

Effects of Redd Superimposition by Introduced Kokanee on the Spawning Success of Native Bull Trout

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Abstract.—Intra- and interspecific competition for spawning space is a commonly observed interaction in salmonids that can result in progeny loss. This study examined the impacts of redd superimposition by kokanee *Oncorhynchus nerka* on the reproductive success of bull trout *Salvelinus confluentus* in the Deschutes River basin, Oregon. The activities of high-density spawning groups of kokanee were hypothesized to place the eggs and alevins of bull trout at risk of displacement and damage wherever the spawning habitats of these two species overlap. Bull trout egg pocket depths and kokanee scouring depths were measured. Fry emergence from redds, a proxy for bull trout reproductive success in the presence of kokanee, was compared between superimposed and undisturbed redds by using fry emergence traps. Our results indicate that groups of spawning kokanee did not scour the stream bed deeply enough to reach bull trout eggs. Data on bull trout fry emergence revealed that kokanee redd superimposition did not affect bull trout egg-to-fry survival rates.

Salmonid reproductive behavior and different indicators of its success, such as egg production, embryo survival, fry emergence, or redd superimposition have been examined in many studies (e.g., McNeil 1964; Peterson and Quinn 1996; Baxter and McPhail 1999). Redd superimposition is a form of competition that takes place among salmonids when the availability of spawning beds is limited in relation to spawner abundance. Superimposition occurs when gravel and other substrate particles in a redd are dug and disturbed by the spawning activities of subsequent females; through egg displacement, it has been inferred as a major cause of density-dependent embryo mortality (Parenskiy 1990; Chebanov 1991; Fukushima et al. 1998).

Egg displacement may be less likely when there are marked size dissimilarities between species, although late-spawning smaller fish still are thought to affect the reproductive success of early spawners through other indirect mechanisms. For example, embryos in redds may be subject to suffocation, entrapment, or physical damage when the composition of the gravel and the integrity of the egg pockets is altered by late spawners (Meyer et al. 2005). During redd digging, salmonids release sediments from the streambed. The excavated

gravels and interstitial fine sediments are exposed to currents and transported downstream (Kondolf et al. 1993). If those fine substrate particles are deposited in downstream redds in high quantities, they can either reduce the permeability of the gravel and the amount of water flowing past the incubating embryos (Chapman 1988) or form sand seals that prevent fry from emerging (Phillips et al. 1975). In addition, during critical developmental stages, salmonid embryos are extremely sensitive to mechanical shock (Johnson et al. 1989); substrate digging activities by late spawners may agitate the eggs that were already laid and thus affect their development.

Empirical evidence of the outcome of interspecific redd superimposition in terms of gravel composition changes and fry production is scarce. Studies that have explored superimposition have focused on anadromous salmon and have examined density-dependent egg loss (e.g., Fukushima et al. 1998) on a stream-wide (e.g., McNeil 1964) and spawning channel scale (e.g., Essington et al. 2000).

The potential incidence of interspecific spawning competition is an issue with management implications in basins where the spawning habitats of different sized salmonids overlap, such as kokanee (a small, land-locked form of sockeye salmon *Oncorhynchus nerka*) and bull trout *Salvelinus confluentus*. Where kokanee spawn in high-density aggregations (spawning cohorts), the redds of the earlier-spawning bull trout can be altered beyond recognition (M. A. Weeber, personal observation). The impacts of this interaction have been

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implicated in the decline of some bull trout populations (USFWS 2002) and are of great concern in basins where kokanee have been introduced and native bull trout numbers are depressed. Adfluvial bull trout are considerably larger than kokanee and should therefore be able to bury their eggs much deeper (DeVries 1997); to our knowledge, however, this hypothesis has not been tested specifically.

The goal of this study was to determine whether superimposition of redds by kokanee has a negative effect on production of bull trout fry. To evaluate this goal, we tested whether the scouring potential of spawning kokanee overlapped that of egg pocket depth for co-occurring bull trout. In another test of whether kokanee redd superimposition affects bull trout fry survival and duration of egg incubation, we compared the number of emergent fry and time-to-emergence between undisturbed and kokanee-altered bull trout redds.

Study Sites

Data were collected over two spawning seasons (the autumns of 2005 and 2006) in two subbasins of the Deschutes River basin, Oregon: Metolius River and Odell Lake (Figure 1). Both study subbasins have populations of adfluvial bull trout and kokanee, yet are geographically isolated from each other. Bull trout are native to both systems; kokanee were introduced into the Odell Lake subbasin, whereas kokanee in the Metolius River subbasin derive from an extirpated run of anadromous sockeye salmon, plus hatchery stocks. Peak spawning for bull trout in the Deschutes Basin normally occurs during the first week of September; peak spawning for kokanee generally occurs about a month later.

In the Odell Lake subbasin, data were collected in Trapper Creek, a second-order perennial stream and the largest lake inflow. A natural upstream barrier restricts spawning to the lower 1.3 km of the creek. Composed of riffle-pool habitat in its lower section, this creek is the only known spawning habitat utilized by bull trout throughout the Odell Lake system. Although all bull trout in the Deschutes River basin are listed as "threatened" under the Endangered Species Act, the population in Odell Lake is considered particularly sensitive (Ratliff and Howell 1992). An average of 10 redds per year has been observed in Trapper Creek over the past 13 years (Oregon Department of Fish and Wildlife, unpublished data).

In the middle of the Deschutes Basin, the Metolius River runs for approximately 41 km before discharging into Lake Billy Chinook, a man-made reservoir. Data were collected in several tributaries, including Candle, Canyon, and Jefferson creeks, as well as Heising

Springs and Roaring Springs. Being a predominantly spring-fed system, flows and water temperatures fluctuate little over the year and spawning habitats are abundant. Unlike the Odell Lake population, Metolius River bull trout are thought to be relatively healthy. Up to 1,000 redds have been counted in the sub-basin in recent years (Oregon Department of Fish and Wildlife, unpublished data).

Methods

Bull trout egg burial depth.—Twenty-six bull trout redds were manually excavated throughout the Metolius River subbasin before kokanee arrived. No bull trout egg burial data were collected in the Odell Lake subbasin because of concerns over affecting the few redds found each year in that system. The examined redds in the Metolius River subbasin were randomly selected from a previously marked pool of redds, which had been located by surveying stream reaches having high bull trout redd densities. Each redd was evaluated by using a manual excavation technique, whereby redd substrate was carefully removed until the top of an egg pocket was reached (see Weeber 2007). An egg pocket was defined as a space in the gravel containing five or more eggs (Crisp and Carling 1989) separated by no more than a few egg diameters (DeVries 1997). Individual egg pockets were referenced to the depth below both prespawning (measured around redd) and postspawning substrate levels (Figure 2). Because our sampling locations were primarily spring-fed and had a low, constant discharge rate, substrate aggradation or scouring were not concerns in this study.

Kokanee scour monitoring.—As with the sockeye salmon observed by Parendskiy (1990), we observed kokanee in our study systems spawning at high densities and disturbing large areas of gravel without building distinct redds. This made locating and reliably identifying kokanee egg pockets difficult. As a result, few kokanee egg pockets could be identified, and their depths could be measured only to the surface of the postspawning bed elevation rather than to the prespawning substrate level. The latter measurement would have been a common reference point needed for comparison with bull trout egg burial depths. Therefore, in this paper we assume that the kokanee prespawning reference bed level equates on average to the postspawning bed elevation of bull trout and analyze the data accordingly. To this aim, we measured the collective scouring ability of kokanee by using 30 sliding-bead monitors in Trapper Creek, within the Odell Lake subbasin. Trapper Creek contains some of the highest densities of spawning kokanee throughout the Deschutes Basin. The monitors operate similarly to

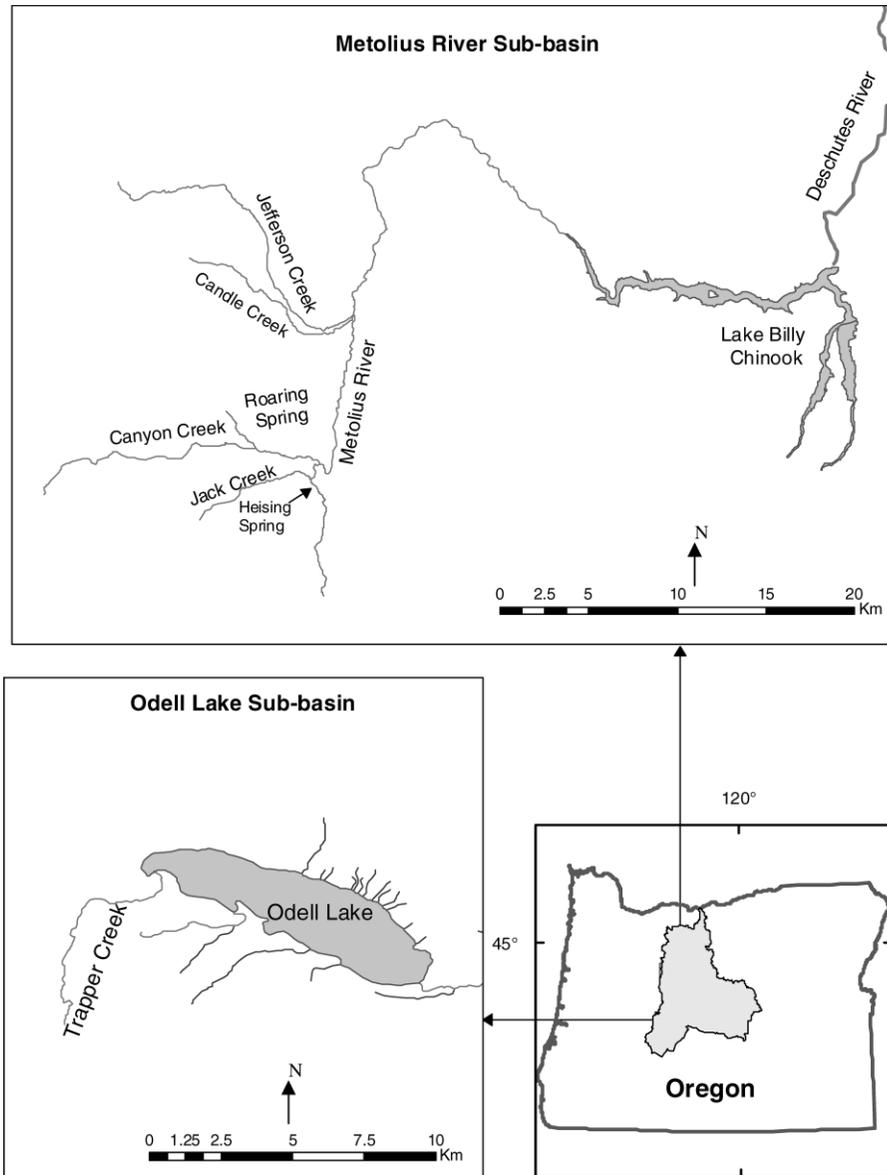


FIGURE 1.—Locations of the Deschutes River basin and the two study subbasins (enlarged): the Metolius River subbasin, which has Heising Spring among its tributaries; and the Odell Lake subbasin, which has Trapper Creek as a tributary.

scour chains and do not interfere with the spawning activities of fish (Nawa and Frissel 1993). When scouring of the substrate surface occurs, buried beads are released into the water column and swept to the end of the unburied portion of the wire on which they were threaded. The number of beads (multiplied by the bead diameter) that move to the end of the braided wire represent the depth of scour. In much the same way, if any sediment is deposited on top of the device, the amount of deposition can be determined by measuring

the length of buried wire. In August 2006, before any spawning, monitors were set 0.5 m apart on eight transects in areas known to support high densities of spawning kokanee. This resulted in three to six monitors per transect, depending on the width of the stream. Throughout the kokanee spawning period, all monitors were examined daily and the numbers of exposed beads recorded. To account for possible scour or fill caused by discharge fluctuations, we monitored the water level with a fixed gauge.

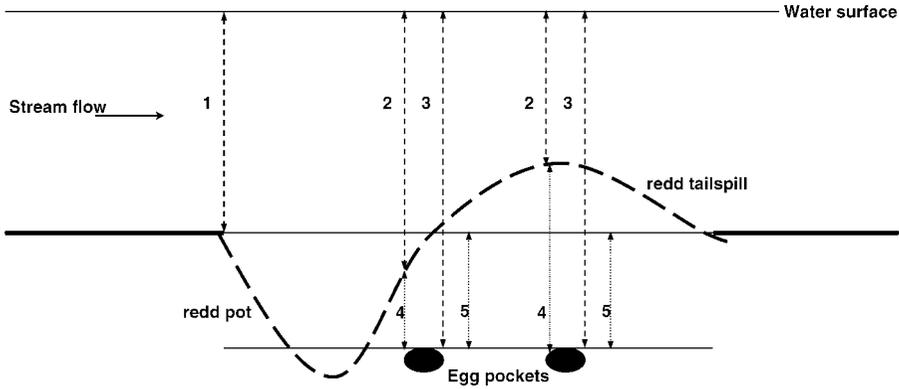


FIGURE 2.—Side-view diagram (not to scale) of the stream substrate at a bull trout redd location. Numbered arrow (1) represents the water column depth referenced to the prespawning substrate level, arrow (2) the water column depth referenced to the postspawning substrate level, and arrow (3) the water column depth to the top of the egg pocket. These measurements were used to determine (4) the egg pocket depth below the postspawning substrate level and (5) the original prespawning substrate level. (Figure adapted from Steen and Quinn 1999).

Bull trout fry emergence.—In fall 2005, Heising Spring, within the Metolius River subbasin, was surveyed two to four times a week. Sixty-four bull trout redds were identified, marked, and measured for physical redd characteristics. Redd surface area ($\pm 0.1 \text{ m}^2$) was approximated according to the formula for an ellipse: surface area = $\pi \cdot (\text{length}/2) \cdot (\text{width}/2)$. Water velocity ($\pm 0.01 \text{ m/s}$) was measured with a digital flowmeter at 60% depth directly upstream of the front edge of the redd. Redd perimeters were defined by positioning six white surveyor ground flags around redd peripheries. Four to five small orange rocks were set on the tailspill of each redd to aid in detecting subsequent disturbances. After the arrival of kokanee, any observations of redd alteration were noted in relation to the surveyor flags and orange rock movements. A 0–2 rating system was developed to identify the degree of redd disturbance caused by kokanee digging. If no disturbance occurred, the score was 0. Redds that sustained minor structural disturbances were scored 1, and those severely altered were scored 2. Only redds with scores of 2 were classified as superimposed, meaning that significant scouring and deposition occurred to the point where the original redd perimeter and shape could not be recognized.

In January 2006, 10–15 d before the time when bull trout fry emergence was predicted to start, a total of 14 redds were selected for emergent fry trap placement. Trapped redds were randomly selected after considering predicted emergence timing and presence or absence of kokanee superimposition: 7 of the 14 traps were set on bull trout redds classified as superimposed by kokanee; the remaining 7 were placed on undisturbed redds. Each trap consisted of a mesh net secured

to a steel frame (208 cm \times 323 cm), a downstream collection tube, and a polyvinyl chloride live-well. Fry emergence traps were similar to those used by Tagart (1984) and described by Sparkman (2004). Traps were set to encompass the entire redd and checked every other day until emergence began to slow. All captured fry and alevins were identified to species, and any morphological abnormalities were noted. After enumeration, the fry were released into the stream margin.

To evaluate potential confounding effects between the number of fry that emerged from superimposed and undisturbed redds, we compared certain physical redd characteristics. In addition to redd surface area and surface water velocity, we measured substrate particle size in our trapped redds. We used geometric mean particle diameter (D_g) as a relative measure of substrate size. Two core samples from the tailspill of each trapped redd ($n = 28$) were collected after fry emergence was over. Collection methods, sorting techniques, and sample-size criteria followed those described by Shirazi et al. (1979). A 25-cm-diameter modified McNeil sampler was used to collect the redd substrates to a depth of 20 cm. The values were calculated by using custom software GRAVEL (Goforth 1992). GRAVEL was used to characterize the entire redd, we pooled the two samples collected.

Statistical analyses.—We used an α value of 0.05 in all tests and S-PLUS statistical software (version 7.0; Insightful Corp.) for all analyses. Two-tailed t -tests were used to test for differences in the depths of bull trout egg pocket and kokanee scour. Two-tailed t -tests were also used to test for differences in physical redd characteristics, emergent fry abundance, and timing between superimposed and undisturbed redds.

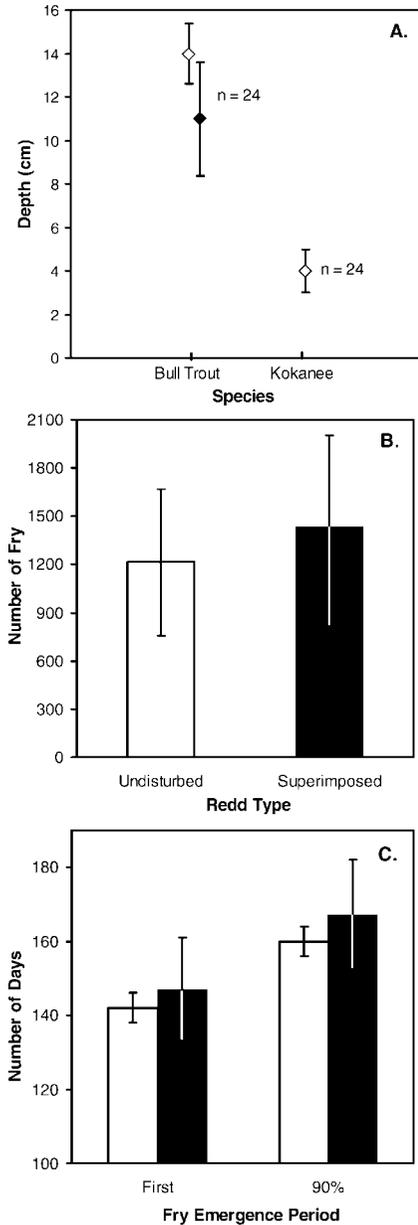


FIGURE 3.—Panel (A) presents a comparison between mean bull trout egg pocket depth (open diamonds = the depth below the postspawning substrate; filled diamonds = the depth below the prespawning substrate) and the mean scouring depth of spawning kokanee groups. Panel (B) shows the mean number of emergent bull trout fry captured from kokanee-superimposed and undisturbed bull trout redds. Panel (C) shows the mean number of days to the first bull trout fry emergence from undisturbed (white bars) and superimposed (black bars) bull trout redds as well as the number of days to 90% emergence. The vertical lines represent 95% confidence intervals.

Results

Bull Trout Egg Burial Depth

Bull trout egg pockets were identified in 24 of the 26 redds evaluated. The number of egg pockets found per redd ranged from 1 to 4. Mean egg pocket depth per redd was 14 cm (SD = 3.5) below the postspawning substrate and 11 cm (SD = 3.5) below the surface of the prespawning substrate (Figure 3A). The deepest egg pocket was 22 cm below the postspawning substrate, and the shallowest was 5 cm. We found a significant difference in mean egg pocket depth below the postspawning and the prespawning substrate elevations (paired $t = 2.19$, $df = 23$, $P = 0.04$). Mean egg pocket depth below the postspawning substrate elevation was 3 cm deeper than the mean depth below the original prespawning surface (95% confidence interval = 0.2–5.3 cm).

Kokanee Scour Monitoring

Kokanee digging was observed on or directly near all sliding-bead monitors. Twenty-nine of the original 30 monitors installed were located; the missing monitor had been either buried or removed. Discharge did not fluctuate during the time the monitors were in place; therefore, scour and deposition depths were attributed to kokanee spawning activity only. Not all monitors recorded changes in substrate depth. No scour was recorded (i.e., no beads were released) at five monitoring locations, and no deposition was recorded at one location. On average, for those monitors that recorded a change in streambed elevation, the net change was positive (i.e., deposition). The mean change in streambed elevation per monitor was 1.3 cm (SD = 3.2), indicating that on average more substrate was deposited on top of the monitoring devices than was scoured away. For monitors that did record scouring by kokanee, the average depth of scour was 4 cm (SD = 2.4), a significantly (two-sample $t = 12.76$, $df = 51$, $P < 0.001$) shallower depth than the postspawning egg burial depth reached by bull trout (Figure 3A).

Bull Trout Fry Emergence

Emergent fry catches ranged from 31 to 2,601 individuals per redd and totaled 17,340. On average, more bull trout fry emerged from superimposed redds than from undisturbed redds (Figure 3B). However, this difference was not significant (two-sample $t = 1.00$, $df = 12$, $P = 0.34$).

Although bull trout fry emerged consistently later from superimposed than from undisturbed redds, we found no significant differences in either days to first emergence (two-sample $t = 0.67$, $df = 12$, $P = 0.38$) or

days to 90% fry emergence (two-sample $t = 0.91$, $df. = 12$, $P = 0.51$; Figure 3C).

Of the three physical variables (water velocity, redd area, and substrate size) we measured among trapped redds, water velocity was the only variable that showed a significant difference (two-sample $t = 3.23$, $df. = 12$, $P = 0.01$) between superimposed (mean = 0.38 m/s; SD = 0.1) and undisturbed redds (mean = 0.53 m/s; SD = 0.1).

Discussion

Our results indicate that in our study streams bull trout buried their eggs in the gravel beyond the depth scoured by kokanee spawning cohorts. Additionally, kokanee redd superimposition did not affect numbers or timing of emerging bull trout fry.

Bull trout egg burial depth measurements were consistent with those reported in previous studies (Block 1955: 20 cm; McPhail and Murray 1979: 10–16 cm; Leggett 1980: 10–15 cm; and Shepard et al. 1984: >14 cm). In addition, we found that most bull trout egg pockets were located near the center of the redd tailspill; hence, their burial depths to the postspawning substrate elevation were greater than the depths were to the level of the original prespawning substrate. Although such “enhanced” burial depth may provide bull trout eggs with some increased protection from redd superimposition by later-spawning females (especially those with smaller body size, such as kokanee), salmonid egg pocket location does not always coincide with the tailspill crest. When egg pockets are located closer to the periphery of the redd or the upstream half of the tailspill, as Steen and Quinn (1999) report for coho salmon, egg pockets may end up nearer to the postspawning substrate surface (for an illustration of this point see Figure 2), making them more vulnerable to displacement. The lateral placement of egg pockets within the redd is especially critical when considering the impacts of superimposition in streams that experience large fluctuations in seasonal discharge. Montgomery et al. (1996) report on chum salmon *O. keta* egg pocket depths being only slightly greater than average natural scour depths at bank full flow. This suggests that a reduction in egg burial depth either before or after a high water event could significantly increase the chances of egg displacement, especially if the eggs were initially closer to the postspawning substrate surface.

Direct behavioral observations revealed that kokanee were superficial spawners, superimposing conspecific redd sites, and leaving many eggs exposed on the substrate surface. For this reason, we were not able to compare their egg burial depths directly with those of bull trout. We therefore relied on sliding-bead monitors

to determine their scouring ability. These devices confirmed our observations of high rates of spawning site reuse. We found that, on average, kokanee deposited just as much sediment at monitoring sites as they scoured, and when scouring did occur, it was minimal. This is possibly attributed to the high densities of kokanee we observed on the spawning grounds. Although some studies conclude that high spawner densities do result in greater superimposition impacts (Chebanov 1991), others have reported that spawning ground overcrowding is accompanied by the formation of “aggregations under stress” that are totally or temporarily excluded from spawning (Parskiy 1990). In our kokanee study populations we observed frequent aggressive interactions, few male–female pairings, shallow egg depositions, and large numbers of eggs scattered on the substrate surface. Hence, kokanee-induced scouring over bull trout redds may be offset in some situations by deposition of substrate by subsequent spawning groups.

Despite kokanee altering the surface structure of some redds, fry trapping revealed no significant differences in the number or timing of emerging fry between superimposed and undisturbed redds. Bull trout fry emerged from all seven of the superimposed redds and, despite high variability, on average they emerged in slightly greater numbers from them than from the undisturbed redds. However, we cannot entirely discount that redd superimposition had negative effects on egg incubation and fry survival, given some physical differences between superimposed and undisturbed redds. Superimposed redds were located closer to the channel margins and in significantly lower velocity waters than were undisturbed redds. Thus, if channel margins provide better spawning habitat and yield better fry survival, then any superimposition effect could be masked. Previous studies have shown that substrates associated with lower water velocity contain a higher percentage of fine sediment (Buffington et al. 2004), which can be detrimental to fry survival (Chapman 1988). However, we saw no difference in substrate particle size between superimposed and undistributed redds.

Conspecific redd superimposition is frequently associated with density-dependent mortality of embryos in anadromous salmonid species (e.g., Essington et al. 2000). Our findings show that, when considering species that differ substantially in size, the effects of redd superimposition are not detectable if the larger species is the one that spawns first. Our results suggest that redd superimposition by kokanee poses limited or no threat to the reproductive success of bull trout, possibly because the latter are much larger than kokanee and can bury their eggs deeper in the

substrate. In view of the unique hydrologic regimes of our study systems, we think that this topic deserves additional consideration in streams with more variable discharge patterns. Redd superimposition studies need to consider egg pocket location within redds, both laterally and vertically. Egg pocket depths in relation to a common reference datum (such as prespawning substrate level) need to be used in such studies but with the awareness that redd structure can change, with discharge, during the incubation period. Redd location across the channel and its associated water velocity, intra-gravel flow, and substrate differences should be considered so their effects can be differentiated from those of superimposition.

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