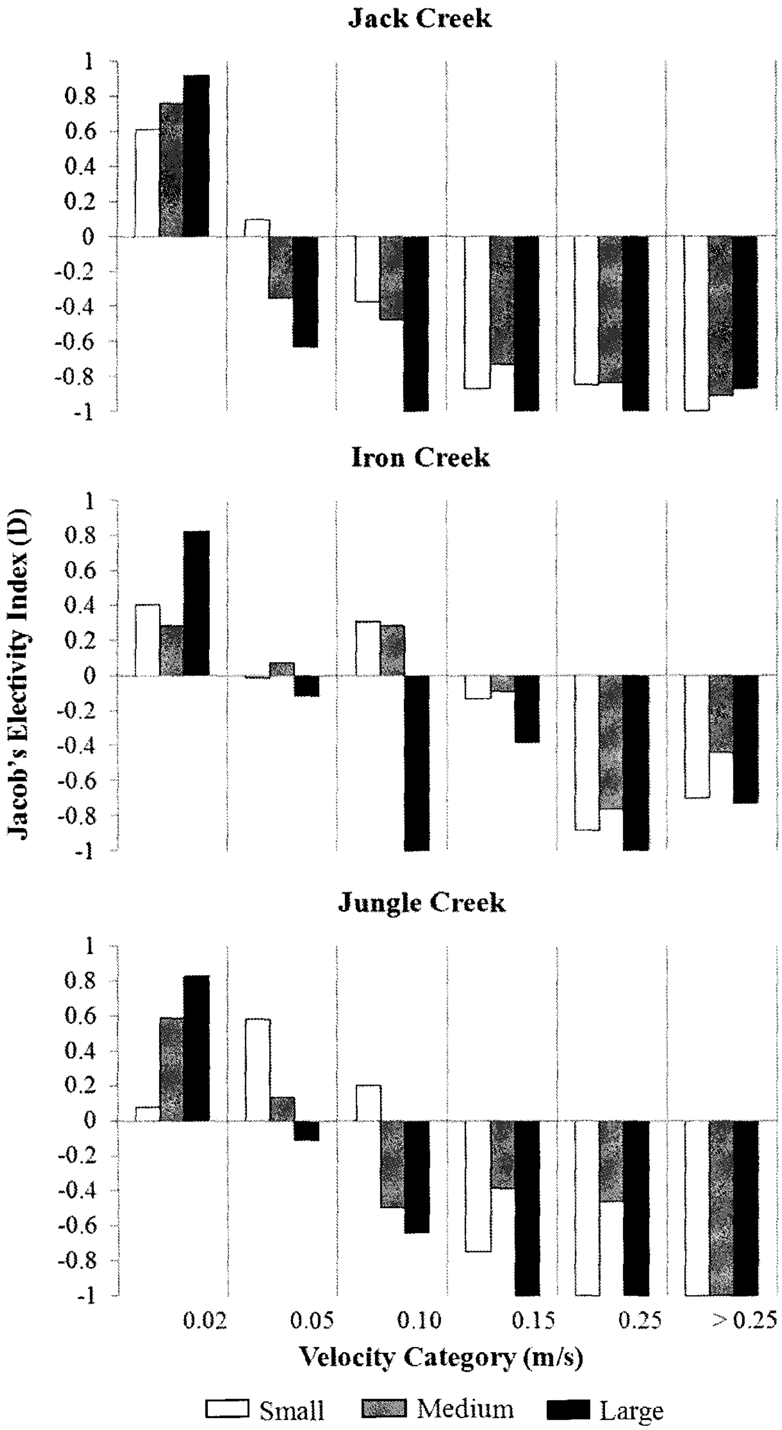

Figure 3. Focal velocity preference values (Jacob's electivity index) for each size-class (small, medium, large) of steelhead *Oncorhynchus mykiss* in Jack, Iron, and Jungle Creeks in central Washington during August-September 2012.

4.64, $P = 0.011$). In Iron and Jungle Creeks large steelhead used slower stream velocities than small and medium rainbow trout (Games-Howell post-hoc tests: Iron Creek, $P = 0.056$, $P = 0.016$; Jungle Creek, $P < 0.001$, $P = 0.037$). In Jack Creek no significant differences were observed (Games-Howell post-hoc tests, $P > 0.073$).

In each stream, steelhead preferred distinct types of microhabitat cover (Jack Creek G = 1470, Iron Creek G = 418, Jungle Creek G = 509; all d.f. = 7, $P < 0.001$; Figure 4). Steelhead in all streams had a strong preference for woody debris, roots, undercuts, boulders, and underwater algae / vegetation. The magnitude of preference for cobble and overhanging vegetation ranged widely among streams. Water turbulence was strongly avoided in Jack and Jungle Creeks, but was used in a neutral fashion in Iron Creek.

Substrate types were not used by steelhead in proportion to their availability (Jack Creek: G = 663, d.f.= 3, $P < 0.001$; Iron Creek: G = 63, d.f.= 3, $P < 0.001$; Jungle Creek: G = 63, d.f. = 4, $P < 0.001$; Figure 5). Steelhead had a strong preference for boulder substrate in all three streams. Cobble substrate was strongly preferred by fish in Jack and Iron Creeks, while it was used in proportion to its availability by fish in Jungle Creek. Sand and silt substrate was largely used in proportion to its availability in the environment at each stream. Steelhead appeared to strongly avoid gravel substrate in Jack Creek, but in Iron and Jungle Creeks gravel substrate was used in proportion to its availability. Jungle Creek was the only stream field site to possess bedrock as a dominant substrate feature, and fish appeared to have a strong preference for this substrate. Caution should be taken in interpreting these preference values, as velocity and depth can be correlated to substrate.

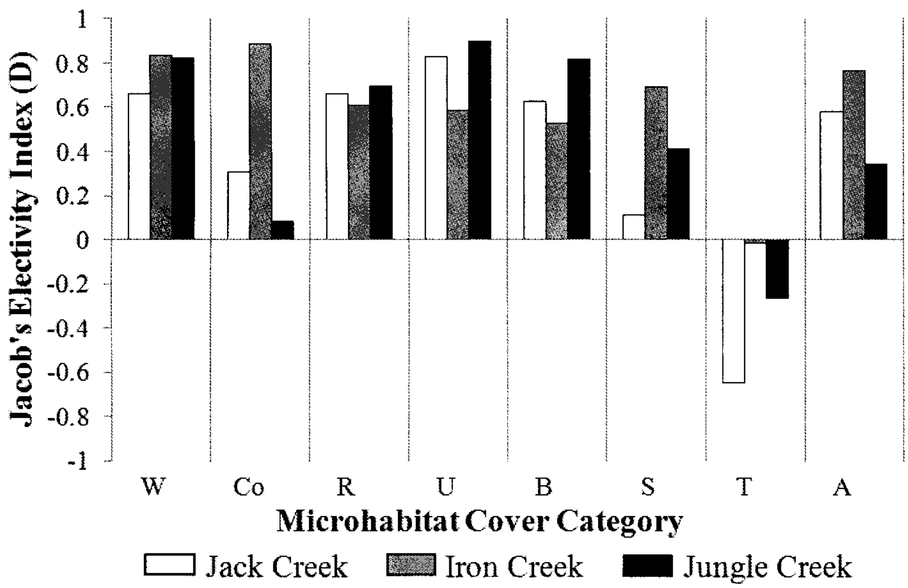

Figure 4. Microhabitat cover preference values (Jacob's electivity index) for steelhead *Oncorhynchus mykiss* in Jack, Iron, and Jungle Creeks in central Washington during August-September 2012. W= woody debris, Co= cobble, R= roots, U= undercuts, B= boulder, S= overhanging vegetation, T= turbulence, A= underwater algae / vegetation.

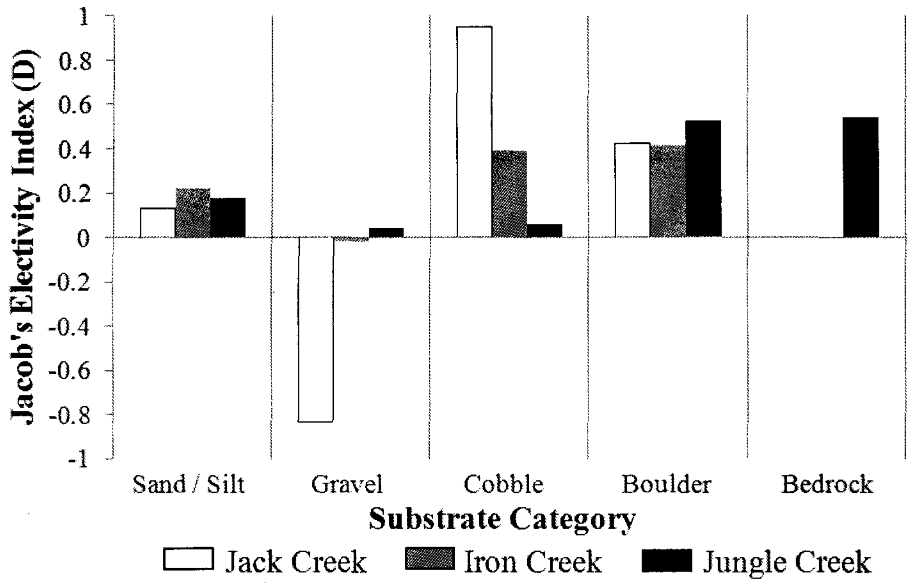

Figure 5. Substrate preference values (Jacob's electivity index) for steelhead *Oncorhynchus mykiss* in Jack, Iron, and Jungle Creeks in central Washington during August-September 2012. Bedrock was not present in Jack Creek or Iron Creek.

Mesohabitat

We sampled 197 mesohabitat units from the study streams during the summer of 2012. This included 82 riffles, 49 glides, 55 pools, and 11 beaver ponds. Beaver ponds occurred only in Jack Creek and were all smaller than 300 m^2 in surface area.

Mesohabitat units differed significantly in depth (Welch's ANOVA: $W_{3, 37.82} = 111.16$, $P < 0.001$), velocity (Welch's ANOVA: $W_{3, 102.4} = 121.58$, $P < 0.001$), habitat complexity (Kruskal-Wallis: H = 46, d.f. = 3, $P < 0.001$), and amount of woody debris (Kruskal-Wallis: H = 37, d.f. = 3, $P < 0.001$). Pool and beaver pond habitat units were significantly deeper than riffles and glides, as would be expected (Games-Howell post-hoc tests, $P < 0.001$; Figure 6). Pool and beaver pond habitat units had the slowest stream velocities, glides had intermediate velocities, and riffles had the fastest stream velocities (Games-Howell post-hoc tests, $P = 0.001$; Figure 6). As stream depth increased, stream velocity significantly decreased (Pearson Correlation: $r = -0.224$, $P < 0.001$; Figure 7). In general, higher stream velocities were seldom encountered at depths greater than 20 cm. Pool and beaver pond habitat units had a higher degree of habitat complexity than riffles or glides (Mann-Whitney post-hoc tests, $P < 0.001$) and contained more woody debris than riffles or glides (Mann-Whitney post-hoc tests, $P = 0.001$).

Mesohabitat types were not used by any size-class of steelhead in proportion to their availability in all three streams (Table 4; Figure 8). Jacob's electivity index showed that riffle habitat was strongly avoided by all size-classes in each stream. However, preference values for glide habitat were variable among the size-classes and streams. Large fish tended to avoid glide habitat, while small and medium individuals had moderate to neutral preference values for glides. Pool habitat was strongly preferred by small and medium individuals in Jack Creek, by all size classes in Iron Creek, and by medium and large individuals in Jungle Creek. Beaver pond habitat in Jack Creek was strongly avoided by small individuals, moderately avoided by medium individuals, and strongly preferred by large individuals.

Overall steelhead density (i.e., all size-classes) differed significantly among mesohabitat unit types (Welch's ANOVA: $W_{3, 39.13} = 39.77$, $P < 0.001$; Figure 9). Steelhead density was higher in pools than in riffles or glides (Games-Howell post-hoc tests, $P < 0.001$). Glides had a higher level of steelhead density than riffles

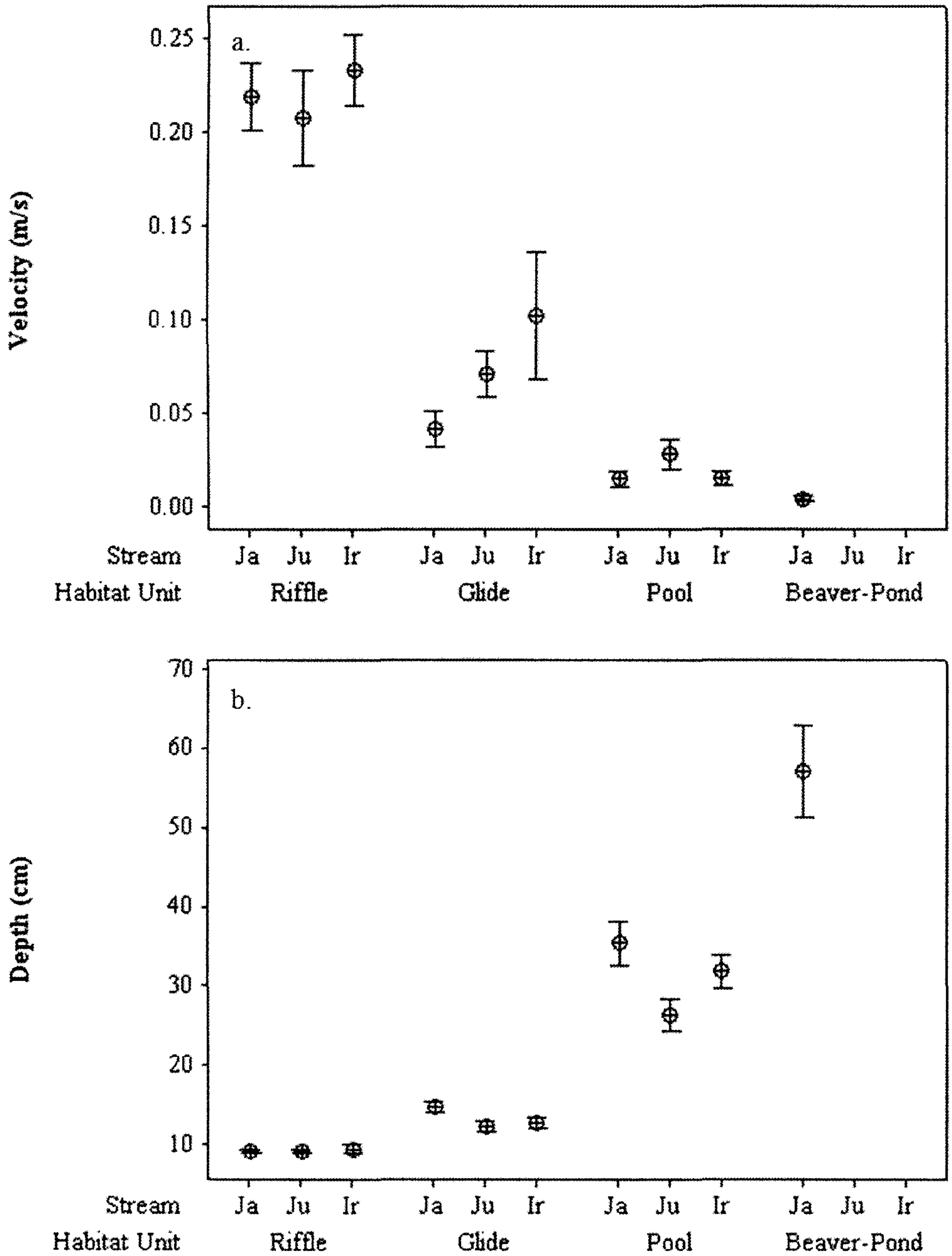

Figure 6. Mean velocity (a) and depth (b) characteristics of mesohabitat types (±SE) for Jack Creek (Ja), Jungle Creek (Ju), and Iron Creek (Ir) in central Washington during August-September 2012. Jack Creek was the only stream that had beaver ponds.

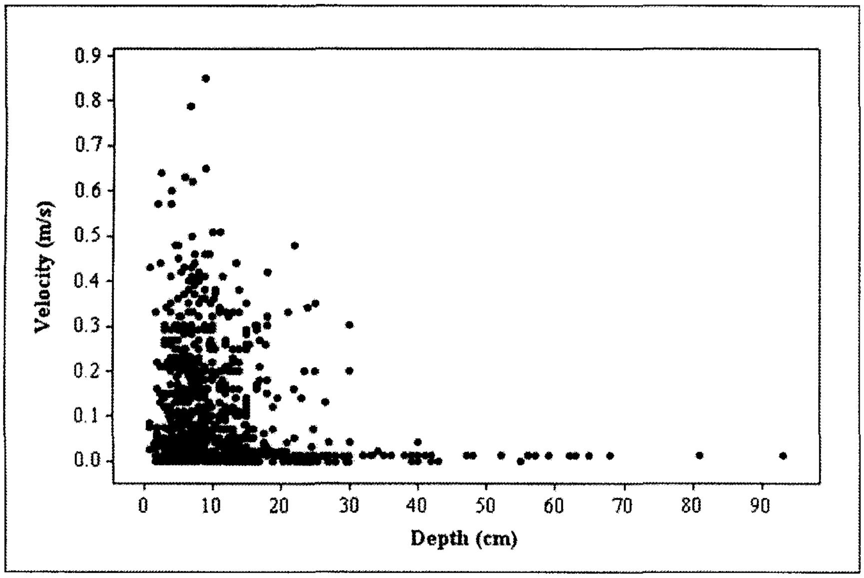

Figure 7. Scatter plot showing the distribution of depth and velocity based on random habitat availability measurements from Jack, Iron, and Jungle Creeks in central Washington during August-September 2012. In general, higher stream velocities were seldom encountered at water depths greater than 20 cm (Pearson Correlation: $r = -0.224$, $P < 0.001$).

Table 4. G-test results comparing the observed level of mesohabitat use with the expected level of use based on mesohabitat availability for steelhead *Oncorhynchus mykiss* by size-class (small, medium, large) for Jack, Jungle, and Iron Creeks in central Washington during August-September 2012.

	Mesohabitat Use		
	G	d.f.	*P*
Jack Creek			
Small	78.68	3	< 0.001
Medium	77.87	3	< 0.001
Large	88.57	3	< 0.001
Iron Creek			
Small	34.27	2	< 0.001
Medium	31.8	2	< 0.001
Large	66.12	2	< 0.001
Jungle Creek			
Small	24.97	2	< 0.001
Medium	25.92	2	< 0.001
Large	46.12	2	< 0.001

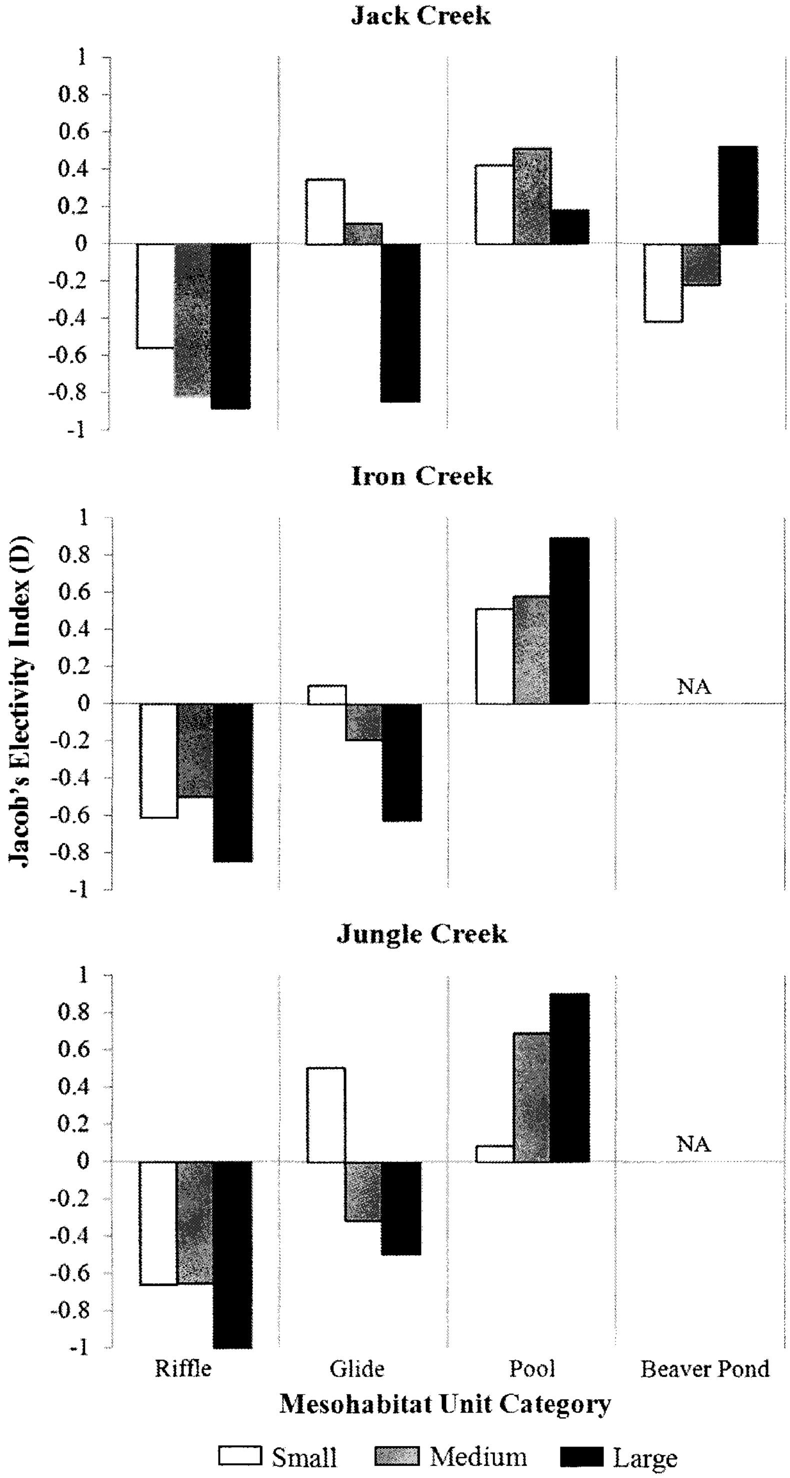

Figure 8. Mesohabitat preference values (Jacob's electivity index) for each size-class (small, medium, large) of steelhead *Oncorhynchus mykiss* in Jack, Iron, and Jungle Creeks in central Washington during August-September 2012. Jungle Creek and Iron Creek did not have any beaver ponds.

(Games-Howell post-hoc test, $P < 0.001$). Beaver pond habitat had intermediate steelhead densities that were similar to both pool and glide habitat densities (Games-Howell post-hoc tests, $P = 0.264$, $P = 0.48$), but higher than riffle densities (Games-Howell post-hoc test, $P = 0.008$). The density of large fish was also significantly different among habitat types (Welch's ANOVA: $W_{3, 36.44} = 21.13$, $P < 0.001$; Figure 9). Pool and beaver pond habitat types had similar densities of large fish (Games-Howell post-hoc test, $P = 1.0$) that were both substantially higher than the densities observed in riffles and glides (Games-Howell post-hoc tests, $P < 0.001$, $P < 0.001$, $P = 0.001$, $P = 0.003$).

Associations between mesohabitat unit type and steelhead size-class were quantified with Pearson's chi-square contingency table test. The Pearson's chi-square test for Jack Creek showed a significant association between size-class and habitat unit type ($Lx^2 = 95.98$, d.f.= 6, $P < 0.001$; Table 5). Odds ratios suggest that large individuals were much more likely to use beaver ponds and less likely to use glides than were small or medium individuals. Pool habitat was more likely to be used by medium individuals than by large individuals. Use of riffle habitat was similar across the size-classes.

The Pearson's chi-square test for Jungle Creek and Iron Creek combined also showed a significant association between mesohabitat unit type and steelhead size-class ($Lx^2 = 42.97$, d.f.= 4, $P < 0.001$; Table 6). Based on odds ratios, large individuals were much more likely to use pool habitat than were small or medium individuals. Small and medium sized individuals used pool habitat at the same level. Conversely, small

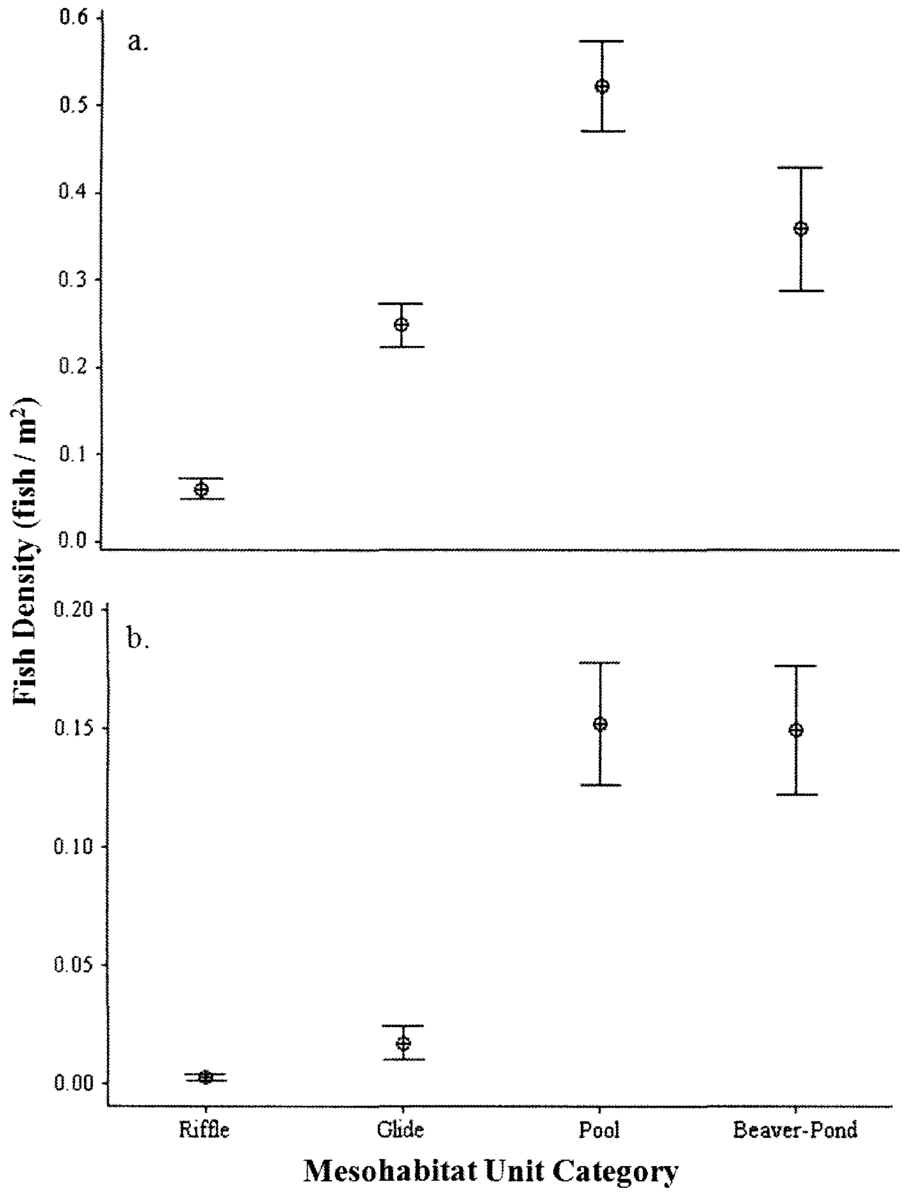

Figure 9. Mean density of steelhead *Oncorhynchus mykiss* among mesohabitat unit types (±SE) for all size-classes combined (a) and for only large steelhead greater than 90 mm in total length (b). Data were collected from Jack, Iron, and Jungle Creeks in central Washington during August-September 2012. Jack Creek was the only stream that had beaver ponds.

individuals were much more likely to use glide habitat than were the larger size-classes. Riffle habitat was used at a similar rate by all three size-classes.

Table 5. Odds ratios for Pearson's chi-square test showing size-related differences in mesohabitat use by steelhead *Oncorhynchus mykiss* in Jack Creek in central Washington during August-September 2012. Size-classes are designated as S (< 50 mm), M (50 - 90 mm), and L (> 90 mm). Bonferroni-correction was used to evaluate significance.

Habitat Unit	Odds Ratio	CI_{95}	*Z*	*P*
Beaver Pond				
L > S	7.67	4.50 - 12.9	7.65	< 0.001
L > M	5.01	2.90 - 8.20	6.08	< 0.001
M = S	1.56	0.94 - 2.59	1.72	0.085
Pool				
S = L	1.70	1.06 - 2.77	2.18	0.029
M > L	2.15	1.31 - 3.54	3.03	0.002
M = S	1.26	0.82 - 1.94	1.04	0.297
Glide				
S > L	24.55	5.92 - 104.19	4.39	< 0.001
M > L	15.09	3.54 - 64.59	3.67	< 0.001
M = S	1.64	0.99 - 2.73	1.92	0.055
Riffle				
S = L	4.61	1.03 - 20.95	2.01	0.046
M = L	1.60	0.29 - 8.88	0.54	0.590
M = S	2.90	0.93 - 9.09	1.83	0.067

Table 6. Odds ratios for Pearson's chi-square test showing size-related differences in mesohabitat use by steelhead *Oncorhynchus mykiss* in Jungle Creek and Iron Creek in central Washington during August-September 2012. Size-classes are designated as S (< 50 mm), M (50 - 90 mm), and L (> 90 mm). The Bonferroni-correction was used to evaluate significance.

Habitat Unit	Odds Ratio	CI_{95}	Z	*P*
Pool				
L > S	8.14	3.74 - 17.80	5.27	< 0.001
L > M	4.09	1.83 - 9.09	3.45	< 0.001
M = S	2.00	1.19 - 3.35	2.61	0.009
Glide				
S > L	6.65	2.69 - 16.53	4.09	< 0.001
M = L	2.25	0.85 - 5.95	1.64	0.102
S > M	2.95	1.61 - 5.44	3.50	< 0.001
Riffle				
S = L	4.30	1.24 - 14.98	2.29	0.022
M = L	5.65	1.62 - 19.66	2.72	0.006
M = S	1.31	0.68 - 2.54	0.81	0.420

Multiple regression was used to further examine how stream velocity, depth, surface area, and woody debris influenced steelhead density (all size classes) at the mesohabitat level (Table 7). Multicollinearity limited the number of important predictor variables that could be included in the overall model. The regression model is described by the following equation:

Fish Density = 0.123 - 0.651 Velocity (m/s) + 0.668 Depth (m) - 0.004 Surface Area (m^2) + 0.090 Woody Debris Rating.

Steelhead density decreased strongly with increased stream velocity, decreased slightly with increased surface area, and increased strongly with both water depth and woody debris cover (S = 0.24, R^2 = 38.95%, PRESS = 12.21, R^2(pred) = 32.44%).

Table 7. Multiple regression coefficients table showing how velocity, depth, surface area, and woody debris are associated with steelhead *Oncorhynchus mykiss* density at the mesohabitat level in Jack, Iron, and Jungle Creeks in central Washington during August-September 2012 (S = 0.24, R^2 = 38.95%, PRESS = 12.21, R^2(pred) = 32.44%).

Coefficients Table:

Term	Coef	SE Coef	T	*P*	VIF
Constant	0.123	0.052	2.377	0.018	
Velocity (m/s)	-0.651	0.167	-3.899	< 0.001	1.41
Depth (m)	0.668	0.002	4.242	< 0.001	1.99
Surface Area (m^2)	-0.004	0.001	-5.566	< 0.001	1.37
Woody Debris	0.090	0.022	4.111	< 0.001	1.24

Discussion

The use of different habitat characteristics by the different size-classes of steelhead suggests that they are partitioning microhabitat and mesohabitat. The strongest microhabitat partitioning appears to operate around stream depth and to a lesser extent around stream velocity, with larger steelhead (> 90 mm TL) occupying slower and deeper water than smaller steelhead (< 90 mm TL). In Jack Creek partitioning based on stream velocity was not observed likely because of the vast availability of slow water habitat (i.e., beaver ponds). Mesohabitat partitioning was evident in the higher preference for glide habitat by small steelhead (< 50 mm TL) compared to large steelhead (> 90 mm TL). Also, smaller steelhead (< 90 mm TL) avoided beaver pond habitat, while larger steelhead (> 90 mm TL) highly preferred it. Pool habitat units were preferentially used by all size-classes, and it appears that within a pool habitat unit, smaller steelhead (< 90 mm TL) use shallower areas that have slightly higher stream velocities, while larger steelhead (> 90 mm TL) use deeper microhabitats with lower velocities.

Size-based habitat partitioning has been documented in other steelhead and rainbow trout populations. Larger steelhead occupy areas with deeper and faster water than those used by smaller steelhead (Baltz et al. 1991; Everest and Chapman 1972; Moyle and Baltz 1985; Muhlfeld et al. 2001). Hirsch (1995) found that microhabitat was partitioned between fry and older individuals, with fry occupying shallow stream margins and backwaters, while older individuals occupied deeper and faster areas of the channel. Other researchers have noted that larger individuals move to deeper and slower water, while smaller subordinate individuals are forced to utilize shallower and faster water (Abbott et al. 1985; Bisson et al. 1988; Edmundson et al. 1968; Jenkins 1969; Keeley 2001; Li and Brocksen 1977). Muhlfeld et al. (2001) found that all size-classes preferentially used pools, all size-classes avoided riffles, and glides were used neutrally by larger individuals and preferentially by smaller individuals. Differences in response by larger steelhead are probably a direct result of differences in stream morphology and habitat availability. Previous research suggests that the causative factors for habitat partitioning and niche compression are intraspecific competition for food and space, with larger more experienced individuals dominating smaller individuals for more advantageous stream positions (Abbott et al. 1985; Jenkins 1969; Keeley 2001; Li and Brocksen 1977).

The brook trout in Jack Creek were most commonly encountered in deep pools and beaver ponds (personal observation), and they may have influenced steelhead habitat use and preference (Cunjak and Green 1983; Larson and Moore 1985). Brook trout have been shown to be highly successful in beaver ponds (Allen 1956; Huey and Wolfrum 1956; Johnson et al. 1992; Rupp 1955). Cunjack and Green (1983) found that brook trout prefer slow stream velocities and deep water, which are the environmental qualities that steelhead appear to prefer in Jack Creek, and suggested that interactive segregation between brook trout and rainbow trout was occurring at their study site in New Brunswick. In the southern Appalachian Mountains, researchers have suggested that rainbow trout are aggressively outcompeting the native brook trout, and restricting their distribution to headwater streams (Larson and Moore 1985). Thus, it is plausible that brook trout and steelhead maybe indirectly or directly competing for resources in Jack Creek.

Differences in stream morphology between large and small streams may lead to a reversal in habitat usage and preference. The use of slow moving habitats like beaver ponds and pools that our study reports appears to directly contradict many previous studies that suggest that rainbow trout and steelhead prefer faster flowing habitats like riffles and glides (Allee 1974; Beecher et al. 1995; Bisson et al. 1988; Bovee et al. 1978; Cunjak and Green 1983; Everest and Chapman 1972; Everest et al. 1986; Fausch 1993; Hartman 1965; Muhlfeld et al. 2001; Scott and Gill 2008; Sheppard and Johnson 1985;

Wydoski and Whitney 2003). Everest *et al* (1986) in particular found that age-0 and age-1+ steelhead substantially avoided beaver pond habitat over four years of study. The researchers also found that riffle habitat supported the largest overall populations of steelhead compared to other habitat types. Researchers from various studies have further pointed out that the diet and body morphology of steelhead have likely developed and adapted to better exploit higher velocity habitats like riffles (Allee 1974; Bisson et al. 1988; Johnson 2007; Johnson and Ringler 1980).

However, a majority of these studies were conducted on much larger streams that have drastically different habitat conditions than the three small streams we studied. In our streams, higher-velocity microhabitat was generally available only at shallower depths (< 20 cm; Figure 10) that are strongly avoided by larger steelhead (Beecher et al. 1993; Bovee et al. 1978; Cramer and Ackerman 2009, 2009b). Furthermore, the riffle and glide mesohabitat units that we sampled generally did not provide the deeper water habitat that is preferred by larger steelhead (Figure 9). Therefore, during the summer months in small streams depth appears to be extremely limiting in a way that makes deep, low-velocity habitats like beaver ponds and pools the best available option, especially for larger steelhead.

Additional evidence for this reversal of habitat preference and use in small streams can be found in several previous studies. In coastal streams in California steelhead preferentially used pools because riffles had shallow depths that rendered them unusable (Harvey and Nakamoto 1996). Hearn and Kynard (1986) conducted a laboratory experiment that only used riffles that were 15 cm deep and found that steelhead preferred pool habitat substantially more. Similarly, steelhead in an Oregon stream primarily used pool habitat in reaches where riffles did not provide adequate depth (Roper et al. 1994). Rainbow trout in a slightly larger stream in Montana preferentially used pool habitat, avoided riffles, and glides were used neutrally by larger individuals and preferentially by smaller individuals (Muhlfeld et al. 2001). The riffles in that stream averaged around 20 cm deep, which is probably why rainbow trout were not using them. Even in much larger streams, pool habitat can be a major limiting factor for age-1+ steelhead production (Everest et al. 1986).

Beaver ponds are often criticized for creating poor habitat conditions that are not beneficial for salmonids (Collen and Gibson 2000; Kemp et al. 2012). In particular, they contain fine sediment that is sometimes viewed as poor quality habitat (Collen and Gibson 2000; Kemp et al. 2012). However, the results of our study and other research show that silt and sand substrates are not avoided (Muhlfeld et al. 2001). In addition, both pool and beaver pond habitat units provided more habitat complexity and woody debris than did riffles and glides. This complements the findings in this study that steelhead strongly preferred woody debris, roots, and undercuts, which are often dominant features in beaver ponds. Boulder and cobble substrates were also strongly preferred by steelhead. All of these preferred microhabitat features should be incorporated into any stream restoration work (Baltz et al. 1991; Cederholm et al. 1997; Cramer and Ackerman 2009; Muhlfeld et al. 2001; Roni and Quinn 2001; Shirvell 1990).

The findings of our research have several important implications for stream restoration and management. Stream restoration for steelhead should incorporate the use of complex cover types like woody debris, roots, undercuts, and overhanging vegetation. Cobble and boulder-sized substrate should also be used to provide high quality cover. The results from this study clearly show that maintaining an adequate supply of deep, pool habitat is paramount to steelhead populations. Our research also fills a knowledge gap about interactions between beaver pond habitat and steelhead. Specifically, our results show that beaver reintroduction programs in small streams have the potential to create deep, complex, pool habitat that will be highly preferred by steelhead populations. Our results in tandem with other research suggests that a decrease in the amount of pool habitat in small streams in central Washington will decrease the availability of preferred habitat and may result in a decrease in stream carrying capacity for steelhead, assuming stream habitat is a major limiting factor (Cramer and Ackerman 2009, 2009b). With that said, riffle habitat should not be discounted in small streams, as it is essential to the production of aquatic invertebrates that are consumed by steelhead and other salmonids (Cramer and Ackerman 2009, 2009b; Hawkins et al. 1983; Waite and Carpenter 2000). Consequently, restoration efforts in small streams that focus on the creation of deep pool habitat, either through artificial means or through beaver reintroduction programs, will have the greatest effect upon increasing the amount of highly preferred stream habitat for larger resident rainbow trout and age-2 and age-3 steelhead.

Beaver reintroduction programs should take into account several important considerations. All beaver ponds sampled as part of this study were less than 300 m^2 in surface area, which means that the results from this study are only informative about smaller beaver ponds. Larger beaver ponds are likely to have different characteristics that can drastically affect habitat use and preference. Beaver dams also have the potential to adversely affect the movement of anadromous fish (Gard 1961; Kemp et al. 2012; Mitchell and Cunjak 2007; Tambets et al. 2005; Taylor et al. 2010; Thorstad et al. 2007). As a result, beaver reintroduction programs are best suited for streams with strong spring and fall flows that will mitigate the potential for beaver dams to become serious migration barriers (Parker and Rønning 2007). Finally, beavers are well known to come into conflict with people (e.g., flooding land and roads) and should only be reintroduced back into areas where there is a low probability for conflict to occur (Kemp et al. 2012; Knudsen and Hale 1965; Macdonald et al. 2000; McKinstry and Anderson 2002).

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