John W. Guzevich[1] and **Russell F. Thurow**, USDA Forest Service, Rocky Mountain Research Station, Boise Aquatic Sciences Lab, 322 East Front Street, Boise, Idaho 83702

Fine-Scale Characteristics of Fluvial Bull Trout Redds and Adjacent Sites in Rapid River, Idaho, 1993–2007

Abstract

From 1993 to 2007, we used single pass, September surveys to locate and measure fluvial bull trout (*Salvelinus confluentus*) redds in Rapid River, Idaho. Here we describe substrate sizes, redd dimensions, and water depths, velocities, and temperatures within and adjacent to 337 redds. Most (79%) spawning sites had fewer than 20% surface fines (< 2 mm) and mean, annual water depths and velocities ranged from 14.2–23.0 cm and 11.6–30.5 cm s^{-1}, respectively. Mean, annual completed redd total lengths and surface areas averaged from 1.03–1.47 m and 0.37–1.07 m^{-2}, respectively. Pea gravel (2 to < 8 mm) and gravel (8–64 mm) were dominant substrates (> 60%) in redds. Bull trout altered channel water depths and velocities during redd construction; pits averaged 5 cm deeper, leading tailspill edges 1.2 cm shallower, and tailspill crests 6.2 cm shallower than adjacent, undisturbed sites. Conversely, pit velocities averaged 2.1 cm s^{-1} slower, tailspill edge velocities 2.3 cm s^{-1} faster, and tailspill crest velocities 10.1 cm s^{-1} faster than adjacent sites. Mean, annual pit water temperatures ranged from 4.5 to 7.7 °C. Water depths and water velocities over undisturbed sites adjacent to bull trout redds were significantly correlated with water depths and water velocities inside completed redds. Improving our understanding of fluvial bull trout redds will increase the accuracy of redd counts, especially in streams with sympatric, fall spawning salmonids. Data describing fine-scale characteristics of redds and adjacent sites will assist efforts to conserve and restore critical bull trout spawning habitats.

Keywords: Bull trout, redds, spawning, fluvial

Introduction

Bull trout are an important ecological and recreational component of many western rivers (Swanberg 1997, Nelson et al. 2002). Life histories of bull trout are highly variable and include fluvial, adfluvial, anadromous, and resident forms (Northcote 1997, Jakober et al. 1998, Mogen and Kaeding 2005, Muhlfeld and Marotz 2005). Migratory bull trout have many unique traits: they attain a large size (up to 87 cm) in cold, relatively unproductive systems (Shepard et al. 1984, Fraley and Shepard 1989); live up to 12 years (Goetz 1989, Downs et al. 2006); may migrate more than 300 km (Bjornn and Mallet 1964); and exhibit high fidelity to natal spawning sites (Schill et al.1994, Elle et al.1994). Results of recent radio-telemetry research suggest bull trout spawning migrations may be more complex than previously reported (Barnett and Paige 2013). Cumulative effects of habitat disturbances in river basins are especially detrimental to migratory forms since they occupy such a wide range of habitats both spatially and temporally during their complex life cycles (Rieman and McIntyre 1995, Swanberg 1997, Baxter and Hauer 2000, Muhlfeld and Marotz 2005). Declines in bull trout are attributed to the obstruction of migratory pathways by dams, irrigation diversion, and channel modification (Meehan 1991); degradation of spawning and rearing habitats (Fraley and Shepard 1989, Rieman and McIntyre 1995); angling mortality (Ratliff and Howell 1992); competition from and hybridization with exotic salmonids (Donald and Alger 1993, Leary et al.1993); and a changing climate (Dunham et al. 2003, Goode et al. 2013). Population declines led to a 1995 listing "of special concern" in Canada and a 1998 listing as "Threatened" under the US Endangered Species Act (ESA) (USFWS 1999).

Bull trout conservation and restoration efforts typically integrate life-stage habitat requirements with the species known distributions (Watson and

[1] Author to whom correspondence should be addressed.
Email: jguzevich@fs.fed.us

Hillman 1997). Accordingly, a growing number of studies are enhancing our understanding of bull trout life-stage-specific habitat requirements. Biologists have investigated spatial scales ranging from micro-habitat assessments (Fraley and Shepard 1989, Saffel and Scarnecchia 1995, Baxter and Hauer 2000, Al-Chokhachy and Budy 2007), to broader, multi-scale approaches (Rieman and McIntyre 1993, Watson and Hillman 1997, Rich et al. 2003). Studies of juvenile bull trout, for example, describe their use of complex stream channels (Fraley and Shepard 1989, Jakober et al. 1998) in close association with unembedded cobble and boulder substrate and large woody debris (Rich et al. 2003, Muhlfeld and Marotz 2005). Adult migratory bull trout migrate from rivers or lakes to ascend natal tributaries several months prior to spawning (Shepard et al.1984, Schill et al. 1994, Swanberg 1997). These pre-spawning adults stage in pools (Fraley and Shepard 1989, Swanberg 1997) or sites with dense accumulations of large woody debris (Schill et al. 1994) and may seek thermal refugia from elevated summer water temperatures (Swanberg 1997). Redds are generally constructed in low gradient channels with abundant, uncompacted gravel substrate (Fraley and Shepard 1989), large woody debris (Hauer et al. 1999), and groundwater exchange (Baxter and Hauer 2000).

Selection of spawning sites by salmonids is complex; as Curry and Noakes (1995) observed, the specific mechanisms of site selection remain to be determined. Field observations suggest stream dwelling salmonids select spawning sites in response to physical cues including water depth and velocity (Knapp and Vredenberg 1996, Schmetterling 2000, Wollebæk et al. 2008), substrate size (Shepard et al. 1984, Thurow and King 1994), discharging groundwater (Witzel and MacCrimmon 1983, Baxter and Hauer 2000, Schmetterling 2000, Muhlfeld 2002) and adjacent cover (Reiser and Wesche 1977, Witzel and MacCrimmon 1983). As Baxter and McPhail (1996) observed, although redds are not necessarily located under cover, mature bull trout migrate and seek refuge prior to spawning.

Expanding knowledge of the fine-scale spawning requirements of bull trout builds upon bull trout habitat utilization databases. These data contribute to our understanding of fluvial bull trout spawning site selection, completed redd characteristics, and how bull trout alter the stream bed during redd construction. Redd surveys are a primary method used to monitor trends in the distribution and abundance of salmonids, including bull trout (Al-Chokhachy et al. 2005, Isaak and Thurow 2006, Howell and Sankovich 2012). In streams that support multiple species of fall spawning salmonids, accurately identifying redds by species may be challenging. Gallagher et al. (2007) suggested that in such cases, redd monitoring programs need to improve redd species identification. For example, Gallagher and Gallagher (2005) applied species-specific redd morphology measurements and redd construction dates to improve discrimination of Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (O. *kisutch*), and steelhead (O. *mykiss*) redds. Consequently, detailed descriptions of redd dimensions and other fine-scale characteristics will guide surveyors in accurately identifying bull trout redds and in correctly differentiating them from redds of fall spawning salmonids they co-occur with. As Howell and Sankovich (2012) observed, redd surveys that estimate redd area and spawner lengths could be used to identify migratory vs resident bull trout redds and to describe the size and distribution of life history forms. Data describing redd and adjacent site substrate composition, water depths and velocities, excavated depths, and dimensions will also assist the design and implementation of projects to restore critical bull trout spawning habitats. These same data may also be applied to identify characteristics of the most critical spawning areas in order to prioritize conservation efforts.

Despite increasing knowledge of bull trout ecology and habitat requirements, few published studies describe fine-scale characteristics of bull trout spawning sites or redds. Although some descriptions of adfluvial bull trout redds exist (Goetz 1989, Fraley and Shepard 1989, Kitano et al. 1994), detailed descriptions of fluvial bull trout redds are scarce in primary fisheries literature. Howell and Sankovich (2012) described fluvial bull trout redd surface areas and no other redd features in the Walla Walla River basin. Consequently, our primary objective was to describe the fine-scale characteristics of fluvial bull trout redds and sites adjacent to redds; including redd dimensions, substrate sizes, water depths, water velocities, and water temperatures. We also sought to determine if conditions outside redds could be used to predict conditions in completed redds. Our secondary objective was to assess how bull trout altered site characteristics during spawning. To meet this second objective, we compared water depths and water velocities in undisturbed sites adjacent to redds with conditions in completed redds. We measured fluvial bull trout spawning sites and redds during 14 field seasons.

Methods

Study Area

We investigated fluvial bull trout in the headwaters of Rapid River, a fourth order tributary to the Little Salmon River in west-central Idaho (Figure 1). Rapid River is a designated Wild and Scenic River and drains a densely forested, roadless basin of 31 000 ha within the Payette and Nez Perce National Forests. Elevations range from 2540 m in the headwater to 580 m at the confluence. The narrow stream channel (mean width < 8 m) is confined by steep hillsides (> 50° slopes) underlain by Seven Devils Meta-Volcanic rock (Overton et al. 1993). Vegetation within the basin is dominated by mixed-coniferous forest (e.g., *Abies*, *Pinus, Pseudotsuga, Larix, Taxus)* with deciduous trees and shrubs (e.g., *Alnus, Populus, Salix)* common in riparian areas. Channel morphology is comprised largely of high gradient riffles, runs, and other fast water habitats (Overton et al. 1993). The flow regime is typical of mountainous central Idaho streams with peak snowmelt-induced runoff typically occurring in late-spring (May–June) and flows decreasing until the onset of fall precipitation (USDA 2007). Major tributaries include: Copper, Fry Pan, Paradise, Rattlesnake, and Sinking creeks, and the Granite, Lake, and West forks of Rapid River (Figure 1).

Rapid River supports both resident and fluvial bull trout forms. Resident forms mature at a comparatively smaller size and complete their life cycle entirely within Rapid River or its tributaries. Prior radio-telemetry and downstream trapping studies (Schill et al. 1994, Elle et al. 1994) described fluvial bull trout life histories as follows: after emerging, juveniles rear for 1–3 years in Rapid River before a spring or fall downstream migration to the Salmon River where they remain for months to years until maturation. Mature adults as well as some immature fish return to Rapid River from March to June. Immature fish return to the Salmon River in contrast to adults that migrate to and stage near headwater spawning areas. Spawning typically begins the third week in August and may extend into November. Post-spawning adults migrate to the Salmon River soon after spawning and adults may return to spawn in alternate or consecutive years. Other native fishes in Rapid River include both resident and anadromous (summer steelhead) redband trout forms, westslope cutthroat trout (*O. clarki lewisi)*, mountain whitefish (*Prosopium williamsoni*), largescale sucker (*Catostomus macrocheilus*), northern pikeminnow (*Ptychocheilus oregonensis*), longnose (*Rhinichthys cataractae*) and speckled dace (*R. osculus*), and sculpin (*Cottus spp.*). Native spring/summer Chinook salmon have been replaced with a mixed-stock Chinook salmon population reared at the Idaho Department of Fish and Game (IDFG) Rapid River Hatchery since 1964. Non-native Brook trout (*Salvelinis fontinalis*) introduced in Black Lake at the headwaters of the Lake Fork Rapid River were recently eradicated via sterile tiger muskellunge (northern pike Esox lucius X muskellunge E. masquinongy) introductions (Koenig et al. 2015).

Sampling Design

From 1993 to 2007, we annually (except for 2002) searched for bull trout redds in headwater reaches of Rapid River during one week in late September. Redds we located were constructed beginning in late August; after peak flows subsided and prior to base flows in November and December (USDA 2007). We completed single pass redd counts and surveyed stream reaches in known fluvial bull trout spawning areas. Known spawning areas were previously identified by relocation of radio-tagged adult bull trout and observation of redds during telemetry studies

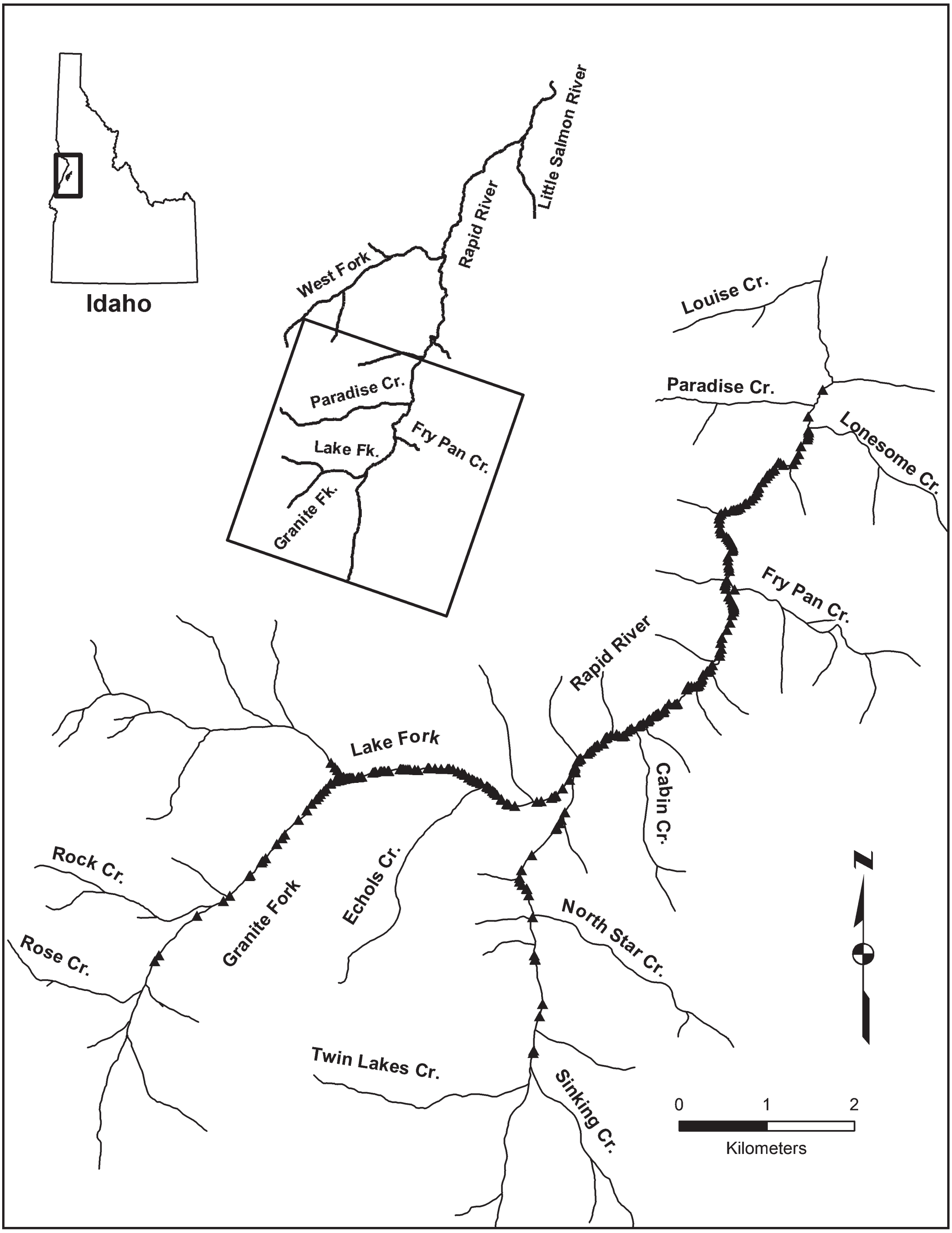

Figure 1. Rapid River basin, Idaho and the distribution of fluvial bull trout redds (▲), 1993–2007.

from 1992 to 1994 (Schill et al. 1994, Elle et al. 1994). We began redd surveys at the confluence of Louise Creek (river kilometer [rkm] 20.5) and walked or waded 11 km upstream to the confluence of Sinking Creek. We also surveyed 3 km of the Lake Fork from its confluence with the mainstem upstream to the Granite Fork; and 3.5 km of the Granite Fork from its confluence with the Lake Fork upstream to Rose Creek.

Fall spawning spring/summer Chinook salmon and brook trout reside in Rapid River and fluvial bull trout redds were easily differentiated by location (salmon spawned downstream from Louise Creek) and smaller brook trout redd sizes. We observed small, resident bull trout (< 25 cm TL) actively spawning or staging in nine redds that ranged from 0.4 to 0.6 m long. Howell and Sankovich (2012) reported that counts of migratory bull trout redds were more accurate and precise than counts of resident bull trout redds, which were significantly smaller and consistently underestimated. We excluded the nine resident bull trout redds from our fluvial bull trout analysis.

Although we annually mapped the total number of redds observed during the week-long surveys in designated study reaches, we did not attempt to estimate the total abundance of redds in the entire Rapid River drainage. A total redd estimate would require multiple pass surveys beginning at the onset of spawning in August and continuing on 4–5 day intervals until November. Prior to 2000, we recorded redds on 7.5 minute topographic maps and thereafter georeferenced redd locations using a global positioning system (GPS). After mapping redd locations, we measured fine-scale attributes including depths, velocities, dimensions, and substrates in all completed redds. Completed redds were identified by their morphological features, (e.g., pit and tailspill) and the absence of adult fish. Pits were identified as the excavated depressions on the upstream portion of redds and tailspills as the mounds of gravel immediately downstream from redd pits; see Burner (1951). We avoided redds if adult bull trout were still constructing or staging in them, or if the redd failed to exhibit a completed pit and tailspill. We waded carefully when collecting data in the vicinity of completed redds to avoid compacting incubating eggs or sweeping fine sediment into the egg pocket. At each complete redd, we measured a series of water depths and mean water column velocities using a top set rod and a Marsh-McBirney current meter, accurate to about 1.5 cm s^{-1}. We measured velocity at 0.6 times the water column depth, the location where velocity approximates a mean vertical water column velocity (Orth 1983). Depth and velocity were measured in four locations at each redd: the undisturbed substrate adjacent to (immediately upstream from) the redd pit; the deepest excavated portion of the pit; the leading 1/3 edge of the tailspill (where eggs are typically buried, Thurow and King 1994); and the crest (top) of the tailspill.

Reiser and Wesche (1977) and Grost (1989) reported that sites immediately upstream from salmonid redd pits represented conditions prior to redd construction. Thurow and King (1994) concurred and measured undisturbed sites both immediately upstream from and within 5 cm next to redd pits and reported no significant differences in water depths, velocities, or particle size distributions between the two sites. We assumed that undisturbed areas adjacent to redd pits were representative of sites selected by spawning bull trout and could be applied as surrogates for site characteristics prior to redd construction.

We measured redd dimensions after Thurow and King (1994). Pit length was measured parallel with the streamflow from the upstream edge of the pit to the upstream edge of the tailspill. Pit width was measured perpendicular to the streamflow across the pit center. We measured the length of the tailspill from its upstream edge located just downstream from the pit to the downstream edge of the mound of disturbed gravel. The width of the tailspill was measured perpendicular to the streamflow at the crest of the mound of gravel. We measured total redd length from the upstream edge of the pit to the downstream margin of the tailspill and calculated redd surface area by summing the pit and tailspill surface areas.

Dimensions of salmonid redds tend to be proportional to the length of spawning fish (Burner 1951, Knapp and Vredenburg 1996) and fish length, rather than localized environmental characteristics, may be the determining factor of redd dimensions (Thurow and King 1994, Muhlfeld 2002). Although we did not capture and measure individual fish on redds, concurrent with our redd surveys during the past 14 years, the number and size of fluvial bull trout returning annually to Rapid River were recorded at the Rapid River hatchery. A permanent velocity barrier and fish trap located 2 km upstream from the confluence with the Little Salmon River permits the handling of all upstream migrants. Bull trout from 180–670 mm TL ascended Rapid River and Elle et al. (1994) reported that fish less than 300 mm TL were age 2 + and 3 + juveniles. Published minimum lengths of mature fluvial and adfluvial bull trout range from 290 to 455 mm TL (Goetz 1989). Pratt (1992) and Howell and Sankovich (2012) similarly reported that mature fluvial bull trout exceeded 300 mm. Most of the bull trout we observed on redds in Rapid River also exceeded 300 mm TL. Consequently, we assumed bull trout larger than 300 mm TL had the potential to be mature, fluvial spawners.

We assessed substrate sizes and water temperatures in and adjacent to all completed redds. Within redds, we visually estimated percentages of substrate sizes in the entire redd pit and tailspill combined. We viewed redds with polarized glasses and visually estimating the percentage of the substrate comprised of fines (< 2 mm), pea gravel (2 to < 8 mm), gravel (8 to < 64 mm), rubble (64 to < 128 mm), cobble (128 to < 256 mm), boulder (> 256 mm), or bedrock (solid rock) modified after Platts et al. (1983). We also recorded the percent surface fines (particles < 2 mm) in the adjacent substrate upstream from redds by tossing a 20 cm square, 56 intersection metal grid onto the substrate; recording the number of intersections lying over fines; and calculating the percent (Overton et al. 1997). When water depth, surface turbulence, or glare precluded substrate observations, we looked through a dive mask held at the water surface. We recorded water temperatures with a Hanna HI 9063 digital thermocouple thermometer and probe with a resolution of 0.1°C and an accuracy of +/– 0.2%. To evaluate water temperature gradients, we measured temperatures in a grid surrounding redd pits. Temperatures were measured in the center of the pit and arrayed at intervals of 1 m to the left, 1 m to the right, 1 m upstream, and 1 m downstream from the pit center; yielding five temperature readings.

Statistical Analyses

To evaluate fine-scale bull trout redd attributes, we examined distributions of water depths and velocities, redd dimensions, substrate compositions, and water temperatures within and adjacent to redds. We plotted water depths, water velocities, and water temperatures and calculated annual and total summary statistics for these metrics as well as redd dimensions and substrate.

Initially, we conducted a Shapiro-Wilk test of normality for water depth and velocity at four locations (adjacent, pit, tailspill edge, and tailspill crest); redd dimensions (pit length and width, tailspill length and width, total redd length, and redd surface area); substrate composition (percent silt, pea gravel, gravel, rubble, cobble, boulder, and bedrock); percent fines; and water temperatures in and adjacent to redd pits. With the exception of water temperature, all data were found to be non-normal or skewed.

We used a Kruskal-Wallis nonparametric one-way analysis of variance (ANOVA) to assess differences in water depth between undisturbed sites outside redds and three locations in redds: pit, tailspill edge, and tailspill crest. Kruskal-Wallis ANOVA was also used to assess differences in water velocity between undisturbed sites outside redds and three locations in redds.

Water temperatures within and adjacent to redd pits were compared with a paired *t*-test. We compared water temperatures measured in redd pits with temperatures measured in a grid 1 m upstream of pits, 1 m downstream of pits, 1 m left of pits, and 1 m right of pits.

We also wanted to determine if conditions outside redds could be used to predict conditions in completed redds. We applied a Spearman's correlation coefficient analysis to identify relationships between water depths and velocities measured upstream from and within redds. First, we correlated water depth at four locations: undisturbed, pit, tailspill edge, and tailspill crest.

Next, we correlated water velocities at the same four locations. All analyses were performed with PC SAS 9.4 (SAS Institute 2012).

Results

From 1993–2007, we located 337 fluvial bull trout redds (Figure 1). Annual adult (> 300 mm TL) bull trout escapements to Rapid River ranged from 111 to 409 fish during our redd surveys (R. Steiner, IDFG, personal communication). From 1993 to 2007, fluvial bull trout that ascended Rapid River ranged from 300 to 670 mm TL and averaged 452 mm TL. Most (85%) exceeded 400 mm TL and 21% and 1% exceeded 500 and 600 mm TL, respectively. Mean lengths of bull trout entering Rapid River fluctuated among years and ranged from 417 mm in 1993 to 476 mm in 2004.

Adjacent (Undisturbed) Spawning Site Characteristics

As described above, undisturbed sites adjacent to completed redd pits are presumed to be representative of spawning sites. Water depths in undisturbed sites adjacent to redd pits ranged from 5.0 to 53.0 cm and averaged 19.7 cm (Table 1). Mean, annual water depths at adjacent sites ranged from 14.2–23.0 cm (Table 1). Most (89%) adjacent sites exhibited water depths from 10.0 to 39.0 cm; 8% were less than 10.0 cm, and 3% were more than 40.0 cm. Water column velocities in adjacent sites ranged from 2.0 to 65.0 cm s^{-1} and averaged 21.4 cm s^{-1} (Table 1). Mean, annual water velocities at adjacent sites ranged from 11.6 to 30.5 cm s^{-1} (Table 1). Most (94%) of adjacent sites exhibited water velocities from 1.0 to 39.0 cm s^{-1}.

Spawning sites exhibited a low percentage of surface fines (particles < 2 mm). Undisturbed sites adjacent to redds averaged 12.6% surface fines (Table 2) and most (79%) adjacent sites had fewer than 20.0% fines. Mean, annual surface fines ranged from 6.5 to 21.8% (Table 2).

Completed Redd Characteristics

Redd dimensions varied within and across years. Pits ranged from 0.19 to 1.40 m long and mean annual pit lengths and widths ranged from 0.32 to 0.74 m and 0.32 to 0.79 m, respectively (Table 3). Fluvial bull trout sometimes constructed redds immediately downstream from large boulders or large woody debris so some redd pits were disproportionately short. Although we observed clusters of redds less than 0.5 m apart, redd superimposition was uncommon. Total redd lengths and surface areas annually averaged 1.03 to 1.47 m and 0.37 to 1.07 m^{-2}, respectively (Table 3). The largest redds, presumably constructed by very large (> 600 mm TL) bull trout, exceeded 2.0 m long with a surface area of more than 2.30 m^{-2}. Redd pits comprised about 46% of redd surface areas and tailspills the remainder.

Water depths varied across the redd morphology. Mean annual water depths in redd pits ranged from 17.5 to 28.1 cm (Table 1) and most (95%) redd pits were from 10.0 to 39.0 cm deep; 5% were more than 40.0 cm. Water depths decreased significantly ($P < 0.001$) progressing downstream from the pit to the tailspill edge and to the tailspill crest (Table 1). Mean annual water depths ranged from 12.6 to 22.8 cm on the tailspill edge and from 9.0 to 17.4 cm on the tailspill crest (Table 1). Most (90%) tailspill edges were from 10.0 to 29.0 cm deep; 5% were less than 10.0 cm, and 5% were more than 30.0 cm. Most (98%) tailspill crests were from 1.0 to 29.0 cm deep.

Water velocities also varied across the redd morphology. Mean annual water velocities in redd pits ranged from 13.9 to 23.7 cm s^{-1} (Table 1) and most (98%) pit velocities were from 1.0 to 39.0 cm s^{-1}. Water velocities varied inversely with water depth and increased significantly ($P < 0.001$) progressing downstream from the redd pit, to the tailspill edge, to the tailspill crest (Table 1). Mean annual water velocities ranged from 16.6 to 29.6 cm s^{-1} on the tailspill edge and from 21.8 to 38.5 cm s^{-1} on the tailspill crest. Most (93%) tailspill edge velocities were from 1.0 to 39.0 cm s^{-1}. Most (96%) tailspill crest velocities were from 10.0 to 59.0 cm s^{-1}; 3% were less than 10.0 cm s^{-1}, and 1% were more than 60.0 cm s^{-1}.

Gravel and pea gravel were the most abundant particles in completed redds. Mean, annual proportions of gravel and pea gravel ranged from 18.3 to 50.9% and 17.1 to 37.8%, respectively (Table 2). Mean, annual proportions of other sub-

TABLE 1. Mean annual attributes of fluvial bull trout redds and adjacent sites, Rapid River, Idaho, 1993–2007. Annual sample sizes for depth and velocity were identical except in 1993 and 1997 when $N = 12$ and $N = 17$, respectively.

	Redd Attributes															
Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2003	2004	2005	2006	2007	All Years	
Number of Redds	13	32	22	20	26	20	14	17	22	51	34	24	20	22	Range	Mean (SD)
Depth (cm)																
Adjacent to Pit	15.3	14.2	21.9	18.9	19.3	21.8	20.1	19.9	19.4	22.4	20.5	18.2	23.0	19.7	5.0–53.0	19.7 (8.3)
Pit	17.5	18.8	27.0	24.5	23.8	24.3	23.6	24.5	21.6	27.6	28.1	24.6	27.8	23.5	10.0–60.0	24.7 (8.0)
Tailspill Edge	12.6	14.7	21.5	19.1	20.2	22.8	17.1	19.9	16.7	19.0	20.7	16.0	20.3	16.0	6.0–48.0	8.5 (6.9)
Tailspill Crest	9.0	10.3	15.6	15.6	17.3	15.4	13.3	17.4	13.7	12.4	14.5	11.0	14.4	10.2	2.0–45.0	13.5 (6.5)
Velocity (cm s-1)																
Adjacent to Pit	22.0	24.1	18.4	23.4	16.9	20.3	11.6	21.6	19.1	22.1	19.7	17.4	30.5	29.0	2.0–65.0	21.4 (11.8)
Pit	22.7	20.0	19.6	22.3	16.6	19.2	13.9	21.4	18.2	20.0	16.9	14.4	23.7	21.7	2.0–51.0	19.3 (9.8)
Tailspill Edge	26.8	22.9	23.6	26.5	24.3	19.8	16.6	22.3	21.8	24.3	20.9	23.8	29.5	29.6	2.0–62.0	23.7 (10.5)
Tailspill Crest	31.4	31.5	32.2	30.1	29.7	29.0	21.8	26.0	26.4	35.2	26.6	32.4	35.9	38.5	2.0–69.0	31.5 (12.5)

TABLE 2. Mean annual substrate composition adjacent to and within fluvial bull trout redds, Rapid River, Idaho, 1993–2007. Annual sample sizes for surface fines and substrate % were identical except in 1997 when $N = 26$.

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2003	2004	2005	2006	2007		
Number of Redds	13	32	22	20	17	20	14	17	22	51	34	24	20	22	All Years	
	Adjacent to Redd														Range	Mean (SD)
Surface Fines %	6.5	9.3	20.4	21.3	16.8	21.8	10.5	8.8	19.7	7.5	10.9	13.2	6.7	10.5	0.0–71.7	12.6 (12.3)
Substrate %	Within Entire Redd Area															
Silt	7.7	14.1	14.3	11.8	11.7	20.0	13.6	9.4	14.1	10.3	10.0	11.3	7.8	12.6	0.0–45.0	12.1 (8.5)
Pea Gravel	33.5	35.1	18.0	17.8	24.1	23.5	27.2	29.4	29.2	22.6	37.8	19.3	17.1	18.7	0.0–75.0	25.5 (14.1)
Gravel	49.2	36.5	22.5	18.3	45.2	29.0	30.5	28.2	33.5	50.9	36.9	47.1	48.1	41.2	0.0–85.0	38.3 (18.7)
Rubble	8.5	11.2	21.1	24.3	10.9	16.0	13.9	17.3	10.3	13.2	11.0	9.2	13.1	13.0	0.0–60.0	13.5 (10.4)
Cobble	1.2	2.8	15.7	20.5	7.4	9.3	9.7	8.9	8.7	2.7	3.2	8.1	8.3	9.9	0.0–40.0	7.5 (8.6)
Boulder	0.0	0.3	8.0	6.8	0.7	2.0	5.1	6.2	4.2	0.3	0.4	5.0	5.1	4.6	0.0–35.0	3.0 (5.7)
Bedrock	0.0	0.0	0.5	0.8	0.0	0.3	0.0	0.7	0.0	0.0	0.6	0.0	0.5	0.0	0.0–15.0	0.2 (1.4)

TABLE 3. Mean annual dimensions of fluvial bull trout redds, Rapid River, Idaho, 1993–2007. Annual sample sizes listed in Table 1.

Redd Attributes															
Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2003	2004	2005	2006	2007	All Years	
Length (m)															Range	Mean (SD)
Pit	0.42	0.55	0.52	0.49	0.42	0.49	0.32	0.37	0.51	0.61	0.74	0.55	0.55	0.50	0.19–1.40	0.53 (0.18)
Tailspill	0.67	0.62	0.79	0.70	0.61	0.70	0.85	0.69	0.58	0.86	0.72	0.75	0.82	0.73	0.18–1.98	0.73 (0.28)
Total Redd	1.09	1.17	1.31	1.19	1.03	1.19	1.17	1.06	1.09	1.47	1.46	1.30	1.37	1.23	0.70–2.28	1.27 (0.38)
Width (m)																
Pit	0.49	0.47	0.58	0.53	0.42	0.42	0.34	0.32	0.42	0.64	0.79	0.51	0.56	0.48	0.18–1.52	0.53 (0.22)
Tailspill	0.53	0.39	0.48	0.44	0.39	0.40	0.42	0.36	0.35	0.61	0.58	0.51	0.66	0.50	0.13–1.10	0.49 (0.18)
Surface																
Area (m-2)	0.60	0.53	0.69	0.58	0.42	0.53	0.44	0.37	0.44	0.98	1.07	0.70	0.91	0.61	0.13–2.38	0.68 (0.43)

strates in redds included: rubble (8.5–24.3%); silt (7.7–20.0%); and cobble (1.2–20.5%). Particles ranging from pea gravel to cobble comprised more than 80% of the substrates in completed redds. Boulder and bedrock substrates were less common; mean, annual proportions ranged from 0.0 to 8.0% and 0.0 to 0.8%, respectively (Table 2).

Water temperatures in redd pits averaged 6.26 °C and ranged from 2.0 to 10.0 °C. Mean, annual water temperatures in redd pits ranged from 4.5 to 7.7 °C and we did not detect a water temperature gradient within the 1 m grid surrounding redd pits.

Changes During Redd Construction

Water depths and velocities in completed redds differed from those attributes measured in undisturbed sites adjacent to redds. Since we assumed undisturbed sites were representative of pre-redd construction conditions, we concluded that bull trout altered water depths and velocities during redd construction. Completed redd pits averaged 5.0 cm deeper (SD 8.3, $P < 0.001$), leading tailspill edges averaged 1.2 cm shallower (SD 6.9, $P < 0.001$), and tailspill crests averaged 6.2 cm shallower (SD 6.5, $P < 0.001$) than undisturbed sites (Tables 1, 3). Mean annual increases in water depths within redd pits ranged from 2.2–7.6 cm (Figure 2, Table 1). As spawning fish completed redds, pits became deeper and more excavated material was deposited downstream, increasing tailspill heights. Mean annual tailspill crest water depths were from 2.0–10.0 cm shallower than undisturbed sites (Figure 2, Table 1).

Bull trout also altered water velocities during redd construction; most pit velocities were slower and tailspill velocities faster compared to adjacent sites (Figure 2, Table 1). Pit velocities averaged 2.1 cm s^{-1} slower (SD 9.8, $P < 0.001$), tailspill edge velocities averaged 2.3 cm s^{-1} faster (SD 10.5, $P < 0.001$), and tailspill crest velocities averaged 10.1 cm s^{-1} faster (SD 12.5, $P < 0.001$) than undisturbed sites (Figure 2, Table1). Mean, annual water velocities in redd pits ranged from 13.9 to 23.7 cm s^{-1} and were slower than adjacent sites in eleven of fourteen years (Figure 2, Table 1). Mean annual tailspill crest water velocities were from 4.4 to 13.8 cm s^{-1} faster than undisturbed sites (Figure 2, Table 1).

Correlations between Adjacent Sites and Redds

Water depths over undisturbed sites adjacent to bull trout redds were significantly correlated with depths inside completed redds ($P < 0.05$). Spearman rank correlation coefficients (*rs*) between adjacent sites and redds equaled 0.83, 0.73, and 0.53, for redd pits, tailspill edges, and tailspill crests, respectively. Water velocities over undisturbed locations adjacent to bull trout redds were also significantly correlated with velocities inside redds ($P < 0.05$). Spearman rank correlation coefficients (*rs*) between adjacent sites and redds equaled 0.69, 0.64, and 0.57, for redd pits, tailspill edges, and tailspill crests, respectively.

Discussion

Spawning Site Characteristics

Rapid River bull trout (mean TL 452 mm) selected spawning sites similar to, and on average shallower with slower water velocities, compared to spawning sites reported for larger, adfluvial bull trout in Montana. Shepard et al. (1984) and Kitano et al. (1994) reported water depths that ranged from 15.0 to 35.0 cm (both studies averaged 28.0 cm) and water velocities that ranged from 24.0 to 61.0 cm s^{-1} (averages of 29.0 cm s^{-1} and 31.0 cm s^{-1}, respectively) in undisturbed sites adjacent to (upstream from) completed adfluvial (mean TL 611 and 580 mm, respectively) bull trout redds.

Other researchers reported that adfluvial bull trout selected spawning sites with low percentages of fines in substrates ranging from 2–64 mm (Shepard et al.1984, Fraley and Shepard 1989) and in stream reaches strongly influenced by hyporheic groundwater exchange (Fraley and Shepard 1989, Baxter and Hauer 2000). Slightly elevated intragravel temperatures from groundwater (Baxter and Hauer 2000) facilitate egg incubation and embryo development and reduce effects of overwinter ice formation in redds. Bull trout in Rapid River similarly spawned in sites with low surface fines and cool water temperatures. Fewer

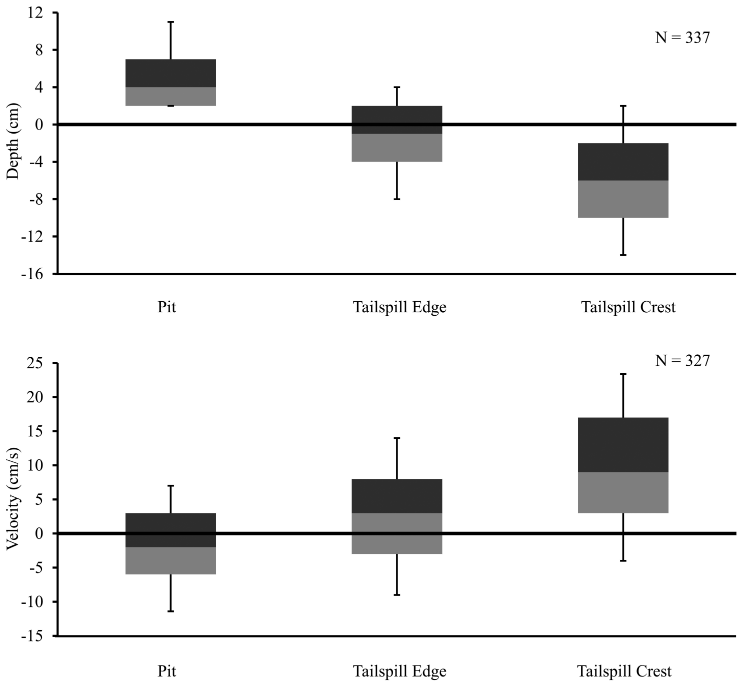

Figure 2. Box-and-whisker plot illustrating changes in water depth (top) and velocity (bottom) between undisturbed sites adjacent to redds and three locations (pit, tailspill edge, tailspill crest) within redds of fluvial bull trout in Rapid River, 1993–2007. Values above the bolded horizontal lines at zero denote increases (+) in depth or velocity after redd construction and those below the line denote decreases (–) in depth or velocity. The horizontal line within each box denotes the median and the upper and lower edges of the box denote the first and third quartiles, respectively. The upper edge of the whisker (vertical line extending outside each box) denotes the 90th percentile and the lower line edge denotes the 10th percentile.

fine sediments enhance spawning success since embryo survival is inversely proportional to the percentage of fines in redds (Chapman 1988). Bowerman et al. (2014) reported that bull trout survival from egg to hatch and from egg to fry emergence were both negatively related to percent fine sediment (< 1 mm) in redds and positively related to the strength of downwelling at spawning sites. We were unable to locate other studies that reported water temperatures in adjacent sites.

Fluvial bull trout are very mobile (Bjornn and Mallet 1964, Swanberg 1997, Mogen and Kaeding 2005) and such mobility presents mature fish with abundant, potential locations for redd construction. Despite the availability of suitable spawning habitat, bull trout redds are often clustered and unevenly distributed within spawning streams (Baxter and McPhail 1996). Dauble and Watson (1990) also reported that fall Chinook salmon (*Oncorhynchus tshawytscha*) redds in the mid-Columbia River were usually aggregated in clusters even though it appeared suitable spawning areas were widely distributed. We similarly observed fluvial bull trout redds clustered in the upper 17.5 km of the Rapid River basin (Figure 1) and many stream reaches with apparently suitable spawning habitat supported no redds. Baxter and McPhail (1996) reported bull trout were prone to spawn in previously disturbed spawning gravels. Although most redds we observed were not constructed in previously disturbed gravels, we did observe new redds constructed immediately adjacent to existing redds while nearby gravels were unused. Most redds were in patches of sorted gravels along the margins of runs, in high gradient riffles, and downstream from boulders or large woody debris. As Kondolf et al. (1991) reported for high gradient channels, we similarly observed most gravel either downstream from boulders or upstream from natural hydraulic controls. Hydraulic controls in Rapid River often resulted from accumulations of large woody debris and sediment as Kondolf et al. (1991) also observed.

Site Modification during Spawning

Bull trout altered water depths and velocities in spawning sites during redd construction. Alteration of the stream bed and coarsening of the gravel by spawning salmonids is well documented (Chapman 1988, Thurow and King 1994). During construction, fish modify water depths and velocities and create the unique salmonid redd morphology (Burner 1951). Accelerated water velocity through redds promotes percolation over eggs incubating in the redd tailspill (Chapman 1988, Schmetterling 2000, Baxter and Hauer 2000). This percolation facilitates gaseous exchange between incubating eggs and ambient water, thereby enhancing embryo development and survival. Bowerman et al. (2014) similarly concluded that redd construction increased hyporheic flow and oxygen delivery through the intragravel environment.

Completed Redd Attributes

Water Depths and Velocities—The depths we measured in completed fluvial bull trout redds were similar to, yet shallower than, depths reported for larger, adfluvial bull trout. Baxter and McPhail (1996) summarized water depths measured "at" bull trout redds and reported mean depths ranging from 23.9 to 56.5 cm. Except for Sexauer (1994), we were unable to determine if the cited studies measured depths in redd pits. Water velocities we measured in fluvial bull trout redds were also similar to velocities reported for larger, adfluvial bull trout. Sexauer (1994) reported water velocities averaging 14.0 cm s^{-1} (range 2.0 to 42.0 cm s^{-1}) in redd pits of adfluvial bull trout in Washington. Baxter and McPhail (1996) also summarized water velocities measured "at" bull trout redds and reported mean velocities ranging from 14.0 to 52.0 cm s^{-1}. As with depth, except for Sexauer (1994), we were unable to determine if the cited studies measured velocities within redd pits.

Substrate Composition—Similar to our observations, others have reported adfluvial bull trout spawning primarily in gravels and cobbles (Shepard et al. 1984, Sexauer 1994, Baxter and McPhail 1996). Baxter and McPhail (1996) described bull trout as capable of moving substrates larger than cobbles. Size of spawning fish influences the range of particle sizes found in completed redds (Thurow and King 1994, Knapp and Vredenberg 1996, Schmetterling 2000). Our observations concur with Chapman (1988) that spawning fish were unable to move the largest substrates and instead removed the overlying layer of small particles exposing larger substrate buried beneath. Kondolf and Wolman (1993) suggested fish spawn in substrate sizes up to 10% of their TL and our data corroborate their findings.

Water Temperature—Cool water is a crucial component influencing bull trout distribution (Dunham et al. 2003), occupied habitats (Rieman and McIntyre 1993, Saffel and Scarnecchia 1995), and spawning sites (Baxter and Hauer 2000). Bull trout redds in Rapid River similarly exhibited cool water temperatures. Baxter and Hauer (2000) observed bull trout redds in bedforms with strong downwelling and high intragravel flow rates.

Redd Dimensions—A number of factors influence redd dimensions, including fish size (Chapman 1988), gravel quality and quantity (Lorenz and Eiler 1989), water velocity (Ottaway et al. 1981, Wollebæk et al. 2008), and spawning pair territoriality (Knapp and Vredenberg 1996). Fluvial bull trout redds measured by Howell and Sankovich (2012) had similar surface areas (median area, 0.99-1.09 m^{-2}) to those we measured. However, Rapid River bull trout constructed redds that were substantially smaller than redds constructed by larger, adfluvial bull trout. Sexauer (1994) reported adfluvial bull trout redds averaging 2.65 m long and 0.77 cm wide for a mean redd area of 2.04 m^{-2} and Shepard et al (1984) reported a mean surface area of 2.31 m^{-2} for redds constructed by similar-sized adfluvial bull trout.

Correlations between Adjacent Sites and Redds

Water depths and velocities over sites adjacent to redds were significantly correlated with depths and velocities in completed redds ($P < 0.05$). Consequently, characteristics of adjacent sites may be useful for predicting completed redd characteristics.

Study Limitations

Our results have important limitations. We completed annual redd surveys during one week in September and did not measure redds across the entire (August–October) spawning season. Redds constructed prior to our surveys may have been undetected if they accumulated periphyton or sediments and additional redds were constructed after our September surveys. We examined weekly bull trout length frequencies recorded at the IDFG fish trap and found no evidence of a time trend in spawner sizes. Consequently, the sizes of redds we measured were likely representative of redds completed during the entire spawning period.

Since bull trout are federally listed as a Threatened species, we avoided disturbing spawning fish, disturbing embryos, and intrusively sampling. Consequently, we relied on published field studies to conclude that undisturbed sites immediately upstream from completed redd pits were representative of spawning site characteristics prior to redd construction. We assumed the undisturbed sites we measured accurately reflected the characteristics of sites adult bull trout selected for redd construction and we applied the characteristics of those sites to assess how spawning fish changed water depths and velocities during redd construction. A more accurate method for confirming pre-redd site characteristics would have been to empirically measure sites at the onset of spawning.

To avoid disturbing developing embryos, our assessments of redd substrate composition were limited to visual estimates of substrate classes rather than empirical particle size measurements. Bunte et al. (2009) reported that visually estimating substrate size-class boundaries can lead to errors. Visual estimates overestimated the amount of 2–16 mm gravel and underestimated the amount of 16–64 mm when compared to measurements (Bunte 2009). Buscombe et al. (2010) described a new, non-intrusive method for characterizing grain sizes that may be applicable for measuring particles in redds of ESA listed species. The authors reported the method utilizes the spectral properties of a digital image and is rapid and inexpensive.

We did not attempt to measure intragravel water temperatures or the influence of hyporheic groundwater exchange. Consequently, we were unable to assess if hyporheic groundwater exchange influenced site selection by bull trout as Fraley and Shepard (1989) and Baxter and Hauer (2000) reported. Despite these limitations, our results contribute to understanding fluvial bull trout redd characteristics.

Conclusions

Improving understanding of fluvial bull trout redds and sites adjacent to redds will improve the accuracy of redd counts, a primary method for surveying bull trout populations. This is particularly relevant in streams with multiple species of sympatric, fall spawning salmonids. These data also directly inform efforts to conserve and restore bull trout habitats and populations. Knowledge of the fine-scale characteristics of bull trout redds will assist the design and implementation of projects to restore critical bull trout spawning habitats. These same data may also be applied to guide conservation of critical spawning areas.

Acknowledgments

We thank Dan Schill and Steve Elle (retired) of IDFG and David Burns (retired) and Dale Olson of the USDA-Forest Service, Payette National Forest for their numerous contributions and suggestions. Rick Lowell, Ralph Steiner, Brad Dredge, Nicola Johnson, Jeff Seggerman and the seasonal staff of the IDFG Rapid River Fish Hatchery provided data and assistance. Numerous seasonal employees of the Rocky Mountain Research Station assisted with data collection, often under challenging field conditions. Nick Gerhardt (retired) of the Nez Perce National Forest provided Rapid River flow records. Three anonymous reviews provided constructive edits that substantially improved the manuscript.

Literature Cited

Al-Chokhachy, R., P. Budy, and H. Schaller. 2005. Understanding the significance of redd counts: a comparison between two methods for estimating the abundance and monitoring of bull trout populations. North American Journal of Fisheries Management 25:1505-1512.

Al-Chokhachy, R., and P. Budy. 2007. Summer microhabitat use of fluvial bull trout in Eastern Oregon streams. North American Journal of Fisheries Management 27:1068-1081.

Barnett, H. K., and D. K. Paige. 2013. Movements by adfluvial bull trout during the spawning season between lake and river habitats. Transactions of the American Fisheries Society 142:876-883.

Baxter, C. V., and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57:1470-1481.

Baxter, J. S., and J. D. McPhail. 1996. Bull trout spawning and rearing habitat requirements: summary of the literature. Fisheries Technical Circular 98. University of British Columbia, Vancouver.

Bjornn, T. C., and J. Mallet. 1964. Movements of planted and wild trout in an Idaho river system. Transactions of the American Fisheries Society 93:70-76.

Bowerman, T., B. T. Neilson, and P. Budy. 2014. Effects of fine sediment, hyporheic flow, and spawning site characteristics on survival and development of bull trout embryos. Canadian Journal of Fisheries and Aquatic Sciences 71:1059-1071.

Bunte, K., S. R. Abt, J. P. Potyondy, and K. W. Swingle. 2009. Comparison of three pebble count protocols (EMAP, PIBO, and SFT) in two mountain gravel-bed streams. Journal of the American Water Resources Association 45:1209-1227.

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. U.S. Fish and Wildlife Service Fishery Bulletin 52:97-110.

Buscombe, D., D. M. Rubin, and J. A. Warrick. 2010. A universal approximation of grain size from images of noncohesive sediment. Journal of Geophysical Research: Earth Surface 115.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1-21.

Curry, R. A., and D. L. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 52:1733-1740.

Dauble, D. D., and D. G. Watson. 1990. Spawning and abundance of fall chinook salmon (*Oncorhynchus tshawytscha*) in the Hanford Reach of the Columbia River, 1948–1988. Technical Report PNL-7289. Pacific Northwest Laboratory, Richland, WA.

Donald, D. B., and D. J. Alger. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71:238-247.

Downs, C. C., D. Horan, E. Morgan-Harris, and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190-200.

Dunham, J., B. Rieman, and G. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management 23:894-904.

Elle, S., R. Thurow, and T. Lamansky. 1994. Rapid River bull trout movement and mortality studies. Job Performance Report, river and stream investigations. Job 1. Idaho Department of Fish and Game, Boise.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133-143.

Gallagher, S. P., and C. M. Gallagher. 2005. Discrimination of chinook salmon, coho salmon, and steelhead redds and evaluation of the use of redd data for estimating escapement in several unregulated streams in northern California. North American Journal of Fisheries Management 25:284-300.

Gallagher, S. P., P. K. Hahn, and D. H. Johnson. 2007. Redd counts. *In* D. H. Johnson, B. M. Shrier, J. S. O'Neal, J. A. Knutzen, X. Augerot, T. A. O'Neil, and T. N. Pearsons (editors), Salmonid Field Protocols Handbook, Techniques for assessing status and trends in salmon and trout populations, American Fisheries Society, Bethesda, MD. Pp. 197-234.

Goetz, F. 1989. Biology of the Bull Trout, *Salvelinus confluentus*: A Literature Review. Willamette National Forest, Eugene, OR.

Goode, J. R., J. M. Buffington, D. Tonina, D. J. Isaak, R. F. Thurow, S. Wenger, D. Nagel, C. Luce, D. Tetzlaff, and C. Soulsby. 2013. Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins. Hydrological Processes 27:750-765.

Grost, R. T. 1989. A description of brown trout redds in Douglas Creek, Wyoming. M.S. Thesis, University of Wyoming, Laramie.

Hauer, F. R., G. C. Poole, J. T. Gangemi, and C. V. Baxter. 1999. Large woody debris in bull trout (*Salvelinus confluentus*) spawning streams of logged and wilderness watersheds in northwest Montana. Canadian Journal of Fisheries and Aquatic Sciences 56:915-924.

Howell, P. J., and P. M. Sankovich. 2012. An evaluation of redd counts as a measure of bull trout population size and trend. North American Journal of Fisheries Management 32:1-13.

Isaak, D. J., and R. F. Thurow. 2006. Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys. Canadian Journal of Fisheries and Aquatic Sciences 63:285-296.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223-235.

Kitano, S., K. Maekawa, S. Nakano, and K. D. Fausch. 1994. Spawning behavior of bull trout in the upper Flathead drainage, Montana, with special reference to hybridization with brook trout. Transactions of the American Fisheries Society 123:988-992.

Knapp, R. A., and V. T. Vredenburg. 1996. Spawning by California golden trout: characteristics of spawning fish, seasonal and daily timing, redd characteristics, and microhabitat preferences. Transactions of the American Fisheries Society 125:519-531.

Koenig, M. K., K. A. Meyer, J. R. Kozfkay, J. M. DuPont, and E. B. Schriever. 2015. Evaluating the ability of tiger muskellunge to eradicate brook trout in Idaho alpine lakes. North American Journal of Fisheries Management 35:659-670.

Kondolf, G. M., G. F. Cada, M. J. Sale, and T. Felando. 1991. Distribution and stability of potential salmonid spawning gravels in steep boulder-bed streams of the eastern Sierra Nevada. Transactions of the American Fisheries Society 120:177-186.

Kondolf, G. M., and M. G. Wolman. 1993. The sizes of salmonid spawning gravels. Water Resources Research 27:2275-2285.

Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conservation Biology 7:856-865.

Lorenz, J. M., and J. H. Eiler. 1989. Spawning habitat and redd characteristics of sockeye salmon in the glacial Taku River, British Columbia and Alaska. Transactions of the American Fisheries Society 118:495-502.

Meehan, W. R., editor. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. Special Publication 19, American Fisheries Society, Bethesda, MD.

Mogen, J. T., and L. R. Kaeding. 2005. Identification and characterization of migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. Transactions of the American Fisheries Society 134:841-852.

Muhlfeld, C. C. 2002. Spawning characteristics of redband trout in a headwater stream in Montana. North American Journal of Fisheries Management 22:1314-1320.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797-810.

Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull char, (*Salvelinus confluentus*), and implications for conservation. Environmental Biology of Fishes 64:321-332.

Northcote, T. G. 1997. Potamodromy in Salmonidae-living and moving in the fast lane. North American Journal of Fisheries Management 17:1029-1045.

Orth, D. J. 1983. Aquatic Habitat Measurements. *In* L. A. Nielsen and D. L. Johnson (editors), Fisheries Techniques, American Fisheries Society, Bethesda, MD. Pp. 61-84.

Ottaway, E. M., P. A. Carling, A. Clarke, and N. A. Reader. 1981. Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. Journal of Fish Biology 19:593-607.

Overton, C. K., M. A. Radko, and R. L. Nelson. 1993. Fish habitat conditions: using the Northern/Intermountain Regions inventory procedures for detecting differences on two differently managed watersheds. USDA Forest Service General Technical Report INT-300. Intermountain Research Station, Ogden, UT.

Overton, C. K., S. P. Wollrab, B. C. Roberts, and M. A. Radko. 1997. R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory procedures handbook. USDA Forest Service General Technical Report INT-346. Intermountain Research Station, Ogden, UT.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian and biotic conditions. USDA Forest Service General Technical Report INT-138. Intermountain Research Station, Ogden, UT.

Pratt, K. L. 1992. A review of bull trout life history. *In* P. J. Howell and D. V. Buchanan, (editors), Proceedings of the Gearhart Mountain Bull Trout Workshop, Oregon Chapter of the American Fisheries Society, Corvallis, OR. Pp. 5-9.

Ratliff, D. E., and P. J. Howell. 1992. The status of bull trout populations in Oregon. *In* P. J. Howell and D. V. Buchanan (editors), Proceedings of the Gearhart Mountain Bull Trout Workshop, Oregon Chapter of the American Fisheries Society, Corvallis, OR. Pp. 10-17.

Reiser, D. W., and T. A. Wesche. 1977. Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations. Water Resources Research Institute, Water Resource Series 64. Laramie, WY.

Rich, C. F., T. E. McMahon, B. E. Rieman, and W. L. Thompson. 2003. Local-habitat, watershed, and biotic features associated with bull trout occurrence in Montana streams. Transactions of the American Fisheries Society 132:1053-1064.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. USDA Forest Service General Technical Report INT-302. Intermountain Research Station, Ogden, UT.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285-296.

Saffel, P. D., and D. L. Scarnecchia. 1995. Habitat use by juvenile bull trout in belt-series geology watersheds of northern Idaho. Northwest Science 69:304-317.

SAS (SAS Institute). 2012. SAS/STAT user's guide; version 9.4. SAS Institute, Cary, NC.

Schill, D., R. Thurow, and P. Kline. 1994. Seasonal movements and spawning mortality of fluvial bull trout in Rapid River, Idaho. Job Performance Report, wild trout evaluations. Job 2. Idaho Department of Fish and Game, Boise.

Schmetterling, D. A. 2000. Redd characteristics of fluvial westslope cutthroat trout in four tributaries to the Blackfoot River, Montana. North American Journal of Fisheries Management 20:776-783.

Sexauer, H. M. 1994. Life history aspects of bull trout, (*Salvelinus confluentus*) in the eastern Cascades, Washington. M.S. Thesis, Central Washington University, Ellensburg.

Received 22 July 2015
Accepted 22 February 2017

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River basin, Montana. Montana Department of Fish, Wildlife, and Parks, Helena.

Swanberg, T. R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126:735-746.

Thurow, R. F., and J. G. King. 1994. Attributes of Yellowstone cutthroat trout redds in a tributary to the Snake River, Idaho. Transactions of the American Fisheries Society 123:37-50.

USDA. 2007. United States Department of Agriculture, Forest Service, Nez Perce National Forest. Stream gauging station number NEAI 15 records for Rapid River, Idaho, 1974-2007.

USFWS. 1999. Endangered and threatened wildlife and plants: determination of threatened status of bull trout in the coterminous US. Federal Register 64:58910-58933.

Watson, G., and T. W. Hillman. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. North American Journal of Fisheries Management 17:237-252.

Witzel, L. D., and M. R. MacCrimmon. 1983. Embryo survival and emergence of brook charr (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) relative to redd gravel composition. Canadian Journal of Zoology 41:1783-1792.

Wollebæk, J., R. Thue, and J. Heggenes. 2008. Redd site microhabitat utilization and quantitative models for wild large brown trout in three contrasting boreal rivers. North American Journal of Fisheries Management 28:1249-1258.