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Dirk Renner for the degree of Master of Science in Fisheries Science presented on June 7, 2005.
Title: Distribution and Habitat Use of Bull Trout Following the Removal of Nonnative Brook Trout

Abstract approved:

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Invasion by nonnative brook trout (*Salvelinus fontinalis*) often results in replacement of bull trout (*Salvelinus confluentus*) in western North America, but the causal mechanisms are not well understood. Removal of brook trout from 1992 to 2000 from Sun Creek in southern Oregon, provided an opportunity to investigate the changes in distribution and abundance of bull trout. This study investigated bull trout distribution over from 1994 to 2003, during and following the extirpation of brook trout in 2000. In 2001 over, 8 km of contiguous stream habitat was examined to investigate bull trout habitat utilization. Bull trout abundance increased almost 300% after the removal of brook trout; however, bull trout distribution did not shift either upstream or downstream into habitat previously occupied by brook trout. This finding suggested that the occupied habitat was either critical for bull trout persistence or that factors restricted dispersal. Temperature did not appear to limit bull trout distribution remaining below 17°C with averages less than 10°C throughout Sun Creek. The downstream distribution of bull trout coincided with a point source increase of turbidity. In regions of the stream where turbidity was low bull trout abundance was positively associated with deep pools, higher average temperatures, and correlated with high densities of springs. The results of this study suggest that brook trout did not displace bull trout, underscoring the importance that point source disturbances (i.e. turbidity) can have on trout distributions. These findings reiterate the value of sampling contiguous streams as a means to identifying factors influencing trout distribution throughout a stream system.

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Distribution and Habitat Use of Bull Trout Following the Removal of Nonnative Brook Trout

By

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

DIRK RENNER

Dirk Renner, Author

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Chapter 1 - Introduction

Bull trout (*Salvelinus confluentus*) a native char of western North America were once distributed from the McCloud River in Northern California to the Yukon River in Canada. During the last 45 years bull trout have declined in abundance and distribution throughout their historic range, especially in the southern margins of the species range (Cavender 1978; Goetz 1989). In 1998, bull trout in the Klamath River and Columbia River basins were listed as threatened under the Endangered Species Act of 1973 (USFWS 1998). Declines in bull trout populations have been primarily attributed to habitat loss and the introduction of nonnative fish.

Bull trout are highly stenothermic found only where stream temperatures average less than 16° C (Buchanan and Gregory 1997; Dunham et al. 2003b). Land management practices or events (i.e. vegetation management, road construction, and climate change) that alter the thermal regime of a watershed can be detrimental to the persistence of bull trout populations (Buchanan et al. 1997). Many bull trout populations were historically potamodromous; habitat fragmentation has relegated these migratory populations to headwater streams resulting in lost gene flow and greater risk of extinction. (Goetz 1989; Buchanan et al. 1997).

Introductions of nonnative fish can alter species assemblages and the organization of aquatic communities. The effects of introduced fish on native populations can be dire when they have not coevolved and adaptations that could allow for their co-existence are absent (Fausch 1988). Brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and brook trout (*Salvelinus fontinalis*) have been introduced throughout the historic range of bull trout. The introductions of brook trout are commonly attributed to declines in bull trout populations (Dambacher et al. 1992; Buchanan et al. 1997).

Competition and hybridization between brook trout and bull trout is often cited as the mechanism responsible for declines in bull trout populations (Dambacher et al. 1992; Markle 1992). Brook trout and bull trout utilize similar ecological resources, increasing the likelihood for direct competition (Wallis 1948; Dambacher et al. 1992). Research on sympatric brook trout and bull trout has demonstrated that brook trout more aggressively pursue food and feeding locations in enclosures than did bull trout, and growth rates for brook trout are often greater than bull trout in these situations (Gunkel 2000). Competitive interactions between brook trout and bull trout may reduce bull trout fitness, ultimately resulting in decreased abundance.

Hybridization between brook trout and bull trout is common because both species spawn in fall and choose similar spawning habitats (Fraley and Shepard 1989). The more aggressive nature of brook trout leads to higher number of hybrids from crosses between bull trout females and brook trout males (Kanda et al 2002). This is compounded by an earlier age at maturity for brook trout of 3 years, compared to 5 years for bull trout, increasing the likelihood that hybridization between these species disproportionately affects bull trout (Leary et al. 1993; Buchanan et al. 1997).

Research behind declines in bull trout populations following the introduction of brook trout has focused on interactions between these species at small (10 m) disconnected sites in stream or laboratory settings. No studies have experimentally manipulated entire populations throughout a stream and examined the results over an extended period. The extirpation of brook trout from the Sun Creek watershed in Crater

Lake National Park, Oregon over a 10-year span provided a rare opportunity to investigate changes in bull trout distribution and abundance with the eradication of sympatric brook trout.

Bull trout were historically distributed throughout Sun Creek. The introduction of brook trout beginning in the 1930s is believed to have restricted the population of bull trout to a 2 km region of stream (Wallis 1948; Dambacher et al. 1992). Dambacher (1992) suggested that brook trout might have excluded bull trout from preferred habitat, adversely affecting survival and reproduction of bull trout.

The goal of this study was to investigate the response of bull trout to brook trout eradication on the distribution and abundance of bull trout. Following the removal of brook trout, a contiguous survey of 8 km of Sun Creek was conducted to assess habitat factors that may be influencing the distribution of bull trout in Sun Creek. The objectives of this study were to:

1. Determine if there was a shift in the bull trout distribution following the removal of brook trout.
2. Determine if bull trout abundance increased with the eradication of brook trout.
3. Describe habitat factors associated with bull trout distribution in Sun Creek.

Chapter 2

Bull Trout Population Response to Brook Trout Extirpation

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Abstract. Invasion by nonnative brook trout (*Salvelinus fontinalis*) often results in replacement of bull trout (*Salvelinus confluentus*) in western North America, but the causal mechanisms are not well understood. Eradication of brook trout over a 10-year period from over 8 km of Sun Creek, a second order stream that flows into the Klamath River basin in Southern Oregon, provided an opportunity to observe changes in distribution and abundance of bull trout. Between 1992 and 2000, bull trout abundance was determined annually through underwater observation and multiple-pass electrofishing, and brook trout were captured, removed, and destroyed. Population abundance of bull trout increased almost 300% between 1994 and 2003. Bull trout occupied a similar portion of the stream during and following brook trout removal and bull trout distribution did not shift either upstream or downstream into habitat previously occupied by brook trout. These results suggest that bull trout in Sun Creek may have occupied source habitat throughout the study period; however, more time may be needed for bull trout densities to increase to the point where bull trout expand into other habitats. Although specific mechanisms are not completely understood, the increase in bull trout abundance with the removal of brook trout suggests that brook trout may have limited recruitment of bull trout.

Introduction

Bull trout (*Salvelinus confluentus*), a native char of western North America, have declined in abundance and distribution during the last 45 years (Goetz 1989). In 1998, bull trout population segments in the Klamath River and Columbia River basins were listed as threatened under the Endangered Species Act of 1973 (USFWS 1998). The primary factors attributed to declining bull trout populations are habitat loss, water diversions, hybridization, and competition with nonnative fishes (Rieman and McIntyre 1995; Buchanan et al. 1997; Kanda et al. 2002).

Habitat fragmentation has limited many bull trout populations to headwater streams, and these small, isolated populations are the most vulnerable to deleterious effects of introduced salmonids (Rieman and McIntyre 1995). Introductions of nonnative fish often result in decreased growth, reduced reproduction, and elimination of native species through competition, predation, hybridization, and novel pathogens (Moyle et al. 1986). The effects of introduced fish on native populations can be especially severe because taxa have not coevolved and adaptations that could allow for co-existence are absent (Fausch 1988).

Bull trout are often sympatric with introduced brown trout (*Salmo trutta)*, lake trout (*Salvelinus namaycush*), and brook trout (*Salvelinus fontinalis*), but brook trout may pose the greatest threat to bull trout persistence (Buchanan et al. 1997). In many pristine the presence of brook trout is often the only factor attributed to the disappearance or declines of bull trout populations (Ratliff and Howell 1992; Buchanan et al. 1997).

Competition for habitat and hybridization with brook trout are suggested to be responsible for declines in bull trout populations (Dambacher et al. 1992; Leary et al. 1993; Buchanan et al. 1997). Similar ecological requirements between bull trout and brook trout increase the probability for direct competition (Wallis 1948; Cunjak and Green 1982; Dambacher et al. 1992). Studies of brook trout and bull trout in sympatry have demonstrated that brook trout more aggressively pursue food and feeding locations in enclosures, and growth rates for brook trout are often greater than that of bull trout in these situations (Gunkel 2000).

Hybridization in streams with sympatric populations of brook trout and bull trout is common because both species spawn in the fall and use similar spawning habitats (Markle 1992; Leary et al. 1993; Kanda et al. 2002). Recent research suggests that hybridization more commonly results from crosses between male brook trout and female bull trout than vice versa possibly disproportionately impacting bull trout recruitment (Kanda et al. 2002).

Although information concerning mechanisms that influence declines of bull trout following invasion of brook trout is increasing, few studies have been conducted at the population scale. A unique opportunity to study distribution, abundance, and interactions between small (<400 mm) brook trout and bull trout occurred in the Sun Creek watershed in Crater Lake National Park, Oregon, during a 10-year bull trout restoration project that extirpated brook trout from this watershed. The objectives of this study were to assess changes in the distribution and abundance of bull trout following the removal of brook trout.

Bull trout were historically distributed throughout Sun Creek from Sun Falls downstream into the Wood River (Wallis 1948; Buchanan et al. 1997). In 1989, a study found the population of bull trout restricted to a 2 km area of the stream (Dambacher et al. 1992). Dambacher et al. (1992) suggested that bull trout had been limited to sub-optimal habitat because of the presence of brook trout. Hypothetically, removal of brook trout would initiate a release from competition, and bull trout would move into areas of the stream previously occupied by brook trout. Such a response would support the hypothesis that habitat availability is limiting in Sun Creek.

Study Area

Sun Creek is a second-order tributary to the Wood River in the Klamath Basin, Oregon, that originates in springs at approximately 2,200 m above mean sea level (amsl) in Crater Lake National Park. Near the source, the stream is <1 m wide with a low gradient, and it is often braided at high flows. At 3.4 km from the source, Sun Creek cascades over a series of waterfalls (Sun Falls) that forms a natural barrier to upstream fish movement and historically constrained the uppermost distribution of bull trout in Sun Creek (Figure 2.1). The portion of Sun Creek immediately below Sun Falls has a moderate gradient (5-7%), and the substrate is dominated by cobble and gravel. The primary pool-forming agent is large wood from nearby hill slopes, but pools formed by roots along stream banks or channel meanders are also present. At 4.8 km below the source, Sun Creek incises deeply into a 25,000-year-old glacial valley filled with pumice ash deposits from the eruption of Mount Mazama 6,850 years bp (Nelson et al. 1994). Pumice has been transported farther downstream where the gradient averages 2-3%.

The Sun Creek watershed is forested with unharvested ponderosa pine (*Pinus ponderosa*), mountain hemlock (*Tsuga mertensiana*), and Shasta red fir (*Abies magnifica*); alder (*Alnus spp.*) dominate the riparian canopy below approximately 1,600 m amsl (Dambacher et al. 1992). The watershed receives an average of 14 m of snow each winter. Peak stream flows occur from late June to early July. During the study, stream flows at the boundary of Crater Lake National Park (~13 km from the source) ranged from 1.8 m^3/sec (July 1999) to 0.2 m^3/sec (November 1992). From June to October, summer stream temperatures in the study area ranged from 2°C in June 2001 to 16 °C in September 2001.

A bull trout restoration program was initiated in 1992 by the National Park Service that sought to restore threatened bull trout in Sun Creek through extirpation of introduced brook trout (Buktenica 1997). Between 1992 and 1994, two upstream migration barriers were constructed near the park boundary to prevent re-colonization of nonnative fish species (Figure 2.1). From 1992 to 2000, annual electrofishing and selective antimycin use (1992, 1997, and 2000) were used to remove over 5,000 brook trout from Sun Creek (Figure 2.2). In 1999 and 2000, all bull trout were captured and moved to a streamside raceway in preparation for chemical treatment; however, in 1999 high stream discharge prevented chemical treatment and bull trout were returned to the stream. In 2000, the entire stream from Sun Falls to the National Park boundary was treated with antimycin. After treatment, bull trout were returned to 50-m stream sections in Sun Creek in proportion to the abundance and size distribution prior to removal (Figure 2.3).

Methods

To evaluate changes in the bull trout distribution following the reduction (1994-1999) and subsequent extirpation (2000) of brook trout, distributions of both species were monitored annually between Sun Falls and the upper artificial barrier (Figure 2.1). From 1994 to 1998, distribution was determined using single-pass daytime snorkel surveys, recorded at a resolution of 50 m. In preparations for chemical treatment, fish distribution data was obtained from multiple-pass electrofishing in 1999 and 2000. Because trout abundance estimates in 1999 and 2000 were based on multiple-pass electrofishing, they are potentially an order of magnitude greater than the snorkeling estimates (Cunjak et al. 1988; Thurow and Schill 1996), consequently 1999 and 2000 abundances are not included in abundance comparisons. In 1999 and 2000, captured bull trout were held in a streamside raceway and returned to the stream in September 2000 following the chemical treatment. In 2000 trout < 60 mm were held over winter in an Oregon Department of Fish and Wildlife hatchery and returned in June of 2001. All brook trout captured were destroyed.

Following chemical treatment and return of bull trout in 2000, Sun Creek was sampled by snorkeling from July 30 –August 17, 2001, July 22 – August 9, 2002, and July 7 – July 29, 2003. Sampling start date was dependent on stream discharge and would commence when discharge at the Park boundary was below 12 cfs. To determine a starting point for sampling each year, a four-person electrofishing crew began at the upper artificial barrier and worked upstream until two bull trout were encountered. At this point a two-person team snorkeled upstream to Sun Falls (Dolloff et al. 1996). The two-person crew was composed of one snorkeler and one data recorder. Crewmembers would switch roles every 50-100 m to avoid fatigue. Location (50-m section and channel-unit type), species, and size class (< 60 mm, 61-100 mm, >101 mm) were recorded for each fish observed

To determine if bull trout abundance changed following the removal of brook trout estimates of bull trout abundance were compared to the mean from all years. Student's t-test was used to determine if abundance after chemical treatment differed from pre-treatment. To determine if the removal of brook trout affected different size classes, snorkeling counts of different size classes of bull trout were compared to the mean from all years for each size class and examined with Student's t-test to determine if pre and post chemical treatment abundances were different.

To detect changes in the distribution of the bull trout population following the removal of brook trout, median location of the summer distribution of both species was compared annually for the period between 1994 and 2003. The median location was defined as the stream location (km from source) where half of the population is upstream and half is downstream (to the nearest 50 m). If expansion at the upstream and downstream ends of the distribution occurred at equal rates the median location would remain constant, therefore we annually evaluated changes in the upstream and downstream extents of the population. To detect trends in the medians and extents of the populations linear regression was used ($\alpha = 0.05$). Additionally, to describe patterns in the bull trout distribution in Sun Creek we examined bull trout abundance at the upstream, middle, and downstream thirds of the distribution; beginning at the downstream extent of bull trout observed during the study extending upstream to Sun Falls. By using both the median, and upstream and downstream extent, and keeping track of bull trout abundance it was possible to describe changes in the bull trout and brook trout distribution.

Results

From 1994 to 2003 bull trout relative abundance increased over 300% following the removal of brook trout. Excluding years sampled with electrofishing bull trout relative abundance ranged from a low of 93 in 1995 to a high of 376 in 2003 (Figure 2.4). Bull trout abundance following chemical treatment was greater than the mean from all years and significantly different from pre-treatment abundance ($t = -5.4$, $p = 0.02$; Figure 2.5). Following chemical treatment abundance of bull trout 60 – 100 mm in length was higher than the mean from all years; however, the difference was not significant when compared to pre-treatment abundance ($t = 1.3$, $p = 0.24$; Figure 2.6). Abundance of bull trout >100 mm in length was higher than the mean from all years following chemical treatment and was significantly different from pre-treatment abundance ($t = -3.82$, $p = 0.009$; Figure 2.6).

The median distribution of bull trout in Sun Creek did not shift substantially after the removal of brook trout from Sun Creek ($P = 0.09$, $R^2 = 0.32$; Figure 2.7). Of approximately 9.0 km of available habitat, the bull trout population median ranged over only 700 m of the stream. In 1999, the median was located 7.1 km from the source. This was the farthest downstream the median was recorded and represented a 4% change from the 1994 baseline of 6.8 km (Figure 2.7). In 2002, 2 years after the final phase of the brook trout removal program was completed, the median was 6.4 km from the source the farthest point upstream and a 5% change from 1994 (Figure 2.7).

The upstream extent of the bull trout distribution varied by approximately 1.6 km in 10 years; however, the difference between 1994 (3.7 km from the source) and 2003 (3.5 km from the source) upstream extents was only 200 m, less than a 1% change ($P = 0.07$, $R^2 = 0.35$; Figure 2.7). In 2000, electrofishing found the bull trout population at its uppermost extent, 2.6 km from the source (a 5% change from 1994). In contrast the upstream extent was the farthest downstream in 1995 (4.3 km from the source), a 16% change from the 1994 baseline (Figure 2.7).

The downstream extent of the bull trout population ranged approximately 3.0 km and was more variable than the upstream extent but had no detectable trend among years ($P = 0.37$, $R^2 = 0.1$; Figure 2.7). In 1994, the downstream extent of bull trout was at 10.5 km from the source. Electrofishing was used from 1999 through 2003 to determine the lower extents, and bull trout were found the farthest downstream at 11.3 km from the source in 1999 (a 7.5% change from the 1994 baseline). In 2001, the downstream extent was the farthest upstream at 8.35 km from the source, a 20% change from the 1994 baseline (Figure 2.7).

During the rehabilitation project, the brook trout distribution was affected by removal. In 1994, the median of the brook trout population was initially located 600 m downstream from the bull trout median at 7.4 km from the source (Figure 2.7). In 2000, the median of the brook trout population was 1.4 km farther downstream (8.8 km from the source) and was separated from the bull trout median by 2.3 km, a 19% change from the 1994 baseline ($P = 0.002$, $R^2 = 0.88$; Figure 2.7). The upstream extent of the brook trout distribution varied by approximately 1 km in 6 years, and ranged from 3.6 km from the source in 1994 to 4.6 km in 1997 ($P = 0.71$, $R^2 = 0.03$; Figure 2.7). The downstream extent of brook trout distribution was more variable than the upstream extent, ranging over 1.8 km. In 1994 the downstream extent was at 10.6 km from the source and 11.65 km in 2000 a 9% change ($P = 0.12$, $R^2 = 0.14$; Figure 2.7).

Examining bull trout abundance at the upstream (3.45 – 6.05 km), middle (6.05 – 8.7 km), and downstream (8.7 – 11.3 km) thirds of the distribution found the majority of bull trout in the middle third. The middle third also showed an apparent upward trend in abundance with an increase from 101 bull trout in 1994 to 255 trout in 2003 (Figure 2.8). Bull trout abundance also increased in the upstream third of the distribution from 23 bull trout in 1994 to 111 trout in 2003 (Figure 2.8). Bull trout abundance in the downstream third did not show an increase in abundance over the study period; however, the results may have been affected by the removal and return of bull trout from Sun Creek during the chemical treatment. Bull trout abundance in the downstream third increased from 5 in 1994 to 31 in 1998 and then decreased following the chemical treatment to 1 trout in 2001, but had increased to 10 trout by 2003 (Figure 2.8).

Discussion

Research examining the relation between brook trout and bull trout has focused on microhabitat interactions often studied in enclosures or laboratory settings (McMahon et al. 1998; Gunkel et al. 2002). No studies have examined salmonid distribution *in situ*, following removal of an introduced species. After 10 years of monitoring over 8 km of stream, there was no substantial shift in the distribution of bull trout with the removal of brook trout. Bull trout maintained their general distribution in the stream with minor annual expansions and contractions, but no directional trend (Figures 2.4, 2.7, and 2.8). Had bull trout been competitively excluded from the optimal habitat as was previously assumed, a downstream shift or redistribution by bull trout into habitat previously occupied by brook trout would have been expected (Dambacher et al. 1992). Previous research on bull trout and brook trout interactions has shown that displacement of bull trout by brook trout is likely when resources are scarce (Gunkel et al. 2002). Although microhabitat interactions or food resources between brook trout and bull trout were not examined in this study, if either food or habitat was a limiting factor for bull trout in Sun Creek, then a stronger population response would have been expected following the removal of over 5,000 brook trout (Figure 2.2). These results suggest that bull trout were not excluded from summer habitat by the presence of brook trout.

The abundance of bull trout in the uppermost sections of Sun Creek may be related to favorable environmental features found in headwater sections of the stream. Ziller (1992) found bull trout generally closer to the headwaters in Sprague River subbasins that are located 100 km to the east of Sun Creek. Headwaters are generally steeper, colder, and have less discharge than downstream reaches, and these factors could be indirectly influencing bull trout distribution by altering the substrate, groundwater dynamics, and possibly brook trout distribution (Ziller 1992). Dunham et al. (2002) hypothesized that brook trout are found in lower gradient reaches of streams and have difficulty dispersing into higher gradient reaches; however, Adams (1994) found that brook trout were able to ascend channels with slopes of 13%. Although brook trout were capable of occupying the upper reaches of Sun Creek and were initially stocked in Sun Meadow upstream of the bull trout population in Sun Creek, they were most abundant in the lower reaches of the stream (Wallis 1948, Dambacher et al. 1992). Bull trout may have had a competitive advantage over brook trout in headwater reaches because of higher gradients, lower temperatures, or higher habitat complexity (Sexauer and James 1997; Paul and Post 2001; Rich et al. 2003). Areas of the stream where bull trout maintained a core population likely coincided with favorable habitat conditions, and combined with higher initial densities, may have allowed bull trout to persist in sympatry with brook trout.

Our results suggest that bull trout occupied "core" habitat throughout the 10 years of this study. If bull trout abundance continues to increase, the areas occupied by bull trout probably will expand. Wallis (1948) reported that bull trout occurred throughout Sun Creek from the park boundary to Sun Falls. Larson et al. (1995) suggested that stream fish populations ebb and flow over time with physical and biotic environmental constraints. Similar dynamics may be occurring in Sun Creek, regardless of interspecific interactions. The bull trout population appears to be focused in a core area of favorable habitat and may radiate upstream and downstream as population densities and environmental variables change, in a similar manner to that observed with species ranges (Brown 1984; Travis 2004). As densities, biotic interactions, life histories, or environmental variables fluctuate, individuals may move out of the core area and into less favorable habitats (VanHorne 1983).

Bull trout once occupied the entirety of Sun Creek and were likely part of a historical population that spawned in headwater streams and migrated downstream to the Wood River or Upper Klamath Lake as adults (Wallis 1948; Buchanan 1997). Movements of bull trout downstream below the artificial barriers is possible as populations increase or as migratory characteristics are expressed.

The increase in bull trout abundance during and following the removal of brook trout from Sun Creek suggests that the presence of brook trout negatively affected the bull trout population. Although the exact mechanism is unclear, it seems likely that reproductive interference may be a factor. Kuno (1992) found that competitive exclusion might occur more readily through reproductive interference than resource competition if species temporally and spatially overlap during reproduction. Disruptive spawning interactions commonly play a role in species displacement (Grant et al. 2002). For example, Scott and Irvine (2000) found that competitive exclusion of brown trout (*Salmo trutta*) by rainbow trout (*Oncorhynchus mykiss*) in New Zealand occurred because rainbow trout superimposed redds directly on top of brown trout redds. Redd superimposition was also suggested as the mechanism responsible for the displacement of brook trout by brown trout in a Minnesota stream (Sorensen et al. 1995). Additionally, Grant et al. (2002) found brook trout and brown trout simultaneously spawning on the same redds, and males of both species attending females of both species. In Sun Creek the increase in bull trout 60 -100 mm in length following the removal of brook trout, although not statistically significant, may indicate that reproductive interference by brook trout was limiting bull trout abundance.

Disruptive spawning interactions between brook trout and bull trout may have been an important factor in Sun Creek because both species share similar spawning requirements (Rieman and McIntyre 1995). Evidence of this disruptive interaction is supported by the finding that hybrids are predominantly from crosses between male brook trout and female bull trout (Kanda et al. 2002). The deleterious effects of this one-sided reproductive interference is compounded by earlier maturity and faster population growth of brook trout leading to decreased recruitment by bull trout when in sympatry with brook trout. Bull trout generally do not spawn until age 5-7 (Fraley and Shepard 1989; Goetz 1989). In contrast male brook trout are capable of spawning at the end of their first summer and females after their second, although it is more common for males to mature in their second year and females in their third (Moyle 1976; Leary et al. 1993). The earlier age at maturity for brook trout allows faster population growth and increased abundance raising the probability of reproductive interference with bull trout.

This study provides insight into the interactions between isolated populations of brook trout and bull trout in a small stream. Previous studies suggested that brook trout are able to competitively dominate bull trout for limited food resources at the microhabitat scale (Gunkel 2000). In Sun Creek, brook trout did not exclude bull trout from optimal habitat at the population scale. Bull trout likely persisted in what appears to be preferred habitat. Our results indicate that the protection of core areas from brook trout influence can assist in bull trout restoration. In streams where populations are not constrained by limited resources, reproductive interference, and hybridization may be the causal factors in the displacement of bull trout by brook trout. Under such conditions, efforts to remove brook trout from bull trout spawning areas could protect bull trout reproductive potential. However, comprehensive restoration of bull trout populations undoubtedly requires the eradication of brook trout in most cases as demonstrated by the rapid increase in bull trout abundance with the removal of brook trout from Sun Creek. Interactions between brook trout and bull trout at spawning sites deserve further study to determine specific factors that influence the success or failure of bull trout reproduction when these species occur in sympatry.

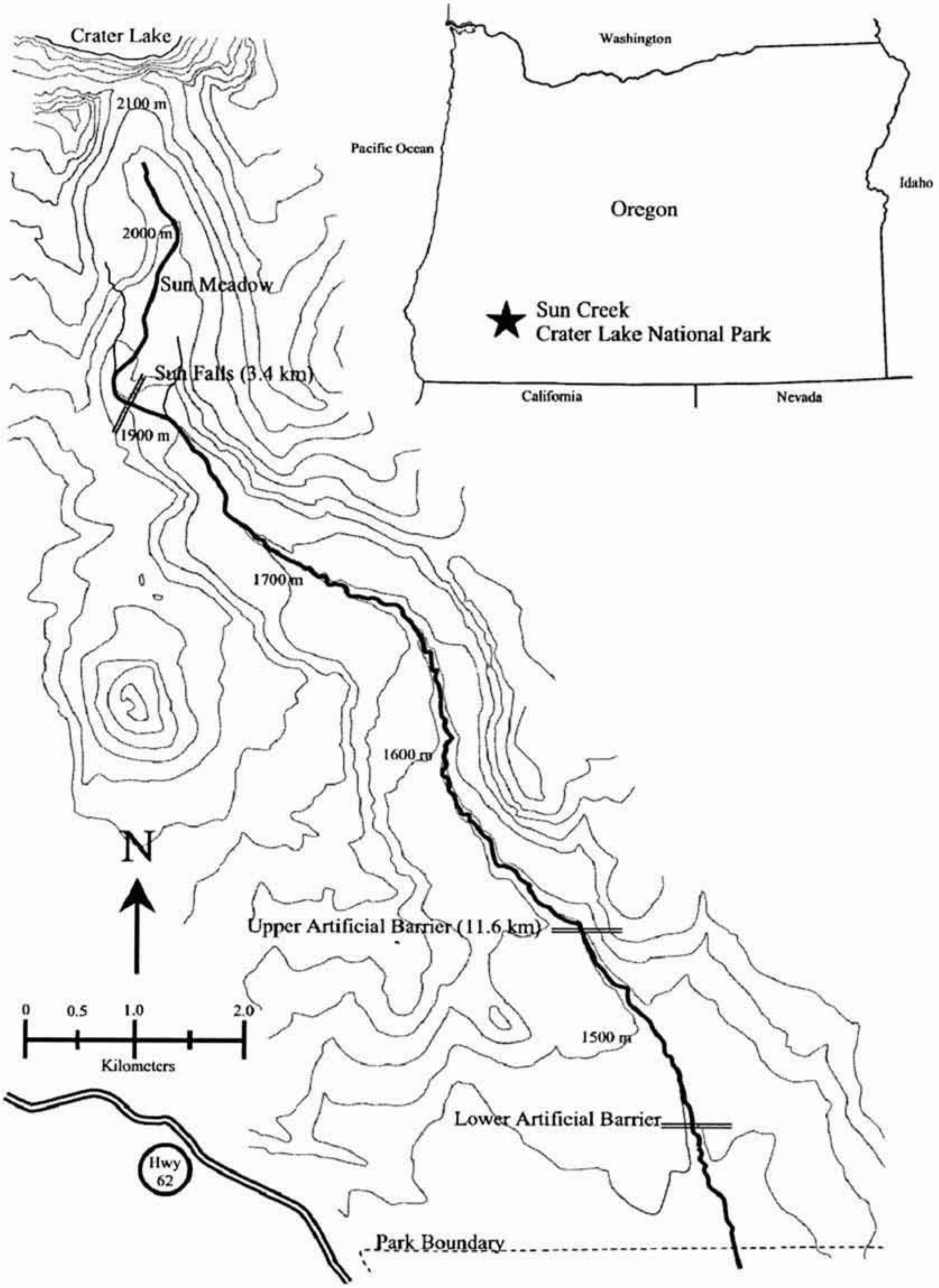

Figure 2.1 – Sun Creek study area including location of fish migration barriers. Flow direction runs from north to south.

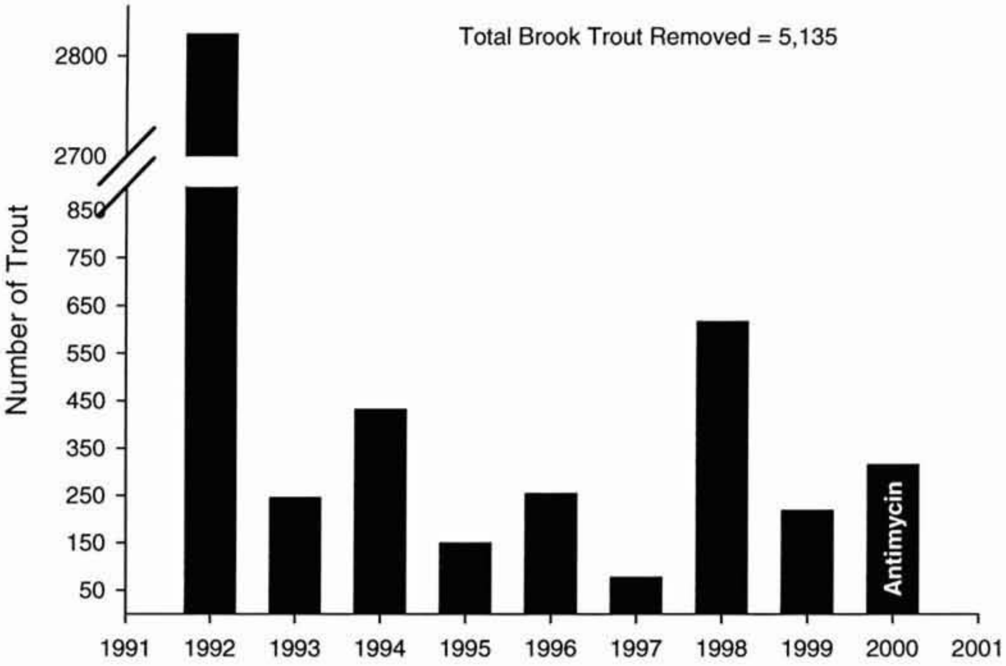

Figure 2.2 - Numbers of brook trout removed from Sun Creek between 1992 and 2000.

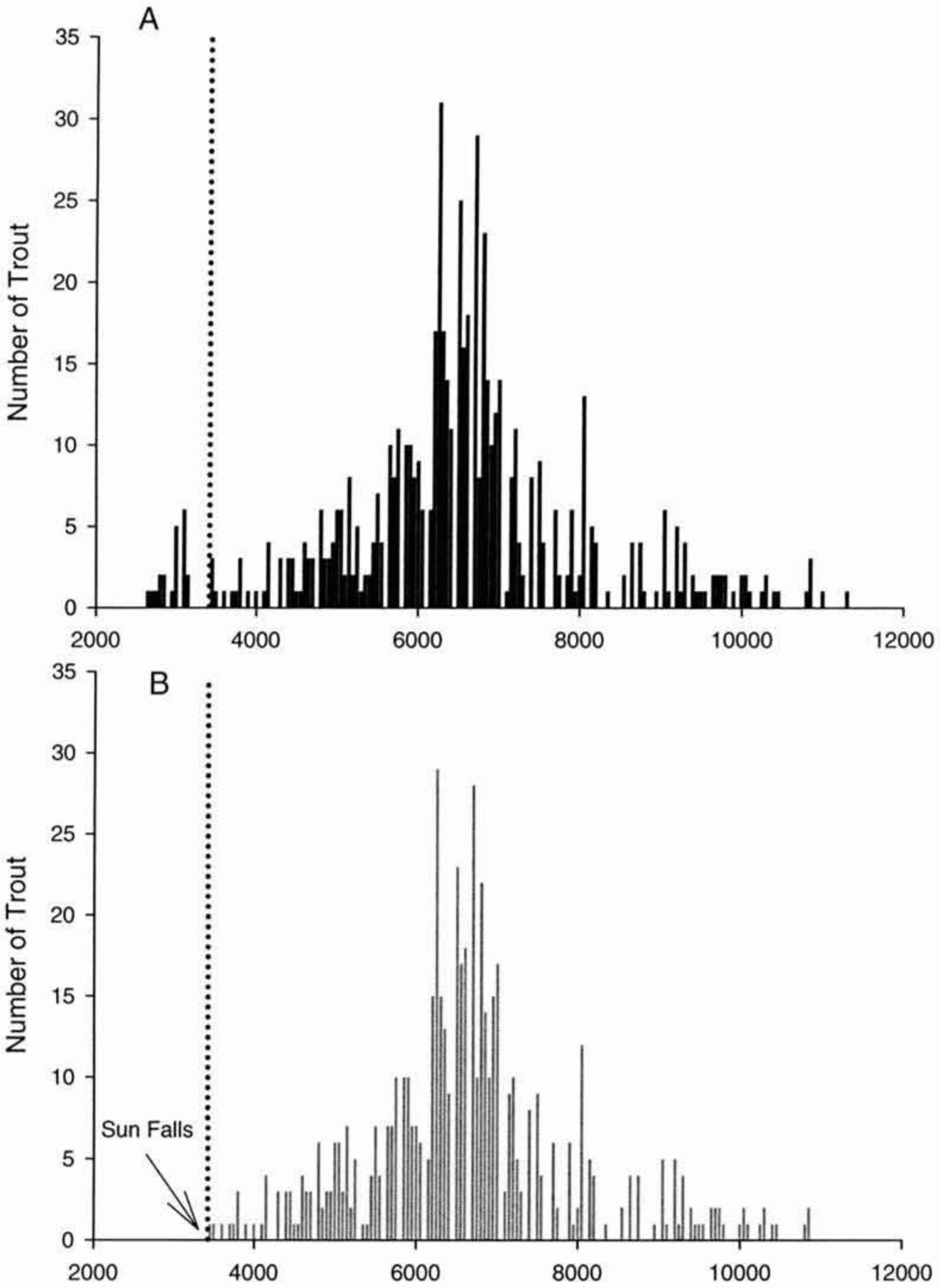

Figure 2.3 - (A) The number and location of bull trout that were removed from Sun Creek prior to chemical treatment in 2000. Bull trout were moved to either a streamside raceway or a state hatchery. (B) The number and location of bull trout returned to Sun Creek in 2000 and 2001 after chemical treatment. Trout returned in 2001 were young of the year that over wintered in a state hatchery to assure positive identification.

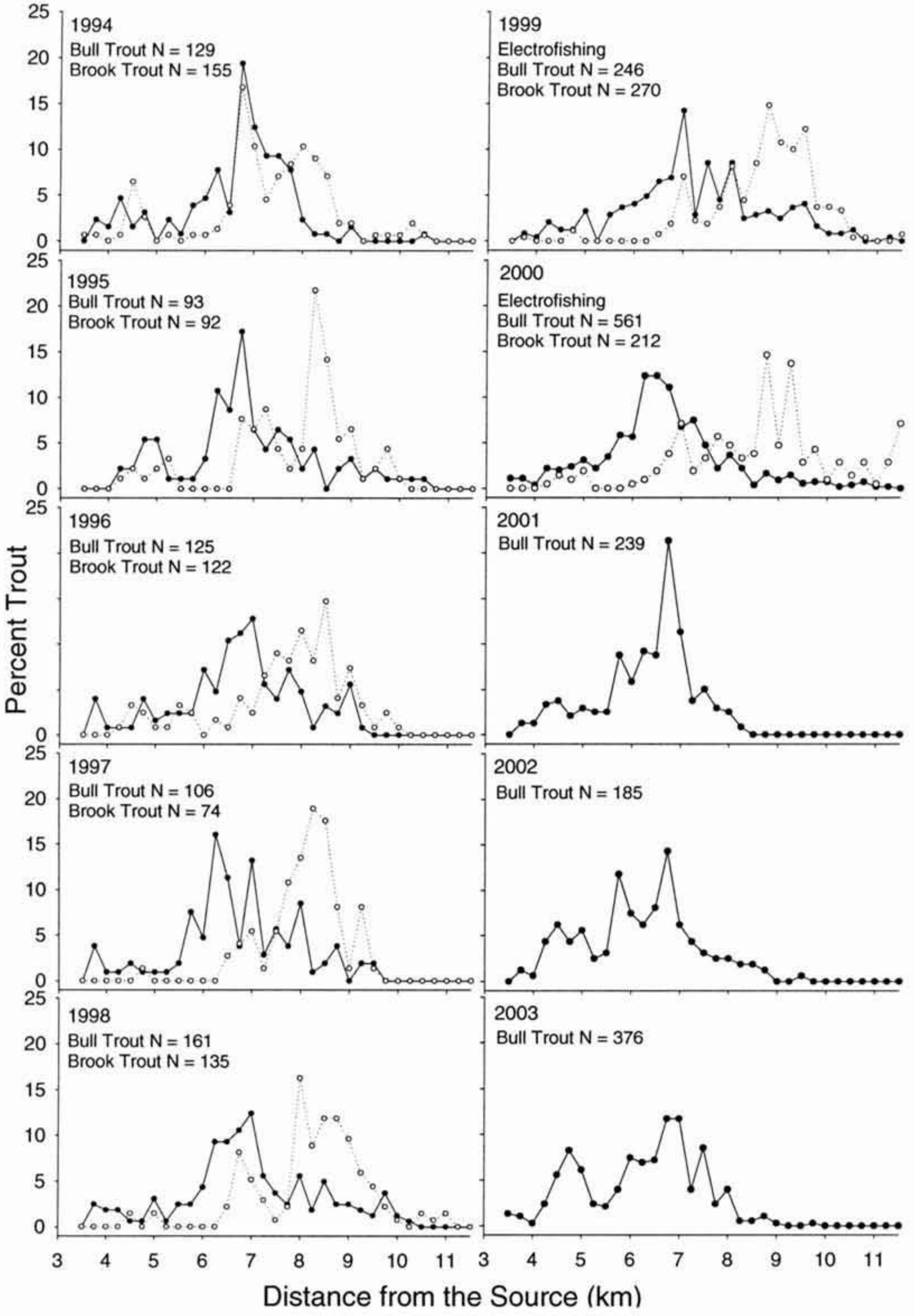

Figure 2.4 - Bull trout (●) and brook (○) trout distribution and abundance in Sun Creek from 1994 – 1999. Data were collected from first pass snorkel counts from 1994 – 1998 and 2001-2003. In 1999-2000, multiple pass electrofishing was used to determine distribution and abundance.

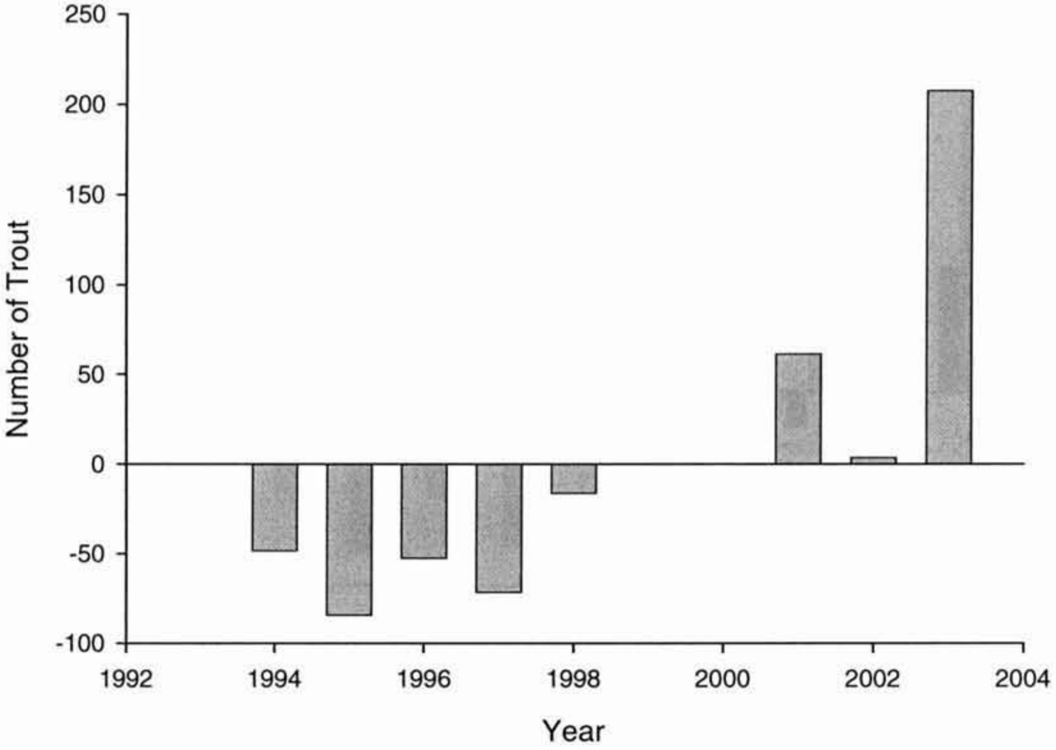

Figure 2.5. Deviation from mean (177) of snorkel counts for all bull trout, before (1994- 1998) and after (2001- 2003) the chemical treatment. The years 1999 and 2000 were excluded because they were sampled by electrofishing and not comparable to snorkel survey abundance estimates.

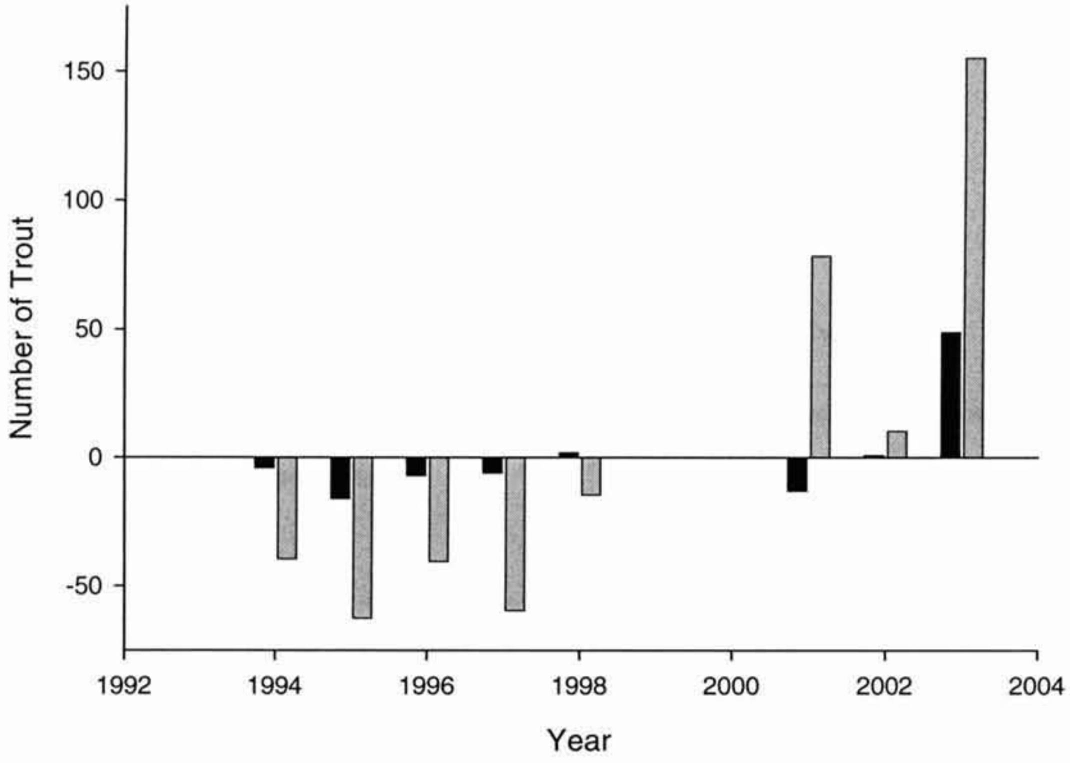

Figure 2.6 – Deviation from mean (25) of snorkel counts for bull trout 60 – 100 mm (black bar), and the mean (148) for bull trout >100 mm (gray bar), before (1994- 1998) and after (2001- 2003) chemical treatment. The years 1999 and 2000 were excluded because they were sampled by electrofishing and not comparable to snorkel survey abundance estimates.

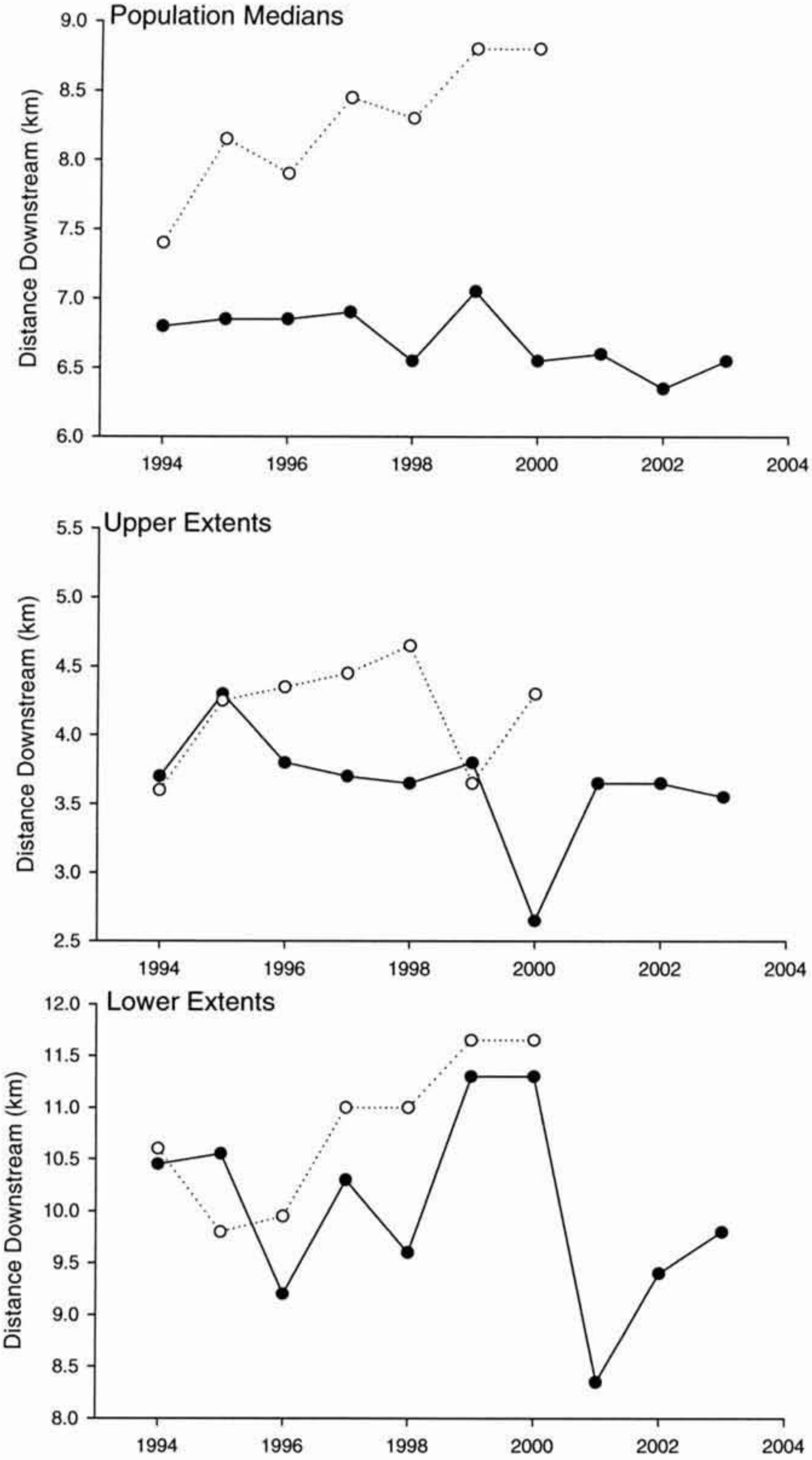

Figure 2.7 - Bull trout (●) and brook (○) trout yearly population medians and upper and lower extents.

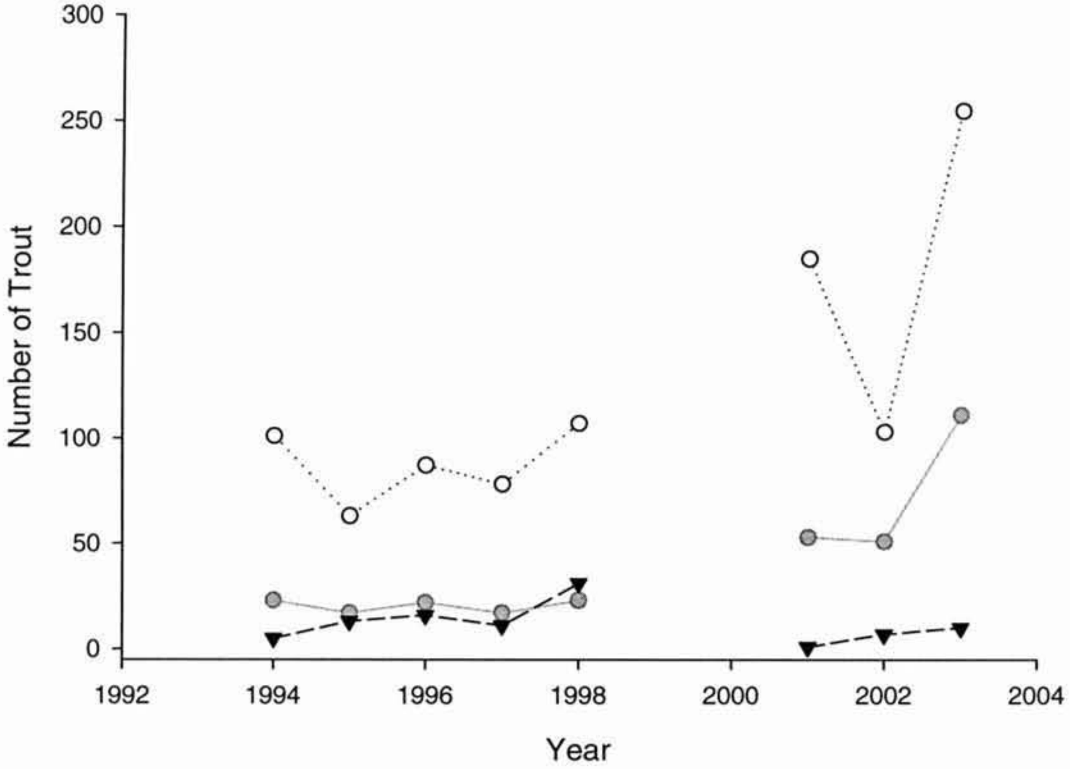

Figure 2.8 - Bull trout abundance at the middle (●), upstream (○), and downstream (▼) thirds of their distribution. The years 1999 and 2000 sampled by electrofishing were excluded.

Chapter 3

Factors Influencing Bull Trout Distribution in a Southern Oregon Stream

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Abstract. Factors influencing bull trout distribution (*Salvelinus confluentus*) have mostly studies examined discrete patches at the watershed and landscape scales. Missing from the literature is a comprehensive study of bull trout distribution over a continuous stream. In 2000, nonnative brook trout (*Salvelinus fontinalis*) were extirpated from Sun Creek in southern Oregon to protect native bull trout. During the process of eradicating brook trout, the bull trout abundance increased over 300%. The distribution of bull trout distribution remained relatively static, suggesting that either occupied habitat was beneficial to their persistence or there were environmental variables limiting dispersal. We examined bull trout distribution at the geomorphic-reach, 250-m section, and channel-unit scales in 8-km of contiguous stream habitat. Average temperatures in the stream ranged between 6.8° C and 8.4° C. At the watershed scale, bull trout were limited to areas upstream of a point source (7.85 km from the source) where spring effluents were associated with turbidity >30 NTU. Multiple regression was used to investigate habitat attributes influencing bull trout abundance patterns in areas of the stream with low turbidity. In reaches and fixed length stream sections, bull trout abundance was higher where pools were deeper and stream temperatures were higher. The presence of springs influenced bull trout abundance at the reach and channel unit scales. Electivity analysis of habitat units found that bull trout selected pools rather than riffles, and plunge pools rather than scour pools. Studies that examine small sites on a multitude of streams are useful in describing general factors influencing bull trout; however, they may miss important relationships occurring at the stream scale where management and restoration occurs. Our results reiterate that point source perturbations, such as turbidity, can influence

trout distribution, and underscore the value of continuous samples as a means of identifying such spatially intermittent factors.

Introduction

Bull trout (*Salvelinus confluentus*), a native char of Western North America, have declined in abundance and distribution during the last 30 years (Goetz 1989). In 1998, the Klamath Basin and Columbia River bull trout population segments were listed as threatened, under the Endangered Species Act of 1973 (USFWS 1998). Bull trout are one of the most thermally sensitive coldwater species in western North America and loss or fragmentation of this habitat has contributed to their decline (Rieman and McIntyre 1993; Buchanan and Gregory 1997). At the patch ($\geq 10^3$ m) scale, temperature is the primary factor for predicting their presence or absence, whereas habitat fragmentation and patch size are important (Dunham and Rieman 1999; Dunham et al. 2003a). At the site scale (10 m) bull trout are generally found in pools or associated with instream cover (Saffel and Scarnecchia 1995; Sexauer and James 1997). Missing from the current literature are factors influencing bull trout at an intermediate scale (10^2 m).

Research on bull trout has typically occurred at discrete sites distributed throughout a stream network, and spatially contiguous samples of habitat are uncommon. On the other hand, a spatially contiguous view of rivers and streams may provide new insights to factors affecting trout distribution and ultimately their conservation (Imhof et al. 1996). A rare opportunity to study bull trout habitat associations at multiple scales occurred in Sun Creek at Crater Lake National Park, Oregon following the extirpation of introduced brook trout (*Salvelinus fontinalis*).

Historically bull trout were distributed throughout Sun Creek and downstream into the Wood River (Wallis 1948; Buchanan et al. 1997). The introduction of brook trout from 1930s to the 1970s is thought to have restricted bull trout to a 2 km reach of Sun Creek (Dambacher et al. 1992). Dambacher et al. (1992) suggested exclusion from preferred habitat by brook trout could adversely affect survival and reproduction of the native char. Renner et al. (in review) found that distribution had changed little 3 years after the removal of brook trout. In order to investigate factors that influence bull trout distribution, a contiguous survey of 8 km of Sun Creek was conducted in 2001.

Study Area

Sun Creek is a second-order tributary to the Wood River in the Klamath Basin, Oregon. The stream originates in Sun Meadow approximately 2,200 m above mean sea level (amsl) in Crater Lake National Park (Figure 3.1). In Sun Meadow the stream is <1 m wide with a low gradient, and it is often braided at high flows. At 3.4 km from the source, Sun Creek cascades over a series of waterfalls (Sun Falls) forming a natural barrier to upstream fish movement that historically constrained the distribution of bull trout in Sun Creek (Figure 1). The portion of Sun Creek immediately below Sun Falls has a moderate gradient (5-7%), and the substrate is dominated by cobble and gravel. The primary pool-forming agent is large wood from nearby hill slopes, but pools formed by root-defended banks or channel meanders are also present. At 4.8 km below the source, Sun Creek incises deeply into a 25,000-year-old glacial valley filled with pumice ash deposits from the eruption of Mount Mazama 7,000 years bp (Nelson et al. 1994).

The Sun Creek watershed is forested with unharvested ponderosa pine (*Pinus ponderosa*), mountain hemlock (*Tsuga mertensiana*), and Shasta red fir (*Abies magnifica*). Alder (*Alnus spp.*) dominates the riparian canopy at elevations below approximately 1,600 m amsl (Dambacher et al. 1992). The watershed receives an average of 14 m of snow each winter. Peak stream discharge occurs from late June to early July.

A restoration program was initiated in 1992 by the National Park Service to restore threatened bull trout in Sun Creek through extirpation of introduced brook trout (Buktenica 1997). To accomplish this goal, two upstream immigration barriers were constructed near the park boundary to prevent colonization of nonnative fish species (Figure 3.1). From 1992 to 2000, annual electrofishing and selective use of antimycin (1992, 1997, and 2000) removed over 5,000 brook trout from Sun Creek. During this period the abundance of bull trout increased (Buktenica 1997, Renner et al. in review). In 2000, all bull trout were captured and moved to a streamside raceway, and the entire stream from Sun Falls to the National Park boundary was treated with antimycin. After the treatment, bull trout were returned to 50-m stream sections in Sun Creek in proportion to the abundance and size distribution found during removal.

Methods

Habitat and bull trout surveys

During June and July 2001, a stream survey was conducted from Sun Falls (3.4 km from the source) to the uppermost downstream artificial barrier (11.6 km from the source). Habitat was classified hierarchically by geomorphic reach and channel units (Frissell et al. 1986). Geomorphic reaches were defined by major changes in valley form, gradient, bed morphology, and pool spacing (Montgomery and Buffington 1997). The minimum length for each individual reach was 10 channel units. Four reach types (cascade, step pool, plane bed, and pool riffle) were identified in Sun Creek (Montgomery and Buffington 1997).

Channel units were categorized as dam pool, plunge pool, scour pool, riffle, cascade, or step (Bisson et al. 1982). During field surveys, the following variables were recorded for each unit: gradient, active channel width, channel unit length, maximum pool depth, dominant and subdominant substrate type, number of wood jams, riparian vegetation, habitat type, reach type, channel type, and channel and valley form. Each channel unit was marked for later identification.

The stream was also systematically divided into 250-m sections in order to examine habitat at a scale smaller than geomorphic reaches but larger than individual channel units. This length is similar to sample sections used in other studies of trout habitat associations (Binns 1994; Bonneau and Scarnecchia 1998; Horan et al. 2000).

Water temperature was recorded using Onset™ H8 thermographs at 16 locations from July 9, 2001 to June 21, 2002. During the week of July 23 - 27, 2001 discharge was calculated at 250-m intervals between Sun Falls and the upper artificial barrier using a Swoffer™ model 2100 flow meter. To locate springs and seeps between Sun Falls and the artificial barrier groundwater inputs that differed ≥0.5°C from the mainstream channel temperature were recorded. A difference of 0.5°C was used in an attempt to differentiate stream water from groundwater and upland sources (Constantz 1998).

Turbidity and pH were measured using an HF^{tm} model 150-turbidity meter and an Altex^{tm} Φ30 pH meter. Conductivity was measured in the field using a Hanna Instruments™ model HI 8733 conductivity meter. In 2002, water samples were collected from reaches that had low levels of turbidity, and reaches with high levels of turbidity for trace element analysis. Filtered and unfiltered water samples were taken at 10 locations, 8 stream water samples taken between 4.5 and 9.5 km from the source, and 2 samples taken from springs. The upper spring sampled was located at 5.3 km from the source, and the downstream spring was located at 8.8 km from the source.

Sun Creek was surveyed by snorkeling between July 30 and August 17, 2001 to determine trout distribution (Dolloff et al. 1996). A four-person electrofishing crew began at the upper artificial barrier located 11.6 km from the source and worked upstream until two bull trout were encountered (Reynolds 1996). At this point, a two-person snorkeling team worked upstream to Sun Falls counting all bull trout. The two-person crew was composed of one snorkeler and one data recorder. Crewmembers would switch roles every 50-100 m to avoid fatigue. Location (channel unit), species, and size class (< 60 mm, 61-100 mm, >101 mm) were recorded.

Data analysis

Habitat features associated with the presence of bull trout were compared using ANOVA ($\alpha < 0.05$). Backward stepwise regression was used to determine variables for input into a multiple regression model. To reduce multicollinearity, correlation between independent variables was examined. If two variables were strongly correlated ($r < 0.60$), the variable correlated strongest with bull trout abundance was included in stepwise regression. Variables that did not meet the assumptions of normality and equal variance were transformed ($\log_{10}(x + 1)$).

Channel units in the reaches that contained bull trout were compared for unit scale factors influencing trout distribution and abundance. Variables examined included: distance from the source, pool depth, unit length, active channel width, substrate, channel unit type, and distance from springs. Ivlev's electivity analysis was used to compare discrete variables including substrate type, unit type, pool type, and spring presence (White and Garrott 1990). Ivlev's electivity index provided a dimensionless number that compared the proportion of a resource used by an animal to the proportion of that habitat available in the study area (Lechowicz 1982). Electivity indices range from –1.0 and approach 1.0, negative values suggest avoidance and positive values suggest selection. Simultaneous Bonferroni confidence intervals ($\alpha = 0.05$) were calculated to determine whether preference or avoidance responses were statistically significant (White and Garrott 1990).

Results

In the study area, temperature did not limit bull trout occurrence. Stream temperatures in Sun Creek during the study period remained below 17° C with the average temperatures between 6.8° C and 8.4° C (Figure 3.2). Summer temperatures recorded between July 10 and September 17, 2001, exceeded 14° C at four locations (5.1 km, 6.1 km, 7.3 km, and 11.6 km from the source) in Sun Creek. Summer stream temperatures dropped below 4° C at 3.65 km and 4.6 km from the source. The warmest temperature recorded was 16° C at 7.6 km from the source on September 21, 2001.

Bull trout were present in the upper portions of the sample area, and none were observed beyond 8.4 km from the source. This point coincides with the presence of springs and turbidity > 30 NTU. Examination at both the reach ($n = 15$) and section ($n = 32$) scales found a strong negative association with turbidity (Figure 3.3). The mean turbidity where bull trout were present at the reach scale was 1.95 NTU and 20.4 NTU where bull trout were absent ($P < 0.0001$). Similarly, at the 250-m section scale, sections that contained bull trout had a mean turbidity of 1.75 NTU and where they were absent turbidity was 34.5 NTU ($P < 0.0001$; Figure 3.3).

Investigating variables that influence bull trout abundance in regions of the stream where the turbidity was low found higher bull trout abundance at the reach scale associated with deeper pools, higher average temperatures, and higher densities of springs ($P = 0.008$, $R^2 = 0.91$; Table 3.1; Figures 3.4 and 3.5). Low turbidity sections were analogous to the reach scale with bull trout abundance positively associated with warmer stream temperatures and deeper pools ($P = 0.003$, $R^2 = 0.56$; Table 3.1).

Channel units ($n= 928$) where bull trout were present were significantly longer and narrower than those where bull trout were absent. Bull trout abundance at the unit scale was positively associated with distance from the source and negatively associated with distance from springs ($P<0.001$, $R^2 = 0.14$; Table 3.1). Electivity analysis of units found that bull trout selected pools rather than riffles when compared to the proportion of these habitats available in the environment. Out of the three types of pools quantified, bull trout selected plunge pools, used dam pools proportionally to their availability in the habitat, and selected against scour pools. Bull trout avoided units dominated by gravel or silt substrates and selected those with sand substrates. At the unit-scale, bull trout occurred where cobble substrates were in proportion to their occurrence in the study area (Table 3.2).

Analysis of trace elements suggested that concentrations of manganese (Mn) and cobalt (Co) were significantly greater in downstream reaches with elevated turbidity. The average concentration of Mn when compared to the control was 3.4 ppb in the upper reaches and 20.3 ppb in the lower reaches (Figure 3.6). The Mn concentration in the upstream spring was 0.54 ppb and 99.2 ppb in the lower spring. Cobalt concentrations also increased in the downstream reaches compared to the control from 0.63 ppt the upstream reaches to 7.6 ppt in the downstream reaches. The concentration of Co in the upper spring was 0.67 ppt and 63.7 ppt in the lower spring (Figure 3.6).

Discussion

Bull trout are one of the most thermally sensitive coldwater species in western North America rarely found where average temperatures exceed 14° C (Buchanan and Gregory 1997; Gamett 2002; Dunham et al. 2003b). The Sun Creek bull trout population is in the southern margin of the species range where temperature may be more important in delineating the species distribution than more northerly populations (Dunham et al. 2003b). Because temperature and elevation are closely correlated, elevation has been used as a surrogate to determine likely bull trout habitat (Dunham and Rieman 1999). Stream temperatures recorded during the study indicated that the entire study area in Sun Creek has mean summer temperatures well within the thermal optima for bull trout; however, bull trout were not distributed equally throughout the area. Interestingly, in Sun Creek bull trout abundance was positively associated with warmer mean temperatures at both the geomorphic-reach and 250-m section scales.

Selong et al. (2001) found that growth in young bull trout peaked at 13.2ºC and McPhail and Murray (1979) found that survival of Dolly Varden (*Salvelinus malma*) eggs decreased when incubation temperatures were below 4ºC. The mean summer temperatures where bull trout occurred in Sun Creek ranged between 6.8ºC and 8ºC, with the peak in bull trout abundance at 7.8ºC. These findings suggest that bull trout may occupy warmer areas where growth and reproductive success is optimized.

Three years after the eradication of brook trout from Sun Creek, the bull trout population exhibited little change in distribution (Renner et al. in review). Belanger and Rodriguez (2002) suggested that habitat quality is difficult to ascertain using fish densities because of effects from seasonal changes, variability in food sources, biotic, and abiotic influences. As an alternative, local movement and distribution may provide a more reliable understanding of habitat selection (Belanger and Rodriguez 2002). For example in environments where habitat conditions vary substantially among years, (e.g., the Southern Appalachian Mountains) the distribution of nonnative rainbow trout (*Oncorhynchus mykiss*) exhibited a pattern of "ebb and flow" in relation to seasonal and abiotic factors (Larson et al. 1995). Strange and Habera (1998) suggested that rainbow trout in southern Appalachian streams were not affecting the downstream limits of brook trout populations, instead, the distributional limits of both rainbow and brook trout fluctuated upstream and downstream over time with changing environmental factors. In Sun Creek, bull trout have fluctuated around a "core" area and did not shift into habitat previously occupied by brook trout. This observation suggested they have continued to occupy habitat that is suitable for survival and recruitment.

Why are bull trout concentrated in a 4 km region of Sun Creek when the entire creek is within their thermal tolerances? It is possible that population density has not reached levels that would prompt downstream movement. This possibility seems unlikely because there is no evidence of a shift downstream after 11 years of brook trout extirpation and a 300% increase in bull trout abundance after brook trout extirpation (Renner et al. in review). If population size is not the regulating mechanism determining bull trout distribution in Sun Creek then the most likely variable explaining the paucity of bull trout in the lower reaches of Sun Creek is the increase in turbidity immediately downstream of the bull trout distribution (Figure 3.3). Comparisons of areas where bull trout were present and absent suggested a strong negative relationship between bull trout and turbidity. High turbidity may deter bull trout by reducing foraging success. Turbidity has been shown to decrease the reaction distance between fish and their prey (Gradall and Swenson 1982; Barrett et al. 1992; Abrahams and Kattenfeld 1997). Very turbid water (>40 NTU) can promote a change in foraging strategies from "lie in wait" to active searching for prey, negatively affecting the ability of trout to feed and limiting growth from increased energy expenditure (Sweka and Hartman 2001b, a).

The increase in turbidity likely originates from a series of anoxic springs that produce an iron flocculent which covers the streambed and appears to be related to the turbidity. If bull trout are not responding to impaired vision from high turbidity then it could be the chemical properties or the turbidity may act as a gill irritant (Redding et al. 1987; Bash et al. 2001). Regardless of the mechanism in the turbidity that bull trout are responding to, this point source impact likely explains why bull trout were not found throughout Sun Creek.

Although the downstream peak in springs appears to be associated with the increase in turbidity, our finding suggest that bull trout abundance in the low turbidity areas of Sun Creek is related to the presence of springs. The peak in the Sun Creek bull trout population occurs immediately downstream from the peak in springs (Figure 3.4). Bull trout are not directly responding to the number of springs, they do appear to respond to the downstream influence of the springs. The influence of cold springs may help maintain stream temperatures within bull trout's thermal optima during periods of drought and above average air temperatures (Buchanan and Gregory 1997; McMahon et al. 1999; Gamett 2002). Conversely, this study found that bull trout abundance was positively correlated with temperature. Indicative that Sun Creek may be colder than needed to support bull trout, and that springs may prevent the stream from getting too cold. In the winter springs may help keep portions of the stream ice free; however, this study did not examine winter bull trout distribution or habitat conditions.

In addition to regulating stream temperatures in Sun Creek, springs may also play an important role in redd site selection and egg survival (Baxter and McPhail 1999; Baxter and Hauer 2000). For example, Baxter and Hauer (2000) found bull trout spawning where groundwater upwelling increases, and Baxter and McPhail (1999), suggested that higher egg survival in upwelling areas was likely due to increased oxygenation of eggs and the prevention of anchor ice.

In reaches and fixed length sections of the stream where the turbidity was low, bull trout abundance increased where pools were deeper. Additionally, electivity analysis at the unit scale found that bull trout preferred pools to riffles an association that has been found for nearly all salmonids (Johnson and Kucera 1985; Bisson et al. 1988; Marcus et al. 1990). Pools and other slow water areas are bioenergetically beneficial to trout by providing areas where trout can forage with minimal effort (Rosenfeld and Boss 2001).

The majority of current research on bull trout habitat associations has focused on the importance of cold temperature (<15ºC); however, throughout Sun Creek temperature was within bull trout tolerances. Turbidity appears to confine bull trout presence to the upstream reaches of Sun Creek emphasizing the influence that point source effects can have in explaining trout distributions in a stream. Studies that examine only several small sites (100 - 200 m) within a stream may miss important point source effects on populations. The findings of this study underscore the importance of examining continuous stream reaches to help identify point source influences.

Bull trout were once distributed throughout Sun Creek and into the Wood River, likely as part of a historic Upper Klamath Basin metapopulation (Wallis 1948; Buchanan et al. 1997). Migratory trout tend to be larger than residents and may be more tolerant of marginal habitats, such as higher turbidity (McPhail and Baxter 1996). The higher turbidity region of Sun Creek may be acting as a sink that may be utilized by bull trout once their abundance increases. Continued monitoring of this population is needed to determine if Sun Creek bull trout still exhibit migratory life histories and if the higher turbidity lower reaches continue to deter bull trout presence.

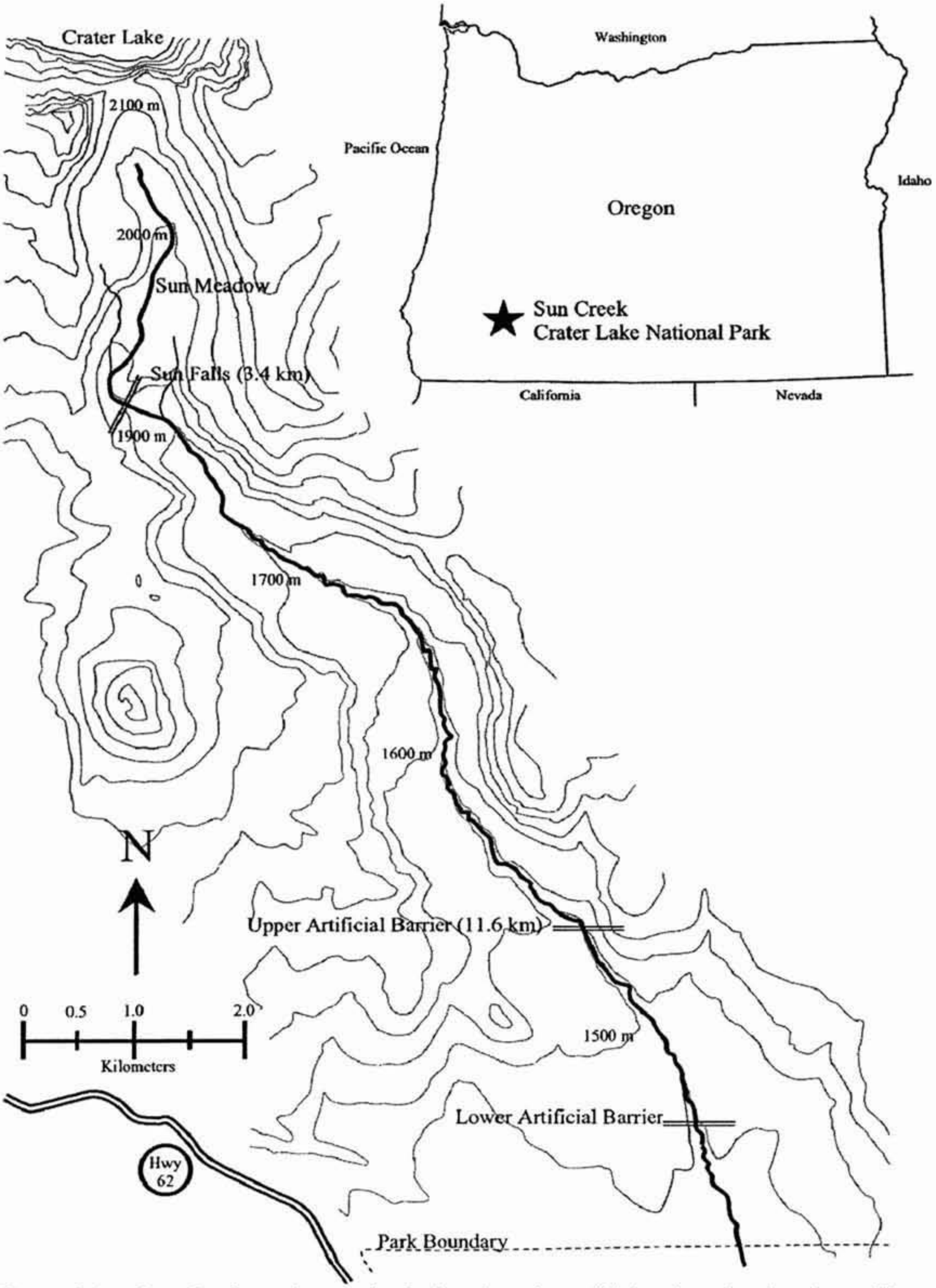

Figure 3.1 – Sun Creek study area including location of fish migration barriers. Flow direction runs from north to south

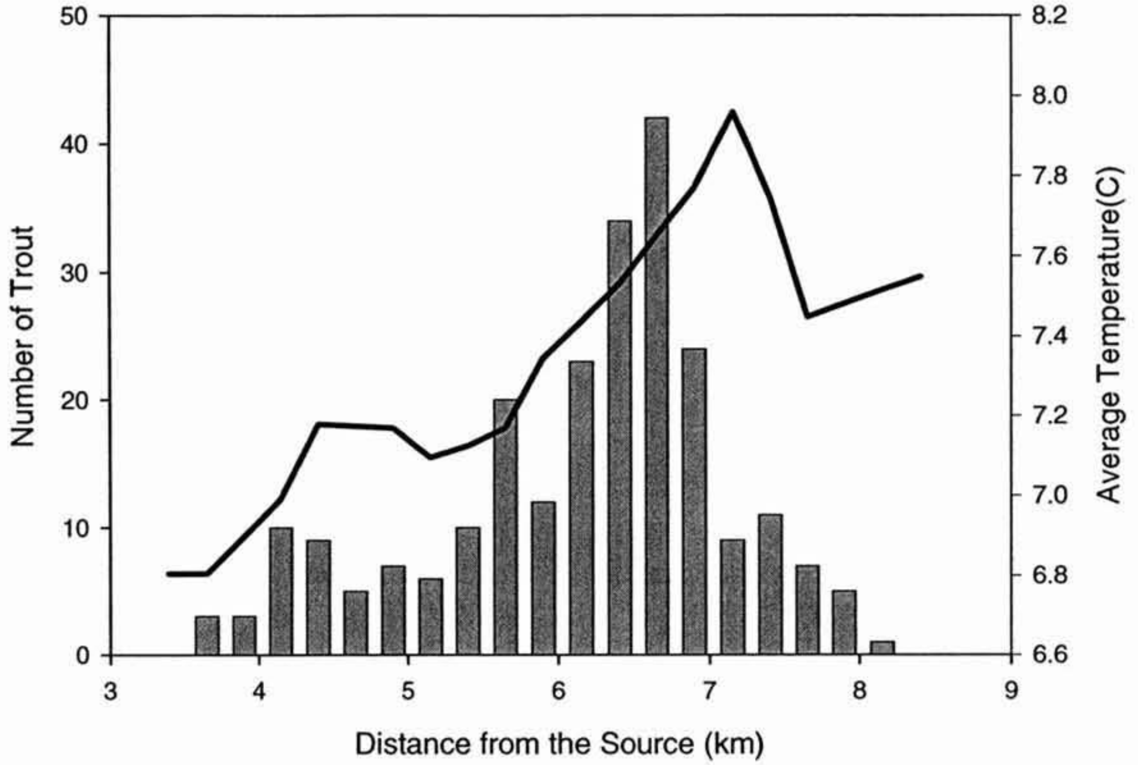

Figure 3.2 - Relationship between bull trout (bars) and average temperature (line) in Sun Creek.

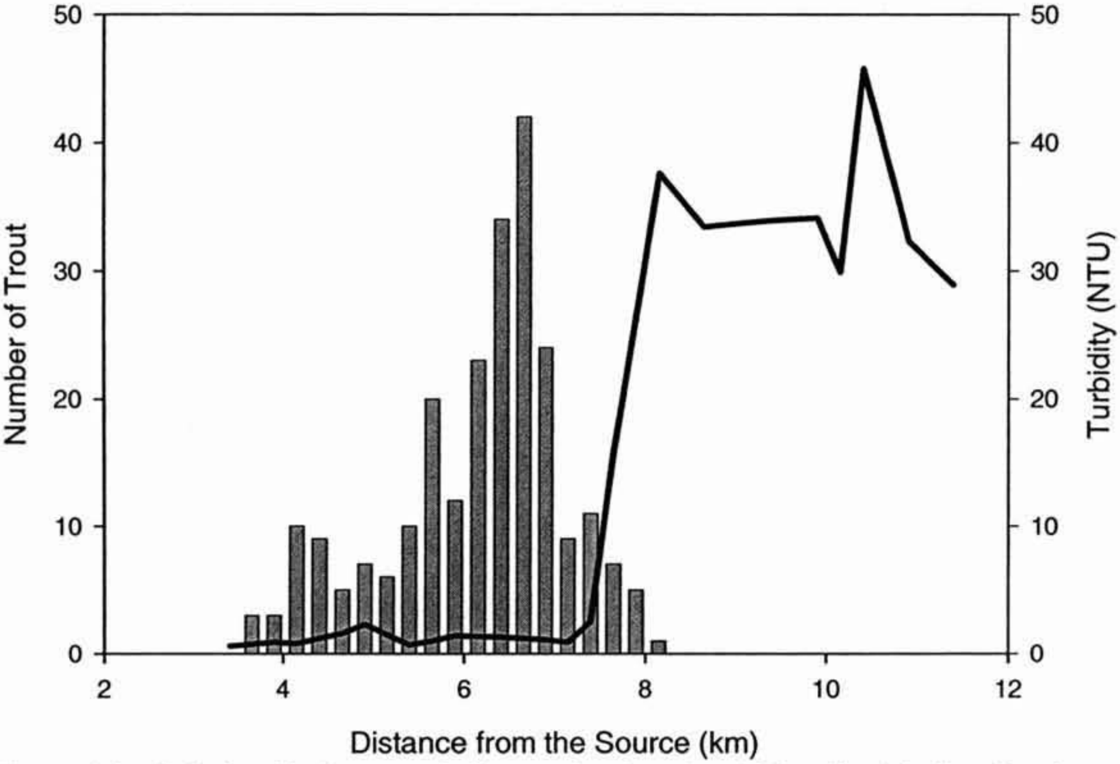

Figure 3.3 - Relationship between bull trout (bars) and turbidity (line) in Sun Creek.

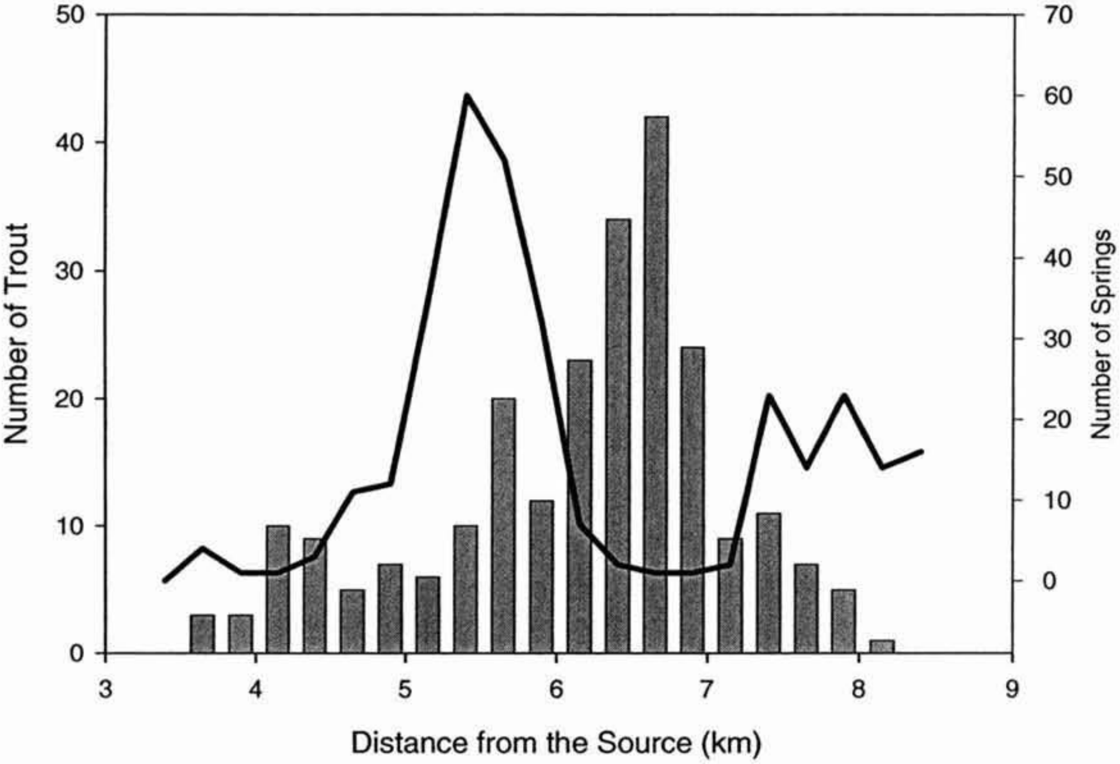

Figure 3.4 - Relationship between bull trout (bars) and spring abundance (line) in Sun Creek

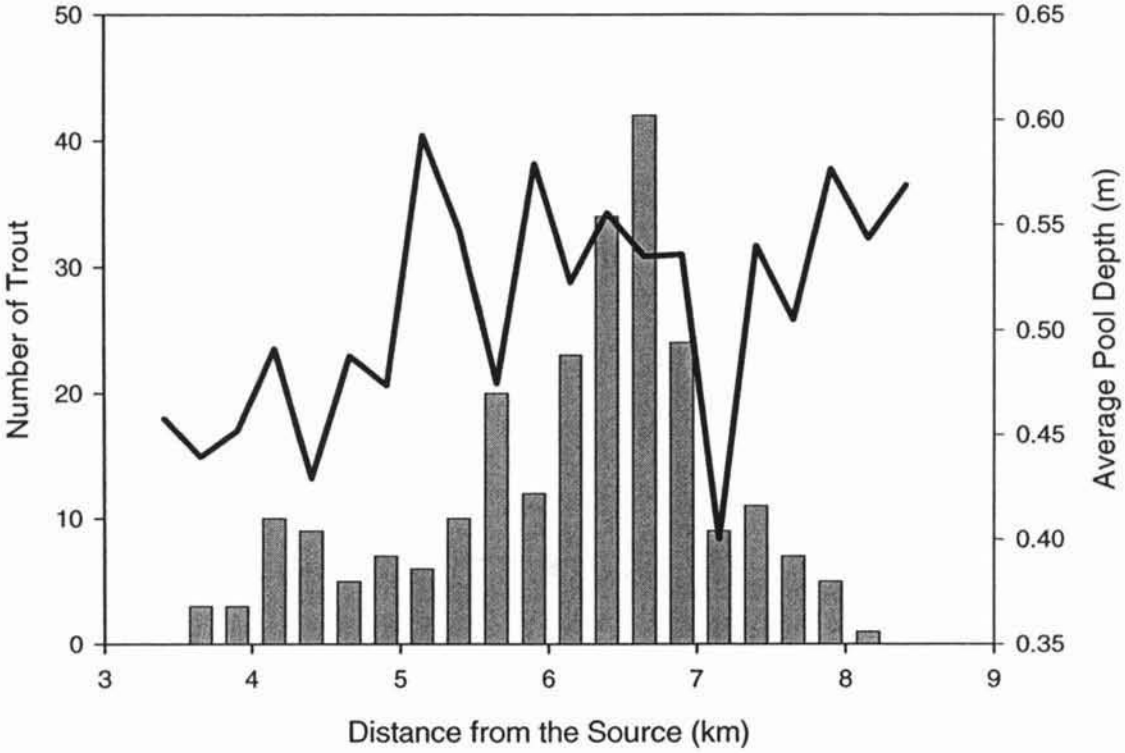

Figure 3.5 - Relationship between bull trout (bars) and average pool depth (line) in Sun Creek

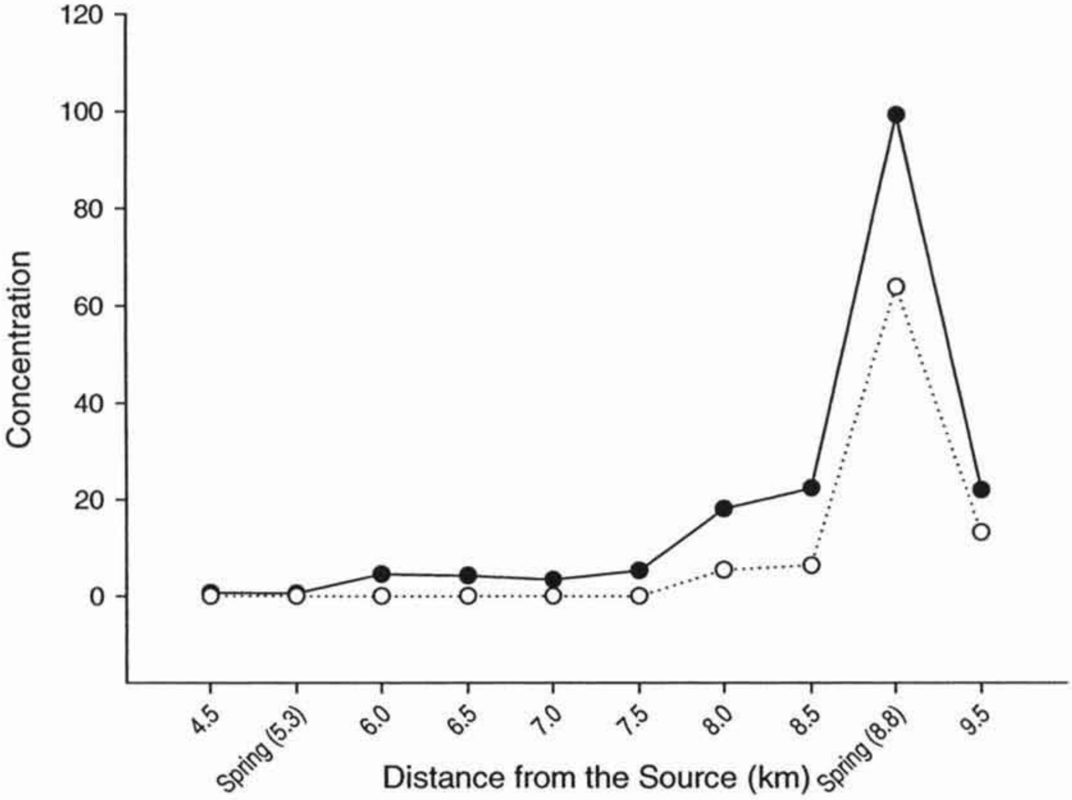

Figure 3.6 - Downstream changes in concentrations of manganese (●; ppb) and cobalt (○; ppt) for eight stream water samples and two springs

Table 3.1 - Stepwise regression results for factors influencing bull trout abundance at the geomorphic reach, 250-m section, and habitat unit scale in low turbidity regions of Sun Creek. Variables included were all significant predictors of bull trout abundance when examined with univariate regression.

Variable	**Regression Coefficient**	***P***	**R^2**	**Model *p***	**Durban Watson Value****
Reach Scale (n = 15)			**0.91^{m}**	0.005	2.37
Mean Pool Depth	26.36 (6.2)	0.008			
Mean Temperature	4.42 (4.0)	0.32			
Spring Density	-0.16 (0.14)	0.3			
250m Sections (n = 33)			**0.56^{m}**	0.003	1.42
Mean Pool Depth	8.012 (4.46)	0.09			
Average Temperature	0.699 (0.14)	0.004			
Unit Scale (n = 926)			**0.14^{m}**	<0.001	1.65
Distance From Source	0.0001 (0.00)	< 0.00			
Distance to Springs	-0.023 (0.01)	0.06			

Table 3.2 - Ivlev's electivity analysis comparing units in reaches that contained bull trout.

Variable	Proportion of Available Habitat	Fish Observed	Fish Expected	Preference	Ivlev's Electivity Index
Pool - Riffle					
Riffle	0.76	62	178.6	Avoids*	-0.48
Pool	0.24	173	56.4	Prefers*	0.51
Type of Pool					
Dam Pool	0.147	22	25.431	-	-0.07
Plunge Pool	0.5483	117	94.8559	Prefers*	0.10
Scour Pool	0.3047	34	52.7131	Avoids*	-0.22
Unit Substrate					
Cobble	0.32	89	75.2	-	0.08
Gravel	0.56	94	131.6	Avoids*	-0.17
Sand	0.11	52	25.85	Prefers*	0.34
Silt	0.01	0	2.35	Avoids*	-1.00
Springs					
Springs present	0.27	73	63.45	-	0.067
No springs	0.73	162	171.55	-	-0.03

Ivlev's electivity Index is calculated as $E_i = (r_i - p_i)/(r_i + p_i)$, where r_i is the proportion of habitat used and p_i is the proportion in the environment. * Significant values lie outside Bonferroni Confidence Intervals (White and Garrott 1990).

Chapter 4 - Conclusion

Research examining relationships between brook trout and bull trout has focused on microhabitat interactions often studied in enclosures or laboratory settings (McMahon et al. 1998; Gunkel et al. 2002). No studies have examined the distribution of a native trout in *situ*, following the removal of an introduced species. After 12 years of brook trout removal, bull trout distribution in Sun Creek did not change. Bull trout maintained their general distribution in the stream with minor annual expansions and contractions, but no directional trend. Had bull trout been competitively excluded from the optimal habitat as was previously assumed, a shift or redistribution by bull trout into habitat previously occupied by brook trout would be expected (Dambacher et al. 1992). Bull trout increased in abundance over 300% following the removal of brook trout. If bull trout had not been relegated to marginal habitat as suggested by Dambacher et al. (1992), then brook trout were negatively influencing the bull trout population through a mechanism other than competition for habitat.

Bull trout and brook trout share similar spawning requirements increasing the likelihood of disruptive spawning interactions affecting bull trout recruitment (Rieman and McIntyre 1995). Evidence of this disruptive interaction is supported by the finding that hybrids are predominantly from crosses between male brook trout and female bull trout (Kanda et al. 2002). A disproportionately greater loss to bull trout recruitment may result from hybridization and this deleterious effect is compounded by earlier maturity and greater population growth of brook trout (Fraley and Shepard 1989; Goetz 1989).

Bull trout are one of the most thermally sensitive coldwater species in western North America rarely found where average temperatures exceed 14° C (Buchanan and Gregory 1997; Gamett 2002; Dunham et al. 2003b). The Sun Creek bull trout population is in the southern margin of the species range where temperature may be more important in delineating the species distribution than more northerly populations (Dunham et al. 2003b). Stream temperatures recorded during the study indicated that the entirety of Sun Creek has mean summer temperatures well within the thermal optima for bull trout; however, bull trout were not distributed equally throughout the creek.

The increase in turbidity in the lower reaches of Sun Creek strongly deterred bull trout at both the reach and 250-m section scales. High levels can reducing foraging success or it could be a chemical or gill irritant (Redding et al. 1987; Bash et al. 2001). Regardless of the mechanism in the turbidity that bull trout are responding to, this point source impact likely explains why bull trout are not found throughout Sun Creek.

Bull trout distribution was associated with springs at the reach and unit scales, and the peak in bull trout abundance was immediately downstream from the peak in springs. Springs may help maintain stream temperatures during periods of drought and above average air temperatures (Buchanan and Gregory 1997; McMahon et al. 1999; Gamett 2002). Springs also play an important role in redd site selection and egg survival (Baxter and McPhail 1999; Baxter and Hauer 2000). Baxter and Hauer (2000) found bull trout spawning in areas of groundwater upwelling and Baxter and McPhail (1999) determined that egg survival in areas of upwelling was due to increased oxygenation and the prevention of anchor ice.

Studies of the interactions between brook trout and bull trout at the microhabitat scale has demonstrated that brook trout are more competitive (Gunkel 2000). The absence of a change in the bull trout population with the removal of brook trout suggests that environmental factors are likely the limiting factor influencing the distribution of bull trout in Sun Creek. The bull trout population appears to be focused in a "core" area of favorable habitat and will likely radiate upstream and downstream as population densities and environmental variables change (Brown 1984; Travis 2004). As densities, biotic interactions, life histories, or environmental variables fluctuate, individuals may move out of the core area and into less favorable habitats (VanHorne 1983).

Our results indicate that the protection of core areas from brook trout influence can assist in bull trout restoration. In streams where populations are not constrained by limited resources, then reproductive interference and hybridization with brook trout may be the causal factor in the displacement of bull trout. Under such conditions, efforts to remove brook trout from bull trout spawning areas may better protect bull trout populations over the short-term However, in most cases comprehensive restoration of bull trout populations undoubtedly requires the complete removal of brook trout. Specific factors that influence the success or failure of bull trout reproduction when these species occur in sympatry deserves further study.

Turbidity in Sun Creek appears to be limiting bull trout presence in the downstream reaches and emphasizes the influence that point source effects can have on trout distributions. Examining continuous streams when determining variables that influence trout distributions will help to identify point source influences. Continued monitoring of the Sun Creek bull trout population is needed to determine if the turbidity in the lower reaches is a chronic variable that continues to constrain the population if abundances continue to increase.

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