

Factors affecting habitat selection by a small spawning charr population, bull trout, *Salvelinus confluentus*: implications for recovery of an endangered species

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Abstract Bull trout, *Salvelinus confluentus* (Suckley), populations are declining in many streams of North America and are listed under the Endangered Species Act in the United States. Many small populations are isolated in fragmented habitats where spawning conditions and success are not well understood. Factors affecting habitats selected for redds by spawning bull trout and redd habitat characteristics within Gold Creek, a headwater stream in the Yakima River within the Columbia River basin, Washington State, USA, were evaluated. Most spawning (> 80% of the redds) occurred in upstream habitats after dewatering of downstream channels isolated fish. Habitats were selected or avoided in proportions different to their availability. For example, most bull trout selected pools and glides and avoided riffles despite the latter being more readily available. Although preferences suggest influences of prolonged fish entrapment, site fidelity could be important. A habitat with redds commonly contained abundant cover, gravel substratum and higher stream flows. The major factors influencing habitat selection by spawning fish and their persistence in streams of the Yakima and Columbia River regions include entrapment of fish by dewatering of channels and geographical isolation by dams. The goal of the US Government's recovery plan is 'to ensure the long-term persistence of self-sustaining bull trout populations'. Recovery plans linked to provisions for protecting and conserving bull trout populations and their habitats were recommended. Landscape approaches are needed that provide networks of refuge habitats and greater connectivity between populations. Concurrent recovery efforts are encouraged to focus on protecting small populations and minimizing dangers of hybridization.

KEYWORDS: bull trout, habitat selection, *Salvelinus confluentus*, spawning, redds.

Introduction

Bull trout, *Salvelinus confluentus* (Suckley) populations are declining in many streams throughout the species range in the Pacific Northwest and western Canada (Mackay, Brewin & Monita 1997; US Fish and Wildlife Service 1997, 2002). Many populations are isolated in fragmented habitats of degraded catchments where they face considerable risk of extirpation (Howell & Buchanan 1992; Rieman & McIntyre 1995).

Conditions of these populations and habitats are not well known. For example, inventories of bull trout stocks in streams throughout Washington State indicated the lack of data for spawning population densities, redd numbers and habitat characteristics (Washington Department of Fish and Wildlife 1998). Other shortcomings include minimal information about factors affecting habitat selection by spawning bull trout (Boag & Hvenegaard 1997; Baxter & Hauer 2000).

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The objective of this investigation was to evaluate factors affecting habitat selection for redds by spawning bull trout, redd habitat characteristics and the distribution of redds and fish within Gold Creek, a headwater stream in the Yakima River drainage of Washington State, USA. The bull trout stock of Gold Creek was designated as critical by the Washington Department of Fish and Wildlife (1998) prior to being listed by the Federal Government. Bull trout are listed throughout the native range in the United States as threatened under the Endangered Species Act (US Fish and Wildlife Service 1999).

In Washington State, the status of some bull trout stocks were identified in regions of western Washington and the Columbia River basin (Washington Department of Fish and Wildlife 1998). The Gold Creek catchment and the Yakima River drainage lie within the upper Columbia River region, an area above Bonneville Dam and east of the Cascade Mountains. The status of 50 bull trout stocks in the upper Columbia River region includes nine healthy, one depressed (below expected production levels), six critical (loss of genetic diversity or risk of extinction) and 34 unknown because of inadequate information. Stock status in the Yakima River drainage includes one healthy, one depressed, one unknown and all six critical stocks of the upper Columbia River region. The large number of critical and unknown stocks in the upper Columbia region emphasizes the need for better information about fish populations and habitats.

Materials and methods

Study area

The Gold Creek catchment (36 km²) originates in the Cascade Mountains (elevation 2111 m) and flows 13 km before entering Keechelus Lake (elevation 767 m, area 10.5 km²) within the Yakima River drainage (15 941 km², Kittitas County, Washington) (Fig. 1). The Yakima River flows into the Columbia River 650 river km upriver from the Pacific Ocean. Gold Creek contains the only habitat used for spawning by bull trout that inhabit Keechelus Lake (Washington Department of Fish and Wildlife 1998). Bull trout spawn and recruit in Gold Creek and adults reside in Keechelus Lake where they find ample forage (Goetz 1997a,b).

During the past hundred years, bull trout in Gold Creek and Keechelus Lake have been exposed to various water and land uses. In 1911, they were isolated in these headwaters when the US Bureau of Reclamation raised the level of Keechelus Lake to

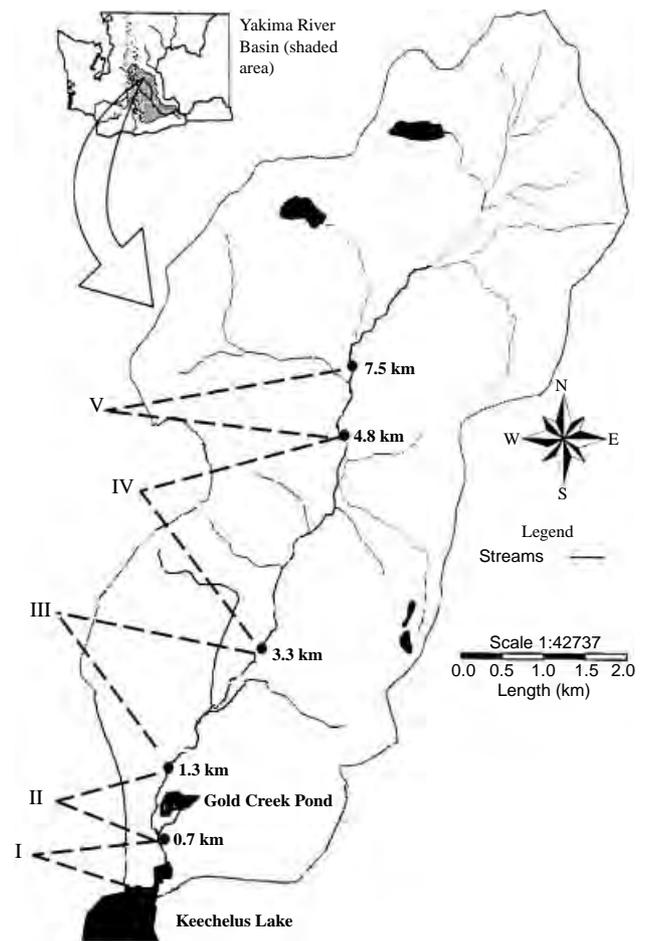


Figure 1. Location of Gold Creek, a tributary to Keechelus Lake in the headwaters of the Yakima River, Washington. Gold Creek originates on the eastern side of the Cascade Mountains of central Washington (86 km east of Seattle).

create a reservoir. Other historical modifications and impacts to fluvial systems in the Yakima River drainage included mining, timber harvest, railway and highway construction, and the creation of dams on all major tributaries (Prater 1981; US Fish and Wildlife Service 2002).

Habitat selected for redds

Habitats selected or avoided by bull trout for establishing redds and probable redds were evaluated using electivity indices (Baltz 1990). Electivity indices (D) were calculated as:

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

where r is the per cent habitat used by spawning bull trout and p the mean proportion of a habitat type

available within a reach. The per cent habitat used for spawning, r , represents the number of redds for a specific habitat type relative to the total number of habitat types within a reach. Electivity indices (D) were described as: strong avoidance (-0.50 to -1.00) moderate avoidance (-0.49 to -0.26), neutral (-0.25 to 0.25), moderate selection (0.26 to 0.49), and strong selection (0.50 to 1.00) (Matthews 1996). Electivity indices were also calculated for probable redds.

Habitat measurements

Habitat types (riffle, pools and glides) were identified within main (M) and side (S) channels of five reaches (I to V) of Gold Creek that span elevations ranging from 767 to 930 m. Reach lengths were identified by major changes in channel gradients. Respective lengths and mean channel gradients for the five reaches were: (I) 0–0.7 km and 0.5%; (II) 0.7–1.3 km and 1.1%; (III) 1.3–3.3 km and 1.2%; (IV) 3.3–4.8 km and 1.6%; and (V) 4.8–7.5 km and 2.7% (Fig. 1). Channel gradients upstream of reach V frequently exceeded 6% with cascades forming barriers to bull trout migration. Channel dimensions and gradients were measured with a laser optic level-stadia rod (Model: Laser-Plane 300). Habitat types, abundances and characteristics (e.g. large wood and streambed substrate sizes) were assessed for each reach using procedures based on Hankin & Reeves (1988). Large woody debris (LWD, diameter > 30 cm) was enumerated as pieces 100 m^{-1} . Dominant substratum was estimated within four size categories (sand < 2 mm, gravel 2–65 mm, cobble 65–254 mm, and boulders > 254 mm).

Stream discharge was estimated weekly at four cross-section sites on the main channel (0.7, 1.3, 3.3 and 4.8 km). Velocity was measured using a Swoffer flow meter (Swoffer Instruments Inc., Seattle, WA, USA). Velocities, widths, depths and areas at cross-sections were used to estimate discharge rates. Daily discharge rates (cm day^{-1}) were calculated by normalizing discharge rates by the sub-drainage area for each reach within the watershed (Dunn & Leopold 1978). Mean daily rates (cm day^{-1}) were used to develop a daily rainfall–runoff relationship for the July to October period (1993 and 1994). Precipitation records (cm day^{-1}) were from the Stampede Pass Weather Station located 4 km south-east of the Gold Creek catchment (National Water and Climate Center, Portland, OR, USA). Water temperatures was recorded (Hobo[®], Onset Computer Corporation, Bourne, MA, USA) at four channel locations (0.7, 1.3, 3.3 and 4.8 km).

Redd and fish measurements

Bull trout redds and probable redds were counted during weekly surveys of Gold Creek channels. Bull trout redds were described as depressions excavated by spawning fish and well-defined tailspill areas (Bjornn & Reiser 1991). Probable redds were identified as areas showing fish excavation activity but without tailspills. No attempts were made to uncover eggs because of the high-risk status of the population. After a spawning site was located, redds and probable redds were recorded relative to habitat type and location. Habitats that contained redds were described by redd areas, channel gradients, wetted channel widths, streambed substrates, mean current velocities and mean depth of water columns beneath cover types (e.g. LWD and boulders).

Identification of bull trout was according to the taxonomic characteristics of Haas & McPhail (1991). Weekly counts were conducted in Gold Creek of the number of bull trout and other major fish species by snorkelling and streamside observations from July to October. These surveys were used to evaluate the mean number of fish present within bull trout spawning habitats. Mean numbers represent weekly counts of fish downstream (reaches I and II) and upstream (reaches III, IV and V) channels.

Results

Habitats selected for redds

Mean proportions for habitat availability (p) indicated that riffles in M-channels were most available in reaches IV and V (0.65 and 0.56, respectively) and ranged from 0.16 to 0.53 in reaches I through III. Riffles were less available in S-channels, ranging from 0.02 to 0.14 in all five reaches. Pool availability was greatest in M-channels of reach III (0.26) and in S-channels of reach I (0.30). Lower pool availabilities occurred in M- and S-channels within the other reaches (range 0.02–0.14). The availability of glide habitats was greatest in M and S-channels (0.20) of reach I and ranged from 0.01 to 0.13 in the other reaches.

In 1993 and 1994 the maximum number of adult bull trout observed in Gold Creek during spawning seasons (July to October) were 24 and 29 fish, respectively. Major portions of these populations, > 71% in 1993 and > 84% in 1994, resided upstream in habitats of reach V after they were isolated by the loss of water in channels of reach II during drought periods. Reach II was dry from 12 August to 8 November in 1993 and

during two periods in 1994 (21 July to 14 September and 16 September to 18 October).

Bull trout established a total of 11 redds and six probable redds in 1993 and 14 redds and two probable

redds in 1994 (Tables 1 and 2). The majority of the redds were placed in habitats of reach V, 82% in 1993 and 86% in 1994, after bull trout were isolated by dry channels.

Table 1. Bull trout selection or avoidance of habitats for establishing redds and probable redds (P. redds) within Gold Creek during 1993. Habitats selected or avoided by bull trout were evaluated using electivity indices (D)*. Habitat units include riffles, pools and glides within main (M) and side (S) channels

Reach	Channel types	Habitat		Redds (n)	P. redds (n)	Habitat availability (p)*	Proportion of Habitat used (r)*		Electivity indices (D)	
		Unit	n				Redds	P. redds	Redds	P. redds
I	M	Riffle	22			0.16				
	S		2			0.02				
	M	Pool	20	2		0.11	0.1		-0.05 (N)	
	S		18			0.30				
	M	Glide	11			0.20				
	S		9			0.20				
V	M	Riffle	28	3	1	0.56	0.11	0.04	-0.82 (SA)	-0.94 (SA)
	S		4	2	3	0.14	0.50	0.75	0.72 (SS)	0.90 (SS)
	M	Pool	14	1	1	0.07	0.07	0.07	0.00 (N)	0.00 (N)
	S		3			0.04				
	M	Glide	17	3	1	0.13	0.18	0.06	0.19 (N)	-0.40 (MA)
	S		3			0.03				

* Electivity indices calculated as: $D = r - p/(r + p) - 2rp$ where r is the per cent habitat used by spawning bull trout and p is the mean proportion of each habitat type available within a reach. Ranges of D values: -0.50 to -1.00 = strong avoidance (SA); -0.49 to -0.26 = moderate avoidance (MA); -0.25 to 0.25 = neutral (N); 0.26 to 0.49 = moderate selection (MS); and 0.50 to 1.00 = strong selection (SS).

Table 2. Bull trout selection or avoidance of habitats for establishing redds and probable redds (P. redds) within Gold Creek during 1994. Channel types include main (M) and side (S) channels

Reach	Channel types	Habitat		Redds (n)	P. redds (n)	Habitat availability (p)*	Proportion of habitat used (r)*		Electivity indices (D)	
		Unit	n				Redds	P. redds	Redds	P. redds
I	M	Riffle	22			0.16				
	S		2			0.02				
	M	Pool	20	1		0.11	0.05		-0.40 (MA)	
	S		18			0.30				
	M	Glide	11			0.20				
	S		9			0.20				
IV	M	Riffle	23			0.65				
	S		9			0.11				
	M	Pool	14			0.11				
	S		2			0.03				
	M	Glide	6	1		0.12	0.17		0.20 (N)	
	S		1			0.02				
V	M	Riffle	28	4		0.56	0.14		-0.77 (SA)	
	S		4	1	1	0.14	0.25	0.25	0.34 (MS)	0.34 (MS)
	M	Pool	14	3	1	0.07	0.21	0.07	0.56 (SS)	0.00 (N)
	S		3			0.04				
	M	Glide	17	4		0.13	0.24		0.36 (MS)	
	S		3			0.03				

* See Table 1 for electivity indices (D).

In 1993, spawning bull trout in reach V showed the strongest selection for riffles within S-channels (electivity indices of 0.72 for two redds and 0.90 for three probable redds) (Table 1). In M-channels there were no preferences for riffles (indices of -0.82 for three redds and -0.94 for one probable redd). Neutral values were observed for pools (0.00 for one redd and a probable redd) and glides (0.19 for three redds). Moderate avoidance (-0.40) was evident for a glide with one probable redd. The remaining redds in Gold Creek were in reach I where neutral values occurred for pools of M-channels (-0.05 for two redds).

In 1994, electivity indices for reach V indicated bull trout once again avoided riffles (-0.77 for redds) in M-channels while being moderately selective for riffles in S-channels (0.34 for one redd and one probable redd) (Table 2). However, fish appeared to prefer pools and glides in M-channels. Indices for pools indicated strong selection for placing redds (0.56) and neutral for probable redds (0.00) and for glides moderate selection (0.36 for redds). During the last 2 weeks of September 1994, moderate avoidance was observed for one redd (-0.40) within a pool of reach I and neutral for one redd (0.20) in a glide of reach IV (Table 2).

Patterns of fish placement of redds in habitats of reach V were similar during 1993 and 1994. During both years, habitat types were selected or avoided in different proportions than their availability. A summary of habitat availability and electivity indices (mean values for 1993 and 1994) in M-channels of reach V indicates bull trout avoided riffles (-0.80) within M-channels during both years even although riffles displayed the highest availability (Fig. 2). The high riffle availability in reach V reflects the large total riffle area (5583 m^2) in M-channels compared with smaller areas for other habitats (range from $45\text{--}999 \text{ m}^2$) in M- and S-channels.

In contrast to the avoidance of riffles, mean electivity indices for pools and glides in M-channels were both 0.28, representing neutral to strong selection (Fig. 2). Respective pool and glide habitat availability in M-channels (0.07 and 0.13) were considerably lower than the riffle availability (0.56). The selection of pool and glide habitats for redd placements occurred where greater amounts of LWD were present (range of mean densities were $1.3\text{--}6.5 \text{ LWD pieces } 100 \text{ m}^{-1}$). LWD densities were over four times lower in riffles (mean $0.3 \text{ LWD pieces } 100 \text{ m}^{-1}$).

Habitats in S-channels were also selected or avoided in proportions different to their availability. Spawning bull trout preferred riffles (mean electivity 0.53) where riffle availability was low (0.14) (Fig. 3). The high

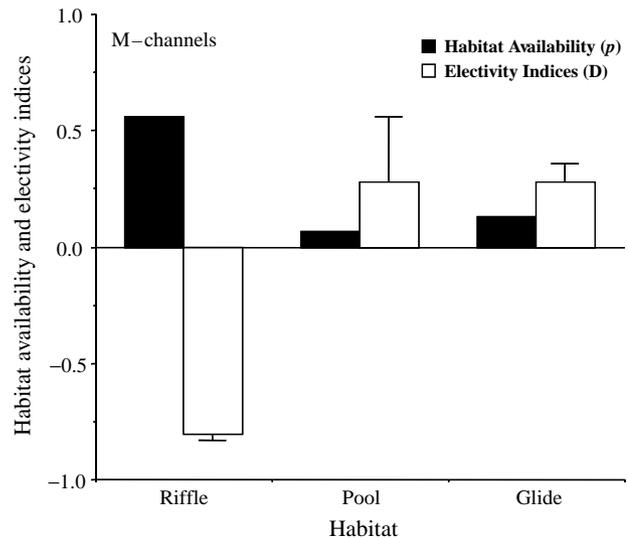


Figure 2. Mean habitat availability and electivity indices for bull trout placement of redd sites within habitats of main channels (M-channels) of reach V during 1993 and 1994. Mean values (and SD) are for riffle, pool and glides habitats. SD is the standard deviation of the mean. Open bars indicate electivity indices and shaded bars indicate habitat availability. Negative electivity denotes avoidance of habitat.

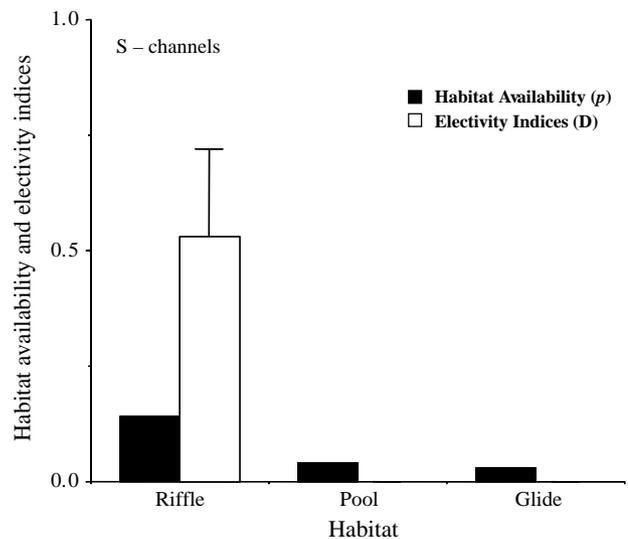


Figure 3. Mean habitat availability and electivity indices for bull trout placement of redd sites within habitats of side channels (S-channels) of reach V during 1993 and 1994. Mean values (and SD) are for riffle, pool and glides habitats. SD is the standard deviation of the mean. Open bars indicate electivity indices and shaded bars indicate habitat availability.

electivity for riffles occurred where more habitat cover was present in S-channels. Riffles in S-channels had more large wood (mean $5.4 \text{ LWD pieces } 100 \text{ m}^{-1}$) and

boulders than riffles in M-channels. No redds were established in pools and glides of S-channels.

Mean redd areas for riffle, glide and pool habitats of reach V ranged from 1.6 to 2.4 m². Habitats containing redds showed mean channel gradients ranging from 0.9 to 2.4% and wetted widths ranging from 4.7 to 7.1 m. Riffles with redds showed the steepest channel gradients, the smallest mean wetted widths and the largest percentage of gravel substrates. Dominant substratum within redd pits and tailspill areas was gravel (82–97%). Mean current velocities at redd locations ranged from 9.1 to 16.5 cm s⁻¹ and mean depths beneath cover types from 0.4 to 1.0 m. A habitat with redds commonly had considerable cover as a result of LWD, boulders and turbulence. Water temperatures when fish were spawning ranged from 9 ° to 11 °C.

Bull trout mortality

Bull trout mortalities relative to the total number of adult fish in 1993 (24 fish) and 1994 (29 fish) were 63 and 24%, respectively. Mortalities were primarily caused by stranding in dry channels at the upstream end of reach II. Carcass fork length ranged from 470 to 550 mm. The upstream isolation of spawning bull trout and fish mortalities during the dewatering of reach II coincided with low rainfall during 1993 and 1994. A daily rainfall–runoff relationship for July to October (1993 and 1994) indicated low rainfall explained much of the variation in low stream flows ($r^2 = 0.60$, $n = 15$).

Other fish species

The mean number of other large-sized fish species (>130 mm in length) present with bull trout (>300 mm in length) in downstream (reaches I and II) and upstream (reaches III, IV and V) channels were estimated from weekly counts from July to October 1994. Four fish species occurred with bull trout: cutthroat trout, *Oncorhynchus clarki* (Richardson), brook trout, *Salvelinus fontinalis* (Mitchill), whitefish, *Prosopium williamsoni* (Girard), and kokanee, *Oncorhynchus nerka* (Walbaum). During this period, these fish were distributed differently downstream and upstream. Downstream, the mean number of bull trout was 3 (SD 3). Low values were also observed for brook trout (three fish, SD 3), cutthroat trout (five fish, SD 5) and whitefish (18 fish, SD 11). Kokanee (568 fish, SD 150) were present downstream but only during the last 4 weeks of the bull trout spawning season (mid-September to mid-October). Upstream of reach II, bull trout (nine, SD 3) and

cutthroat trout (20, SD 12) were the only fish species present.

Discussion

A majority of the habitats selected for placement of redds by spawning bull trout in Gold Creek during 1993 and 1994 occurred after the fish were isolated upstream by drying of downstream channels during drought periods. Consistent patterns of redd placements revealed habitat types were selected or avoided in different proportions than their availability. Although habitat preferences suggest influences of prolonged fish entrapment by blocked channels, site fidelity by spawning fish could be important. For instance, a habitat with redds commonly contained abundant cover, gravel substrates and higher stream flows. These redd habitat characteristics were similar to those observed in other streams of the Pacific Northwest and Canada (Mackay *et al.* 1997; Baxter, Frissell & Hauer 1999).

At the catchment and large regional scales, the major physical factors influencing habitat selection by spawning fish and the species persistence appeared to be entrapment of fish by dewatering of channels and geographical isolation by dams. A regression analysis of long-term data, US Fish and Wildlife Service (2002) records for annual redd counts in Gold Creek and precipitation data (1992–2001) (Stampede Pass Weather Station, National Water and Climate Center, Portland, OR, USA), indicated a direct relationship between redd count and annual precipitation rates ($r^2 = 0.51$). The annual mean redd count for 1992–2001 was low (25 redds, SD 14). Impacts of channel dewatering on spawning bull trout populations in other tributaries of the Yakima River were reported by Craig (1997), Washington Department of Fish and Wildlife (1998) and Meyer (2002). Observations for streams in northern Idaho and northwest Montana also showed that the timing of both low and high flows can be important to bull trout movements and annual variation in reproductive success (Rieman & McIntyre 1996; Swanberg 1997).

The long-term geographical isolation of the local bull trout population in the Gold Creek–Keechelus Lake drainage due to dam construction in 1911, and the presence of no alternative spawning areas in the drainage other than Gold Creek, could be contributing to lower genetic diversity in the population. The lack of gene flow through dispersal and recolonization by bull trout populations from outside the catchment may pose an immediate threat to the persistence of this remnant population (Rieman & Dunham 2000). A

situation similar to Gold Creek has been documented in northern Idaho. Local isolated small bull trout populations in tributaries of Lake Pend Oreille showed minimal dispersal in ways consistent with metapopulation structure and implied some populations could become extinct (Spruell, Rieman, Knudsen, Utter & Allendorf 1999). The metapopulation concept suggests a network of populations provides balance between local adaptations and evolutionary advantages (Harrison & Taylor 1996; Dunham & Rieman 1999).

Regardless of the limited distribution of redds and influences of flow and habitat conditions, several biological factors could play important roles in the persistence of bull trout in the Gold Creek. Repeat spawning (iteroparity) within the multiple age structure of a bull trout population might be very important to survival. Adult bull trout most likely spawn several times in Gold Creek, but generally not in successive years (Fraley & Shepard 1989; Pratt 1992; Conner, Reiser, Binkley, Paige & Lynch 1997; Reiser, Connor, Binkley, Lynch & Paige 1997). The fecundity of different bull trout age groups of alternating years could spread risks of poor reproduction under extreme environmental conditions (Thorpe 1994). For example, while a portion of the population is spawning in Gold Creek during low flow conditions in a drought year, different year-classes remain in Keechelus Lake. Genetic reserves of the fish in the lake might provide opportunities for more successful reproduction in subsequent years.

Concern for potential bull trout interbreeding because of the presence of non-native species in Gold Creek appeared minimal. The chances that brook trout could hybridize with bull trout (Leary, Allendorf & Forbes 1993; Kanda, Leary & Allendorf 2002) were low as most of the bull trout in Gold Creek spawned in upstream reaches where brook trout were not present. Similar observations have been made for bull trout in other streams throughout the Pacific Northwest (Watson & Hillman 1997). There is also the possibility that brook trout spawn later in the autumn within Keechelus Lake (Blanchfield & Ridgway 1997).

Competitive interactions for foraging microhabitats among bull trout, brook trout and cutthroat trout can be important factors for the regulation of bull trout densities at local scales (Nakano, Kitano, Nakai & Fausch 1998). However, competition between bull trout and these species for food and space in Gold Creek was most likely low. Adult bull trout that spent 1–2 months waiting to spawn in Gold Creek commonly have little inclination to feed (Bjornn 1991). Low densities for bull trout, brook trout and cutthroat trout suggested minimal competition for space. Short residence times of whitefish and spawning kokanee in

the downstream reach of Gold Creek indicated little competition with bull trout for space. However, competitive interactions for foraging habitats might have important influences on the densities of juvenile fish when they rear in Gold Creek.

In summary, vulnerabilities of spawning bull trout populations to combined effects of changing environmental conditions (e.g. physical and biological) and anthropogenic actions are poorly understood throughout the species range in North America (Mackay *et al.* 1997; Rieman, Lee & Thurow 1997; Neraas & Spruell 2001; US Fish and Wildlife Service 2002). The Bull Trout Draft Recovery Plan (US Fish and Wildlife Service 2002) considered the Yakima River drainage to contain core habitats important for recovery. The goal of the recovery plan is to ensure the long-term persistence of self-sustaining bull trout populations across the species native range. The plan recommended reducing factors that threaten fish populations.

Before recovery plans are implemented, it is recommended that drainages be surveyed to delineate locations, spacing and sizes of suitable habitats (e.g. spawning and rearing) (Regier, Welcomme, Stedman & Henderson 1989; Wissmar & Bisson 2003). Landscape scale investigations are needed to identify networks of refuge habitats that would increase connectivity between catchments, facilitate genetic exchanges between populations and benefit the development of diverse life histories. Field investigations are also needed to understand what biological factors allow bull trout populations to adapt and persist (e.g. habitat selection, migration behaviour, age class structure and competition). These recovery efforts should contain provisions for reducing sources of sampling errors for fish populations, redd counts and habitat measurements (Hankin & Reeves 1988; Dunham, Rieman & Davis 2001).

A primary concern in recovery plans should be avoiding bull trout hybridization with other species (Kanda *et al.* 2002). The system to be rehabilitated should be surveyed to ensure that non-native populations or species (e.g. brook trout) have not become established and cannot hybridize with the native bull trout population. In extreme situations, actions may be required that remove non-native fish and restrict their distributions.

For the small bull trout population in Gold Creek–Keechelus Lake system, and those in other streams throughout the species range, the lack of access to available spawning habitats is most likely becoming more critical as populations continue to decline. Recovery efforts should give considerable attention to small fish populations that may have reduced

genetic diversity (Reisenbichler, Utter & Krueger 2003). Where a small population occurs, managers may wish to introduce individuals of the same ancestral lineage from nearby catchments. However, before implementation of this approach, there should be convincing evidence that reduced fitness is caused by low diversity in the population. For most small populations, the prudent action would be no transfers of fish from other populations. Such introductions could compromise potentially unique genetic combinations in the native population under restoration.

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