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Spawning and rearing behavior of bull trout in a headwater lake ecosystem

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Abstract Numerous life histories have been documented for bull trout *Salvelinus confluentus*. Lacustrine-adfluvial bull trout populations that occupy small, headwater lake ecosystems and migrate short distances to natal tributaries to spawn are likely common; however, much of the research on potamodromous bull trout has focused on describing the spawning and rearing characteristics of bull trout populations that occupy large rivers and lakes and make long distance spawning migrations to natal headwater streams. This study describes the spawning and rearing characteristics of lacustrine-adfluvial bull trout in the Quartz Lake drainage, Glacier National Park, USA, a small headwater lake ecosystem. Many spawning and rearing characteristics of bull trout in the Quartz Lake drainage are similar to potamodromous bull trout that migrate long distances. For example, subadult bull trout distribution was positively associated with slow-water habitat unit types and maximum wetted width, and negatively associated with increased stream gradient. Bull trout spawning also occurred when water temperatures were between 5 and 9 °C, and redds were generally located in stream segments with low stream gradient and abundant gravel and cobble substrates. However, this study also elucidated characteristics of bull trout biology that are not well documented in the literature, but may be relatively widespread and have important implications regarding general characteristics of bull trout ecology, use of available habitat by bull trout, and persistence of lacustrine-adfluvial bull trout in small headwater lake ecosystems.

Keywords Bull trout · Life history · Stream habitat · Spawning · Rearing

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Introduction

Bull trout *Salvelinus confluentus* is a species of char endemic to western North America that exhibits a broad array of life histories that reflect the variable environmental conditions to which the species has adapted (sensu Warren and Liss 1980). For example, bull trout exhibit both non-migratory (resident) and migratory (potamodromous and anadromous) life histories; however, potamodromous bull trout are perhaps the most well studied and characterized. Potamodromous bull trout can exhibit fluvial, fluvial-adfluvial, lacustrine-adfluvial, or allacustrine migratory patterns (Varley and Gresswell 1988; Northcote 1997; Dupont et al. 2007), and more than one pattern can occur in the same population (e.g., Homel and Budy 2008). Despite the expression of a broad array of life history variation that may allow bull trout to exploit a variety of environmental situations, bull trout were listed as threatened in the Columbia River drainage under the U.S. Endangered Species Act in 1998. Many of the remaining strongholds for this species occur in watersheds under public ownership that are managed specifically for protection of natural resources (e.g., national parks and wilderness areas; McMahon et al. 2007; Dunham et al. 2008).

Exploring relationships between environmental and life history variation can provide important insights concerning the evolutionary history of species, and this type of information is critical for protecting biodiversity and managing for persistence in spatially and temporally heterogeneous environments (Den Boer 1968; Gresswell et al. 1994). The spawning and rearing characteristics of potamodromous bull trout that make long distance migrations (e.g., hundreds of kilometers) from large lakes and rivers to small headwater streams have been studied extensively (Fraley and Shepard 1989; Muhlfeld and Marotz 2005; Monnot et al. 2008; Howell et al. 2010). However, lacustrine-adfluvial bull trout populations may exhibit short distance migrations (i.e., a few hundred meters to a few kilometers) to natal tributaries. For example, lacustrine-adfluvial bull trout in Lake Cushman, Washington, migrate 6 km or less to spawning areas in the North Fork Skokomish River (Brenkman et al. 2001), the largest population of lacustrine-adfluvial bull trout in Lake Pend Oreille, Idaho, spawns within the lowermost 12–15 km of Trestle Creek (see Fig. 1 in Downs et al. 2006), and lacustrine-adfluvial bull trout in Odell Lake, Oregon, migrate 1.3 km or less to spawning areas in Trapper Creek (USFWS 2002). Lacustrine-adfluvial bull trout occupy numerous headwater lakes in Glacier National Park, Montana (Meeuwig et al. 2008). Documentation of high density spawning in close proximity to Quartz and Cerulean lakes, Glacier National Park, coupled with population genetic data (Meeuwig et al. 2010) suggest that bull trout in this system exhibit short distance spawning migrations, are demographically isolated, and therefore use specific and restricted spawning and rearing habitats. Despite the potential for short distance migrations to be common among lacustrine-adfluvial bull trout, especially those occupying headwater lake systems, the spawning and rearing characteristics of bull trout exhibiting this life history have received little attention.

Bull trout that exhibit, or have adapted to, short distance spawning migrations in remote, headwater lake ecosystems may become more important to the species' persistence as landscapes become more fragmented due to anthropogenic alterations and climate change, which can reduce connectivity among populations (Rieman et al. 1997, 2007). Additionally, short distance migrations may be beneficial or have adaptive significance (e.g., short distance spawning migrations are energetically less demanding, and rearing in close proximity to lake environments may allow progeny to volitionally select preferred rearing habitat). However, bull trout that exhibit short distance migrations may be particularly susceptible to certain types of environmental perturbations. For example, natural disturbances (e.g., floods, wildfires, landslides, and glacial outbursts) have the potential to influence a substantial portion of spawning and rearing habitat for species that exhibit spatially restricted habitat use. Additionally, the invasion or introduction of nonnative predators into lake environments [e.g., the introduction of lake trout *S. namaycush* into many lakes containing native bull trout populations (Martinez et al. 2009)] may negatively affect subadult bull trout rearing in lake environments or even in streams near lakes.

The goal of this study was to characterize the spawning and rearing characteristics of lacustrine-adfluvial bull trout in the Quartz Lake system (Quartz Lake and Cerulean Lake), Glacier National Park, Montana. Bull trout in this system exhibit short distance spawning migrations and are genetically well-differentiated from other bull trout populations in the area (Meeuwig et al. 2010), despite the lack of contemporary natural barriers that restrict movement among many bull trout occupied lakes in the western portion of Glacier National Park (Meeuwig et al. 2008). The specific objectives were to 1) quantify the influence of abiotic and biotic factors on the distribution of subadult bull trout, 2) characterize the spatial and temporal dynamics of bull trout spawning activity, and 3) characterize the abiotic factors associated with areas of high redd density in tributary streams to Quartz Lake. Additionally, the adaptive significance of this life history and its significance to bull trout conservation are discussed.

Methods

Study area

Quartz and Cerulean lakes are located in the North Fork Flathead River drainage on the west side of the Continental Divide in Glacier National Park, Montana. The lakes are situated in a glacially carved basin and are primarily fed by snow and glacial meltwater. Bull trout occupy Quartz and Cerulean lakes in moderate to high relative abundance compared to other lakes in Glacier National Park (Meeuwig et al. 2008).

Quartz Creek, the main tributary to Quartz Lake, flows about 7.0 km (stream length) from the outlet of Gyrfalcon Lake to Quartz Lake; Gyrfalcon Lake is located upstream from a putative fish barrier and is not occupied by bull trout. Rainbow Creek flows downstream about 2.0 km (stream length) from the outlet of Cerulean Lake to the confluence with Quartz Creek, about 1.3 km (stream length) upstream from Quartz Lake. The study area encompassed Quartz Creek from the inlet of Quartz Lake upstream to a putative fish barrier and Rainbow Creek from the confluence with Quartz Creek upstream to the outlet of Cerulean Lake (hereafter referred to as the Quartz Lake drainage; Fig. 1).

The Quartz Lake drainage was partitioned into three stream segments based on hydrology and stream order. Lower Quartz Creek included main-stem and side-channel habitat between the inlet of Quartz Lake and the confluence of Quartz and Rainbow creeks. Upper Quartz Creek included main-stem habitat that extended from the confluence of Quartz and Rainbow creeks to a putative fish barrier on Quartz Creek, and Rainbow Creek included main-stem and side-channel habitat between the confluence of Quartz and Rainbow creeks and the outlet of Cerulean Lake (Fig. 1). Sampling occurred from August through October of 2008.

Physical habitat characteristics

Physical habitat surveys were conducted at summer base flow to quantify stream habitat characteristics in the Quartz Lake drainage prior to subadult bull trout and redd surveys. Habitat unit classification began at the inlet of Quartz Lake and proceeded upstream. Each habitat unit in main-stem and side-channel areas was classified as a pool, riffle, glide, or rapid (Bisson et al. 1982).

Length (nearest 0.1 m) of each habitat unit was measured, and maximum wetted width (nearest 0.5 m) was visually estimated. Actual maximum wetted width (nearest 0.1 m) was measured every tenth habitat unit, and a correction factor for visual estimates was established using simple linear regression (r^2 = 0.94; Hankin and Reeves 1988). Maximum depth (nearest 0.1 m) was measured in each pool. Substrate composition in each habitat unit was visually estimated as percent silt (<0.059 mm), sand (0.06–2 mm), gravel (2–64 mm), cobble (64–256 mm), boulder (>256 mm), and bedrock (Moore et al. 2002). Cover type was visually estimated as the areal percent of the habitat unit occupied by boulder, overhanging vegetation <1.0 m above the water surface, woody debris (Kaufmann et al. 1999), alcove, and backwater. Undercut bank was measured as the percent of the bank with a horizontal undercut depth deeper than 0.2 m within the habitat unit. Physical habitat characteristics in both main-stem and side-channel habitat units were averaged by stream segment, and 95 % confidence limits were used to evaluate differences in mean habitat characteristics among stream segments.

Water temperature (°C) was recorded every 2 h with a temperature data logger that was anchored to the substrate in the stream channel immediately upstream from the inlet of Quartz Lake. Stage (water height, m) was recorded every 2 h with a data-logging staff gauge that was placed in lower Quartz Creek in a low-velocity area next to the stream bank. The staff gauge was relocated in mid-September to avoid wildlife interactions. Stream discharge (m^3/s) was measured biweekly at a site in Quartz Creek downstream from the staff gauge to develop a stage–discharge relationship (Buchanan and Somers 1969). Stage-discharge relationships were established using simple linear regression (initial gauge site: r^2 = 0.99; relocated gauge site: r^2 = 0.95).

Subadult bull trout presence and distribution

Single-pass backpack electrofishing was used to determine the distribution of subadult bull trout throughout the Quartz Lake drainage (Bateman et al. 2005). Subadult bull trout in this study were defined as bull trout without sexually dimorphic characteristics. Sampling occurred August 14 through 28 at base flow and prior to spawning migrations of adult bull trout into the stream network. Electrofishing locations were selected using a systematic sampling design with two

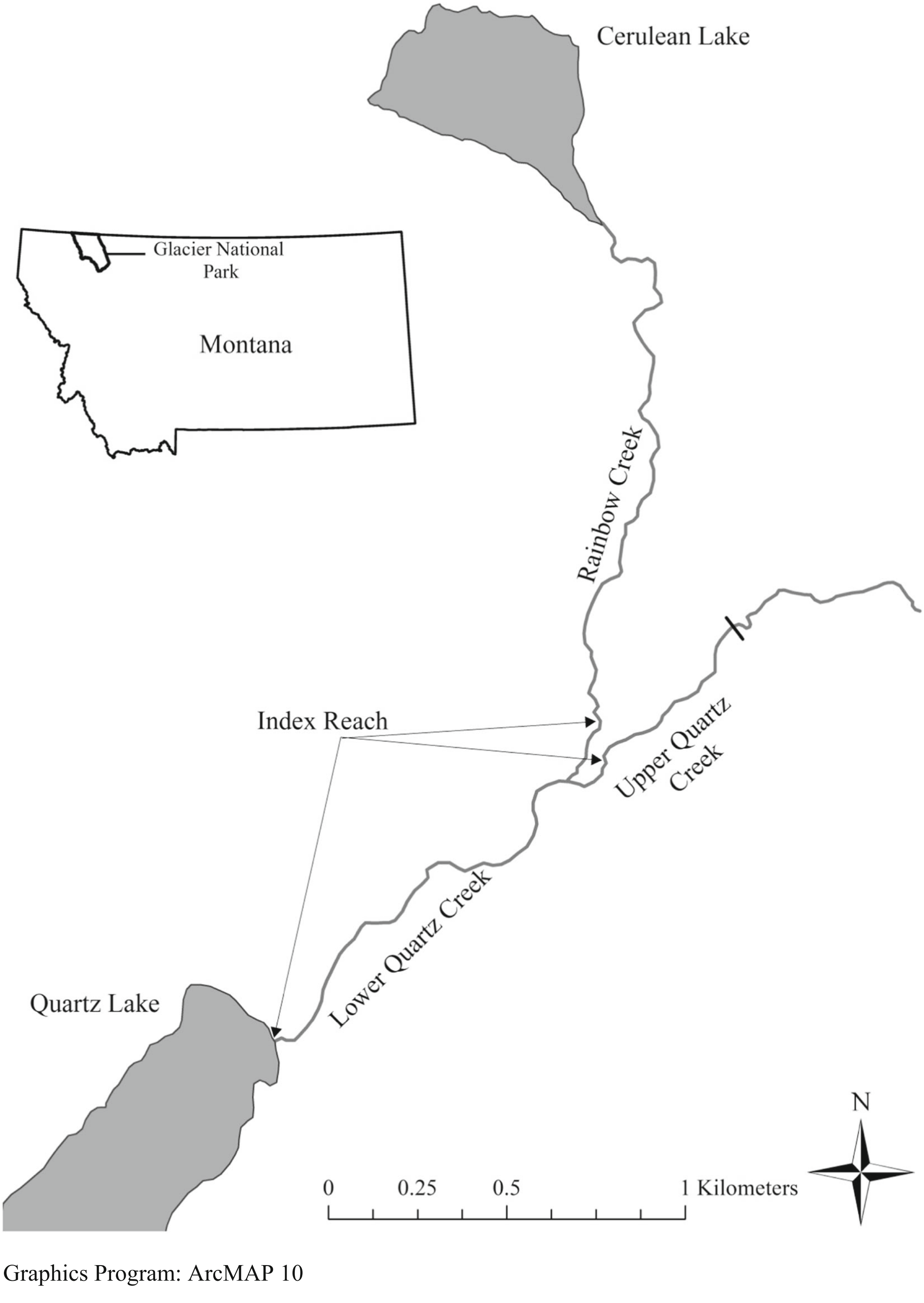

Fig. 1 Study area, stream segment designations, and index reach boundaries in the Quartz Lake drainage. Stream segment designations (lower Quartz Creek, upper Quartz Creek, and Rainbow Creek) were based on hydrology and stream order. Index reach boundaries were established based on the boundaries used for redd surveys conducted in previous years

random starting points (Hansen et al. 2007). Pools and glides were grouped as slow water habitat units, and riffles and rapids were grouped as fast water habitat units (Arend 1999). Habitat units selected for electrofishing were geospatially referenced and marked with a unique identifier during physical habitat surveys. Every fourth slow water unit and every fifth fast water unit was sampled for subadult bull trout without the use of block nets. All salmonids (i.e., bull trout and westslope cutthroat trout *Oncorhynchus clarkii lewisi*) sampled during electrofishing were identified to species, measured for total length (nearest mm), and returned to the habitat unit where they were collected. Subadult bull trout and westslope cutthroat trout occurrence (i.e., presence or absence) was designated for each habitat unit sampled.

The influence of physical habitat characteristics on subadult bull trout presence was examined with 11 candidate multiple logistic regression models (Table 1). Pearson correlation coefficients were examined for all combinations of explanatory variables and only those explanatory variables that were not strongly correlated ($-0.41 < r < 0.25$) were retained for analysis. All models included habitat unit type (i.e., slow water or fast water) and stream gradient as explanatory variables (Table 1) because these variables have been shown to be important for predicting subadult bull trout presence (Fraley and Shepard 1989; Dambacher and Jones 1997; Earle and McKenzie 2001; Al-Chokhachy et al. 2010). An indicator variable was assigned to habitat unit type (0 = fast water, 1 = slow water). Stream gradient was estimated at 100-m intervals starting at the beginning of each stream segment using an orthoimagery layer (NAIP; UTM projected coordinate system, NAD 1983) and a digital elevation model (10 m DEM; NAD 1983) of the study area using ArcGIS 9 software (ArcMap Version 9.2). All habitat units located in the 100-m interval were assigned the resulting gradient value. Additional explanatory variables included coarse substrate (i.e., the sum of percent gravel, cobble, and boulder), width (i.e., habitat unit maximum wetted width), percent woody debris, and percent undercut bank (Table 1).

Candidate models were ranked based on Akaike's Information Criterion (Akaike 1973) adjusted for small sample size (AIC_c; Hurvich and Tsai 1989) using Program R, package qpcR, Version 1.4-0 (Spiess 2014). Delta (Δ) AIC_c values were calculated and models with $\Delta\mathrm{AIC}_c$ values $\leq$2.00 were considered for inferences (Burnham and Anderson 2002). Model parameter estimates, Akaike weights, and adjusted coefficients of determination (Nagelkerke 1991) were estimated in Program R, using packages AICcmodavg, Version 2.0–3 (Mazzerolle 2015) and fsmb, Version 0.5.1 (Nakazawa 2014). Model averaging was used to construct a composite model from the models with $\Delta\mathrm{AIC}_c$ values $\leq$2.0 (Burnham and Anderson 2002). A model averaged parameter estimate and unconditional standard error was calculated for each composite model parameter in Program R, using package AICcmodavg, Version 2.0–3 (Mazzerolle 2015).

A length-frequency histogram was used to estimate age structure of subadult bull trout (Devries and Frie 1996). The cumulative frequency of subadult bull trout and westslope cutthroat trout was plotted as a function of the distance from the inlet of Quartz Lake to evaluate differences in the distributions of these species in lower Quartz Creek and Rainbow Creek.

Distribution of bull trout redds

Bull trout redd surveys were used to characterize the temporal and spatial accumulation of redds in the Quartz Lake drainage. Temporal variation in redd construction was assessed by conducting redd surveys every other day from September 16 through October 11. If a survey could not be conducted because of inclement weather, it was conducted on the next suitable day. Redd surveys

Table 1 Model number and the variables in the model for 11 combinations of variables used to examine the relationship between subadult bull trout presence and physical habitat characteristics in the Quartz Lake drainage

Model	Explanatory variables in model
Global	Unit type, gradient, coarse substrate, width, woody debris, undercut bank
2	Unit type, gradient, coarse substrate, width, woody debris
3	Unit type, gradient, coarse substrate, width, undercut bank
4	Unit type, gradient, coarse substrate, width
5	Unit type, gradient, coarse substrate, woody debris
6	Unit type, gradient, coarse substrate, undercut bank
7	Unit type, gradient, coarse substrate
8	Unit type, gradient, width
9	Unit type, gradient, woody debris
10	Unit type, gradient, undercut bank
11	Unit type, gradient

occurred in a section of Quartz and Rainbow creeks that had previously been established as an index reach (Fig. 1) because it encompassed the area assumed to have the greatest bull trout redd density (Meeuwig and Guy 2007). On each survey day, newly constructed redds were identified and geospatially referenced by two, trained observers walking upstream along the stream channel. Omission and false identification of redds are sources of observer bias that have been documented for bull trout redd surveys (Dunham et al. 2001); however, using the same two experienced observers to conduct all redd surveys in the Quartz Lake drainage likely reduced observer bias associated with the redd detection (Muhlfeld et al. 2006). A brightly painted washer was placed in close proximity to newly identified redds to avoid recounting redds. Habitat units that contained at least one redd were marked by attaching flagging to nearby vegetation. Each subsequent observation of a new redd in the same habitat unit was recorded on the flagging.

Redd surveys were conducted in areas beyond the index reach to assess the spatial distribution of spawning throughout the study area. These surveys were conducted on October 1 and October 11 in the index reach and Rainbow Creek and on October 6 in the index reach and upper Quartz Creek to the putative fish barrier (Fig. 1). Referencing and identification procedures were the same as those used for the index reach.

Geospatial coordinates of redd locations were integrated with an orthoimagery layer (NAIP; UTM projected coordinate system, NAD 1983) and a digital elevation model (10 m DEM; NAD 1983) of the study area using ArcGIS 9 software (ArcMap Version 9.2). The elevation (m) of each redd and stream distance (m) of each redd from the inlet of Quartz Lake were estimated using ArcGIS 9. Discharge, water temperature, and the number of new redds per survey (index reach only) were plotted by survey date to assess the relationship between discharge and water temperature and the beginning, peak, and end of the spawning period. Redd locations (index reach only), measured as the distance from the inlet of Quartz Lake, were plotted by survey date to investigate temporal and longitudinal trends in redd accumulation.

Redd abundance and distribution data gathered beyond the index reach were combined with redd abundance and distribution data from within the index reach to estimate total redd abundance and spatial distribution of redds. The cumulative frequency of redds was plotted as a function of the distance from the inlet of Quartz Lake to evaluate longitudinal trends in redd accumulation. Elevation of each redd was plotted as a function of distance from the inlet of Quartz Lake to investigate the change in elevation associated with redd location. Physical habitat characteristics measured in the study area were compared to the number of redds identified in each stream segment to investigate the relationship between stream segment habitat and redd abundance.

Results

Physical habitat characteristics

Main-stem and side-channel habitats were present in lower Quartz Creek and Rainbow Creek; only main-stem habitat was present in upper Quartz Creek. Side-channel habitat units comprised 71 of 142 (50.0 %) habitat units in lower Quartz Creek and 31 of 140 (22.1 %) habitat units in Rainbow Creek. Habitat unit lengths and maximum pool depths were similar among stream segments (Table 2). The dominant substrate type among stream segments was gravel (lower Quartz Creek) and cobble (upper Quartz and Rainbow creeks). Additionally, lower Quartz Creek had the greatest percent of sand substrate, and Rainbow Creek had the greatest percent of boulder substrate. The percent of silt and bedrock substrate was low in all stream segments (Table 2). Undercut bank and woody debris were the most common cover types in the study area. Rainbow Creek had the least amount of cover present among stream segments (Table 2). Lower Quartz Creek had the lowest mean stream gradient, and upper Quartz and Rainbow creeks had greater, but similar mean stream gradients (Table 2).

Subadult bull trout presence and distribution

Fifty-seven subadult bull trout and 72 westslope cutthroat trout were collected in 87 habitat units in the Quartz Lake drainage. Subadult bull trout were most abundant in lower Quartz Creek, and westslope cutthroat trout were most abundant in Rainbow Creek (Table 2). Lower Quartz Creek contained about 80 % of the subadult bull trout and about 25 % of the westslope cutthroat trout captured (Fig. 2). Additionally, both subadult bull trout and westslope cutthroat trout occurred in fast and slow water habitat units; however,

Table 2 Mean (± 95 % CL) for habitat unit dimensions, substrate (%), and cover type (%) summarized by stream segment sampled in the Quartz Lake drainage. Stream gradient (%) and biotic characteristics summarized by stream segment sampled in the Quartz Lake drainage

	Stream Segment		
	lower Quartz Creek	upper Quartz Creek	Rainbow Creek
Mean habitat unit dimensions			
Length (m)	15.3 ± 2.0	16.5 ± 5.7	16.6 ± 2.7
Maximum wetted width (m)	6.3 ± 1.0	4.0 ± 0.3	5.2 ± 0.5
Maximum pool depth (m)	0.8 ± 0.1	0.8 ± 0.1	0.7 ± 0.1
Mean habitat unit substrate (%)			
Silt	3.2 ± 1.6	0.8 ± 1.4	1.6 ± 1.4
Sand	19.5 ± 3.2	10.2 ± 3.7	4.6 ± 1.7
Gravel	49.9 ± 3.5	40.6 ± 5.0	23.5 ± 3.8
Cobble	26.4 ± 4.4	44.7 ± 7.2	36.0 ± 3.3
Boulder	0.3 ± 0.3	3.8 ± 3.2	29.5 ± 4.6
Bedrock	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Mean habitat unit cover type (%)			
Woody debris	14.8 ± 2.4	10.4 ± 3.2	6.4 ± 1.5
Undercut bank	18.6 ± 4.1	22.8 ± 8.8	10.2 ± 3.6
Boulder	0.0[a] ± 0.1	0.2 ± 0.4	4.7 ± 1.0
Alcove	0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Overhanging vegetation	2.9 ± 1.6	4.7 ± 3.6	1.9 ± 1.3
Backwater	1.1 ± 0.8	0.3 ± 0.5	2.5 ± 2.0
Stream segment gradient and biotic characteristics			
Gradient (%)	1.2	3.3	3.3
Redd count	61	2	30
Subadult bull trout count	46	1	10
Westslope cutthroat trout count	18	2	52

[a] value <0.05

both species were more frequently found in slow water habitat units. Neither species was sampled in fast water habitat units in upper Quartz Creek.

Subadult bull trout varied in length from 44 to 167 mm. The presence of two distinct length groups (i.e., 40–65 mm and 95–125 mm) suggested that there were at least two age groups of subadult bull trout in the Quartz Lake drainage (Fig. 3). Based on data from bull trout populations in the Flathead River Basin (Fraley and Shepard 1989) and surrounding areas (Mogen and Kaeding 2005), these groups were likely age-0 and age-1 individuals.

Three of the 11 candidate models used to examine the relationship between subadult bull trout presence and physical habitat characteristics were considered for inference (Table 3). All of these models had ΔAIC_c values of ≤2.00. The most likely model describing subadult bull trout presence included habitat unit type, gradient, coarse substrate, and width (Table 3). The second ranked model included habitat unit type, gradient, and width, and the third ranked model included the variables habitat unit type, gradient, coarse substrate, width, and woody debris (Table 3). Evidence ratios (w_1/w_j) suggested that the highest ranked model was 1.41 times more likely than the second ranked model and was 2.67 times more likely than the third ranked model (Table 3). Composite model averaged parameter estimates indicated subadult bull trout presence was positively associated with slow water habitat units, width, and woody debris, and negatively associated with gradient and coarse substrate (Table 4).

Distribution of bull trout redds

Spawning was first documented on September 23, and peak spawning occurred on October 3 (Fig. 4). October 11 was assumed to be the end of the spawning period because only two new redds were documented in the index reach, and water temperature had consistently dropped below 6 °C near the inlet of Quartz Lake

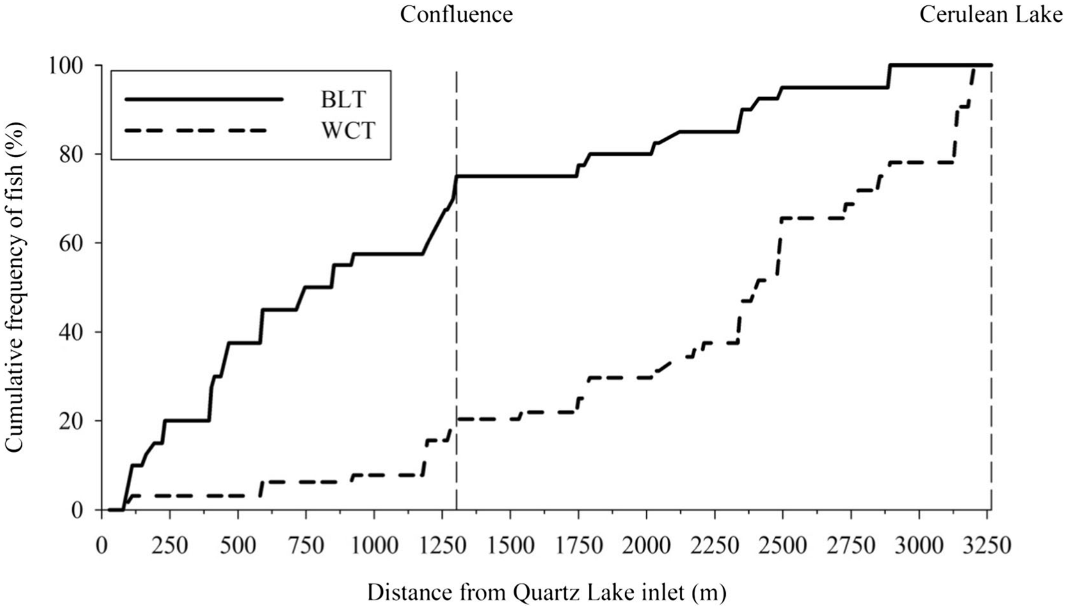

Fig. 2 Cumulative frequency of subadult bull trout (*solid line*) and westslope cutthroat trout (*dashed line*) in lower Quartz Creek (0 to 1303 m from the Quartz Lake inlet) and Rainbow Creek (1303 to 3265 m from the Quartz Lake inlet). The confluence of Quartz and Rainbow creeks is at 1303 m

(Fig. 4). The presumed last date of spawning was preceded by 2 days of inclement weather that precluded sampling, but previous surveys indicated that spawning activity was decreasing.

The number of new redds observed varied with time; however, there was no apparent longitudinal relationship between the number of new redds and the distance from Quartz Lake (i.e., there was not a positive relationship between the date of redd detection and distance upstream from Quartz Lake; Fig. 5). Ninety-eight percent of all redds (91 of 93) were located in lower Quartz and Rainbow creeks; lower Quartz Creek contained 65 % of the redds (61 of 91) detected in these two segments (Table 2; Fig. 6). Only two redds were

Fig. 3 Length-frequency histogram of subadult bull trout sampled within the Quartz Lake drainage

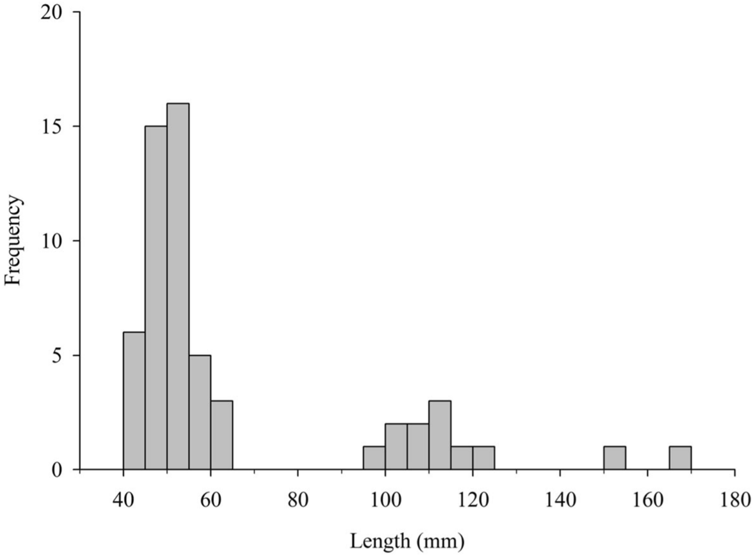

Table 3 Subadult bull trout presence model rank, model number, Akaike's Information Criterion adjusted for small sample size (AIC_c), AIC_c difference (ΔAIC_c), Akaike weight (w_i), and evidence ratio (w_1/w_j) for comparing models used to examine abiotic effects on subadult bull trout occurrence in the Quartz Lake drainage

Rank	Model	Explanatory variables in model	AIC_c	ΔAIC_c	w_i	w_1/w_j
1	4	Unit type, gradient, coarse substrate, width	113.66	0.0	0.48	
2	8	Unit type, gradient, width	114.35	0.69	0.34	1.41
3	2	Unit type, gradient, coarse substrate, width, woody debris	115.61	1.95	0.18	2.67

located in upper Quartz Creek. Fourteen redds were observed within about 450 m from the outlet of Cerulean Lake; spawning activity had not been documented in Rainbow Creek near the outlet of Cerulean Lake prior to this study (Fig. 6). All bull trout redds were observed in main-stem habitat (i.e., redds were not observed in side channel habitat).

Stream gradient of lower Quartz and Rainbow creeks was inferred based on the change in redd elevation associated with the distance from Quartz Lake (Fig. 6). Stream gradient varied from the Quartz Lake inlet upstream to the outlet of Cerulean Lake, and redds were more abundant in low stream gradient areas, including lower Quartz Creek (0 to 1300 m) and Rainbow Creek near the outlet of Cerulean Lake (about 2800 to 3200 m; Fig. 6). Conversely, fewer redds were observed in areas of high stream gradient (e.g., Rainbow Creek from about 1500 m to 2800 m; Fig. 6).

Table 4 Subadult bull trout presence model rank, model number, model parameters, parameter estimates, parameter estimate standard errors, and model R^2 values used to examine the relationship between subadult bull trout presence and physical habitat characteristics in the Quartz Lake drainage. The composite model includes model parameter, model averaged parameter estimate, and unconditional standard error (SE) for each model averaged parameter estimate

Rank	Model	Model parameter	Parameter estimate	SE	R^2
1	4	Intercept	0.02	1.37	0.21
		Unit type = slow water	0.08	0.53	
		Gradient	−3.09	11.67	
		Coarse substrate	−0.02	0.05	
		Width	0.31	0.11	
2	8	Intercept	−1.96	0.74	0.17
		Unit type = slow water	0.38	0.50	
		Gradient	−8.60	11.11	
		Width	0.27	0.10	
3	2	Intercept	−0.47	1.58	0.21
		Unit type = slow water	0.02	0.54	
		Gradient	−1.76	11.93	
		Coarse substrate	−0.02	0.02	
		Width	0.33	0.11	
		Woody debris	0.01	0.02	
		Model parameter	Model averaged parameter estimate	Unconditional SE	
Composite model		Unit type = slow water	0.17	0.54	
		Gradient	−4.72	11.87	
		Coarse substrate	−0.02	0.01	
		Width	0.30	0.11	
		Woody debris	0.01	0.02	

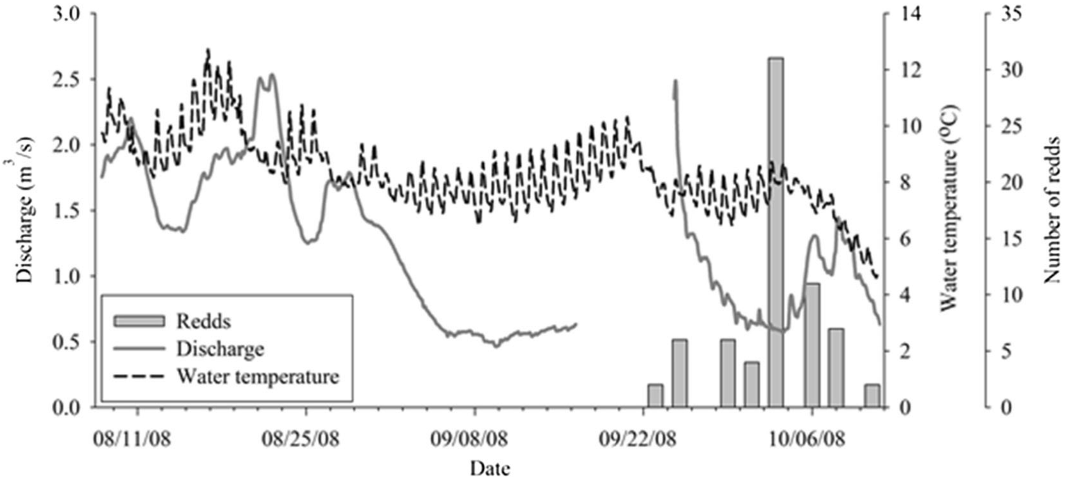

Fig. 4 Discharge (*gray line*), water temperature (*dashed line*), and number of new bull trout redds (*gray bars*) in the Quartz Creek redd survey index reach upstream of Quartz Lake

Discussion

Physical habitat characteristics associated with spawning and rearing of lacustrine-adfluvial bull trout in the Quartz Lake drainage were generally similar to those exhibited by bull trout occupying larger, or more spatially extensive, lake-stream networks. In the present study, subadult bull trout presence was positively related to slow water habitat units and habitat unit maximum wetted width, and negatively related to stream gradient and coarse substrate. Similar relationships have been observed in other studies. For example, in the Clearwater River drainage, subadult bull trout were generally associated with low water velocities (Spangler and Scarnecchia 2001), and in the Flathead River system, subadult bull trout used pools more frequently than runs, riffles, or pocket water (Fraley and Shepard 1989). Similarly, bull trout presence was positively related to channel width and negatively related to gradient in the Bitterroot River drainage (Rich et al. 2003). Subadult bull trout are also reported to have a positive relationship with coarse substrates (Shepard

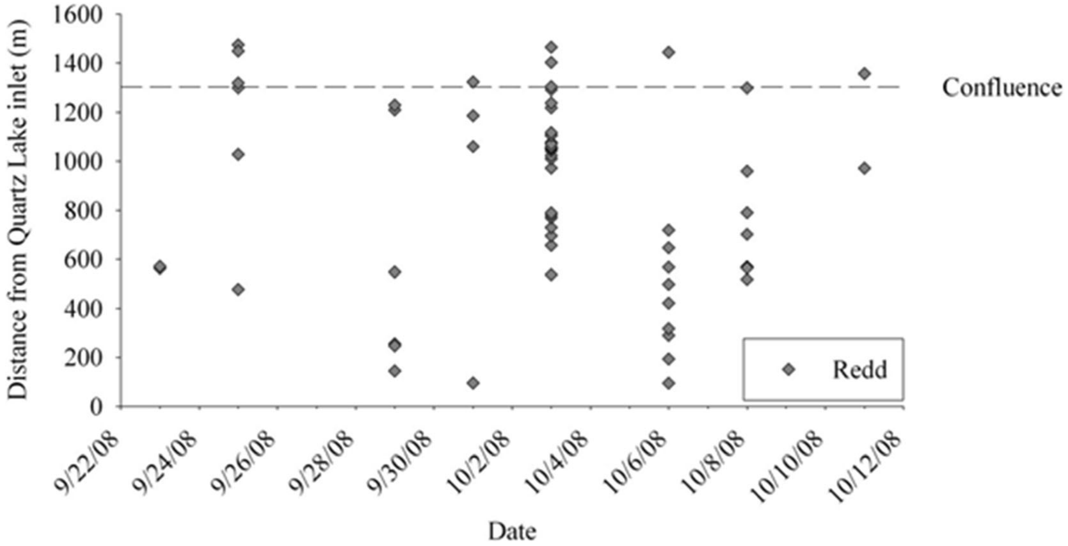

Fig. 5 Distance of each bull trout redd (*gray diamonds*) from the Quartz Lake inlet and its associated date of detection in the Quartz Creek redd survey index reach upstream of Quartz Lake. The confluence of Quartz and Rainbow creeks is at 1303 m

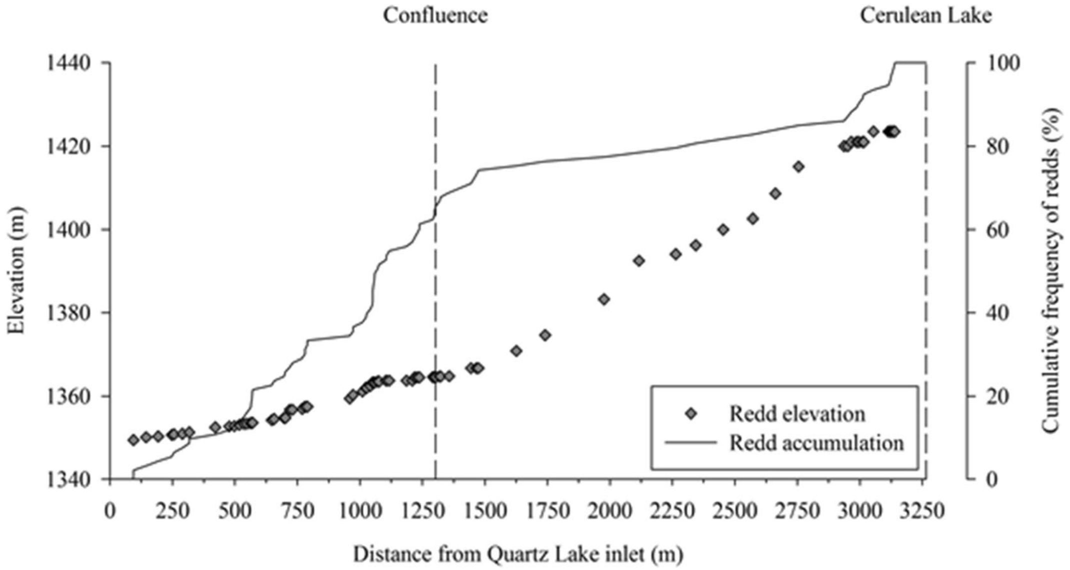

Fig. 6 Elevation of each bull trout redd (*gray diamonds*) and cumulative frequency of redds (*solid line*) in lower Quartz Creek (0 to 1303 m from the Quartz Lake inlet) and Rainbow Creek (1303 to 3265 m from the Quartz Lake inlet). The confluence of Quartz and Rainbow creeks is at 1303 m and the Cerulean Lake outlet is at 3265 m

et al. 1984; Watson and Hillman 1997; Spangler and Scarnecchia 2001). However, in the present study coarse substrate was negatively associated with subadult bull trout presence. This difference may be related to the way coarse substrate was summarized for the purpose of model simplicity as the sum of percent gravel, cobble, and boulder, which may mask untested relationships between subadult bull trout presence and individual substrate types.

Three statistical models were identified as having the greatest support; however, these models explained a relatively small proportion of the variability in subadult bull trout presence at the habitat unit scale. Habitat units were partitioned into three stream segments and many of the physical habitat characteristics were collected at the habitat unit scale. Stream habitat interacts across multiple spatial scales (e.g., habitat unit, stream reach, and stream segment) and likely influences fish distribution and occurrence (Watson and Hillman 1997; Sindt et al. 2012). Therefore, measuring physical habitat characteristics at a single spatial scale may result in poor predictive performance of statistical models because they are not representative of scale-dependent processes and interactions. Additional insight and model refinement might be gained from a study that samples multiple headwater lake-stream bull trout populations. This type of study would increase the number of habitat units sampled and allow for analysis of the relationships between subadult bull trout presence and physical habitat characteristics across multiple spatial scales by increasing the number of stream reaches, segments, and basins sampled. Although, imperfect detection may have also influenced model performance (e.g., MacKenzie et al. 2006) and should be estimated in future studies, it has been suggested that single-pass backpack electrofishing without the use of blocknets is adequate for assessing patterns in the spatial distribution of trout (Bateman et al. 2005).

Bull trout spawning occurred in the Quartz Lake drainage when water temperatures were between 5 and 9 °C, but there were periods prior to the initiation of spawning when water temperature temporarily decreased below 9 °C for several days. Stream discharge data were temporarily unavailable when spawning activity was first observed, but there was an apparent increase in stream discharge during the period when spawning commenced. These findings are consistent with previous studies that suggest the initiation of spawning is related to a complex interaction of photoperiod, stream discharge, and water temperature (Fraley and Shepard 1989; Brenkman et al. 2001).

Bull trout redds were present throughout the Quartz Lake drainage, but the highest number of redds were observed in lower Quartz Creek, Rainbow Creek near the outlet of Cerulean Lake, and near the Quartz Creek and Rainbow Creek confluence. These areas were characterized by high percentages of gravel and cobble substrates and relatively low stream gradient. Similarly, bull trout throughout the Flathead River drainage spawn in areas characterized by gravel substrate, low compaction, and low gradient (Fraley and Shepard 1989). Groundwater exchange also appears to have an important role in bull trout spawning site selection (Baxter and Hauer 2000), and egg and fry survival (Baxter and McPhail 1999; Bowerman 2013), and spawning sites in the Flathead River drainage are generally located close to cover in areas with groundwater influence (Fraley and Shepard 1989). Although groundwater influence was not measured in this study, it likely affects bull trout selection of spawning sites in the study area.

Upper Quartz Creek was also characterized by high percentages of gravel and cobble substrate, but only two redds were observed in this stream segment. A large portion of the stream channel appeared to be recently affected by flood or debris flow, and a new channel was developing. In 2004, redds were observed in an old stream channel adjacent to the current active channel (Meeuwig and Guy 2007). If the recent disturbance is related to a reduced level of bull trout spawning activity in upper Quartz Creek, spawning may increase as the new channel stabilizes in the future. Alternatively, high stream discharge events may have obscured redds that were constructed before surveying upper Quartz Creek; however, relatively high discharge events that occurred in September (Fig. 4) did not appear to be sufficient to scour lacustrine-adfluvial bull trout redds in the index reach.

The present study elucidated three characteristics of bull trout biology that are not well documented in the literature, but that may be relatively widespread and have important implications regarding general characteristics of bull trout ecology, use of available habitat by bull trout, and persistence of lacustrine-adfluvial bull trout. Specifically, bull trout in headwater lake-stream ecosystems may not be required to make extensive spawning migrations if suitable spawning habitat is spatially proximate, subadult bull trout may emigrate from streams to lake environments at early ages, and bull trout and westslope cutthroat trout may exhibit habitat partitioning or density dependent habitat use over small spatial extents.

Spawning and rearing data from the current study and a previous population genetic assessment (Meeuwig et al. 2010) suggest that lacustrine-adfluvial bull trout in Quartz and Cerulean lakes spawn and rear in tributaries close to the lakes despite the lack of passage barriers downstream from Quartz Lake that would prevent movement into or out of the system (see Meeuwig et al. 2008). The construction of a partial barrier to upstream movement (ca. 2004) and a completion of this putative barrier to upstream movement (ca. 2012) on Quartz Creek downstream from Quartz Lake currently limits upstream movement into the study area by bull trout and other fishes from downstream sources (Downs et al. 2015). However, population genetic characteristics that were assessed based on sampling conducted in 2004 through 2006 (Meeuwig et al. 2010), results of previous fisheries surveys (Meeuwig and Guy 2007), and results presented here within (field surveys conducted in 2008) were not likely influenced by the constructed barrier. The life history variation displayed by bull trout in the Quartz Lake drainage is likely common among bull trout occupying headwater lakes associated with relatively small stream networks that have suitable spawning and rearing habitat, but it has rarely been explicitly discussed in the literature. Brenkman et al. (2001) noted spawning migrations of less than 6 km for lacustrine-adfluvial bull trout in the Lake Cushman-North Fork Skokomish River system. Additionally, they noted a shorter-duration spawning season relative to other populations of lacustrine-adfluvial bull trout, and suggest that understanding life history variation in bull trout associated with local environmental conditions is essential for development of appropriate management and conservation strategies.

The advantages of short spawning migrations are potentially numerous. Energetic benefits may occur because adult bull trout would likely not require energy stores for migration and could instead use reserve energy for gamete production, mate selection, or redd construction. Short-distance spawning migrations may also limit exposure to avian and mammalian predators that feed in stream corridors. Additionally, barring local catastrophic extinction events, life histories that require small home ranges may be more likely to persist than life histories that require vast, unfragmented home ranges given current land-management activities. Conversely, localized disturbances and changes to disturbance regimes may have a greater effect on populations that exhibit small home ranges relative to populations that occupy more spatially extensive or diverse habitats. Therefore, in order to conserve life history variation special conservation measures may be needed to mitigate against anthropogenic perturbations that may fragment or contract already limited habitat occupied by some lacustrine-adfluvial bull trout populations (Rieman and McIntyre 1995; Rieman et al. 1997).

Subadult bull trout may also benefit from being spawned in close proximity to potentially productive lake habitats. The majority of subadult bull trout in the Quartz Lake drainage appear to emigrate from natal tributaries before age 2. Length-frequency data suggest that two distinct age classes of subadult bull trout (most likely age 0 and age 1) were present at the time of sampling, and only two individuals with total lengths of 151 and 167 mm appear to be older than age 1. In the larger streams of the Flathead River drainage, subadult bull trout remain in tributaries for 1–3 years before emigrating to main-stem habitats of the Flathead River (Fraley and Shepard 1989). However, early emigration from low productivity natal streams to other relatively high productivity habitats is common among salmonids. For example, coho salmon *O. kisutch* exhibit early life history variation that includes migration to productive estuarine habitats at age-0 (Jones et al. 2014), and the "lake-type" of sockeye salmon *O. nerka* and kokanee migrate from streams to lake environments almost immediately after emergence (Quinn 2005). Additionally, Yellowstone cutthroat trout *O. c. bouvieri* fry from most of the smaller tributaries to Yellowstone Lake migrate into the lake within a few weeks of emergence, but in larger, more complex tributary drainages, some individuals remain for 1–3 years (Gresswell et al. 1997). Harsh winter conditions, such as anchor ice, that can limit the amount of available winter rearing habitat (Jakober et al. 1998) could also promote early emigration from natal tributaries.

Thousands of age-0 bull trout have been shown to emigrate annually from Trestle Creek, a spawning tributary to Lake Pend Oreille, Idaho, but data suggest that none of these individuals returned to spawn (Downs et al. 2006). For bull trout, lack of recruitment to the adult population by age-0 emigrants may represent some form of compensatory mortality; however, selection against this life history is likely. Therefore, an alternative explanation is that current environmental conditions may reduce survival of early life history emigrants. For example, many western lakes occupied by lacustrine-adfluvial bull trout have been invaded by, or intentionally stocked with nonnative fishes, such as lake trout *S. namaycush*, and these nonnative species have the potential to alter food webs, and prey on or compete with bull trout at various life history stages (Martinez et al. 2009). Modeling conducted by Ferguson et al. (2012) indicates that coexistence of native bull trout and nonnative lake trout is most dependent on the age at which subadult bull trout emigrate from natal tributaries. Consequently, if subadult bull trout emigrate from natal tributaries earlier than age 2, both predatory and competitive age structure models predict further declines in bull trout abundance, potentially to the point of extirpation (Ferguson et al. 2012). These findings could have negative implications in Quartz Lake where lake trout were discovered in 2005 and the data presented here suggest that the majority of subadult bull trout emigrate before age 2.

In addition to short distance migrations and potential early subadult migration, subadult bull trout and westslope cutthroat trout appear to partition habitat or exhibit density dependent habitat selection in the Quartz Lake drainage. The native distributions of bull trout and westslope cutthroat trout overlap, and westslope cutthroat trout occur sympatrically with bull trout in portions of the Flathead River drainage in northwest Montana (Fredenberg 1997). Evaluation of cumulative frequency data for both species lower Quartz Creek and Rainbow Creek suggests that the abundance of these species may be negatively related. For example, the majority of subadult bull trout sampled occupied habitat units in lower Quartz Creek, but the majority of westslope cutthroat trout sampled occupied habitat units in Rainbow Creek. Therefore, this may be indicative of habitat partitioning or variability in use of particular microhabitats by each species at a stream segment scale.

This study has yielded novel insights concerning spawning and rearing of bull trout in a headwater lake ecosystem. Moreover, it has expanded the understanding of the adaptive capacity of bull trout by providing additional examples of adaptation to the broad variety of systems where the species persists. This may be especially important given the continued fragmentation of habitats in the historic range of bull trout related to land-management activities. Understanding the adaptive capacity associated with the life history variation of a species is critical to adequately accommodate and manage for its persistence. In the Quartz Lake drainage, and other locations where bull trout make spatially restricted spawning migrations, enhanced protection for the limited spawning and rearing habitat currently used by lacustrine-adfluvial bull trout may be warranted. Additionally, further studies should evaluate the effects of emigration age or size on susceptibility of subadult bull trout to novel predators to understand interactions between bull trout and nonnative piscivores more completely.

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