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Use of cover habitat by bull trout, *Salvelinus confluentus*, and lake trout, *Salvelinus namaycush*, in a laboratory environment

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Abstract Lacustrine-adfluvial bull trout, *Salvelinus confluentus*, migrate from spawning and rearing streams to lacustrine environments as early as age 0. Within lacustrine environments, cover habitat provides refuge from potential predators and is a resource that is competed for if limiting. Competitive interactions between bull trout and other species could result in bull trout being displaced from cover habitat, and bull trout may lack evolutionary adaptations to compete with introduced species, such as lake trout, *Salvelinus namaycush*. A laboratory experiment was performed to examine habitat use and interactions for cover by juvenile (i.e., <80 mm total length) bull trout and lake trout. Differences were observed between bull trout and lake trout in the proportion of time using cover ($F_{1,22.6}$=20.08, P<0.001) and bottom ($F_{1,23.7}$=37.01, P<0.001) habitat, with bull trout using cover and bottom habitats more than lake trout. Habitat selection ratios indicated that bull trout avoided water column habitat in the presence of lake trout and that lake trout avoided bottom habitat. Intraspecific and interspecific agonistic interactions were infrequent, but approximately 10 times greater for intraspecific interactions between lake trout. Results from this study provide little evidence that juvenile bull trout and lake trout compete for cover, and that species-specific differences in habitat use and selection likely result in habitat partitioning between these species.

Keywords Bull trout · Lake trout · Cover habitat · Competition · Nonnative species

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Introduction

Nonnative species may interact with native species through competition, predation, disease transfer, and hybridization (Moyle and Cech 1996). Nonnative species introductions may also result in intraguild predation (Polis et al. 1989; Polis and Holt 1992) if both competitive and predator-prey interactions occur simultaneously between a native species and the nonnative species. Intraguild predators both prey on and compete with their prey, which may result in complex population dynamics. Additionally, intraguild predation may be asymmetrical (i.e., one species preys on and competes with the other) or symmetrical (i.e.,

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both species prey on and compete with the other) and can result in persistence of both species; unlike competitive exclusion (i.e., Hardin 1960).

Bull trout, *Salvelinus confluentus*, and lake trout, *Salvelinus namaycush*, occupying lacustrine environments may provide an example of intraguild predation. Bull trout are distributed throughout the northwestern United States and southwestern Canada. Habitat degradation and interactions with nonnative species have caused declines in the abundance of bull trout through much of their historic range (Leary et al. 1993; Rieman and McIntyre 1993; Kanda et al. 2002) resulting in bull trout being listed as threatened under the U.S. Endangered Species Act of 1973. Lake trout are a popular sport fish that have been introduced into many western lakes and reservoirs outside of their historic range (Crossman 1995; Martinez et al. 2009). There is a growing body of evidence suggesting that the introduction of lake trout into areas occupied by lacustrine-adfluvial bull trout may result in the displacement (Donald and Alger 1993) or reduction in abundance (Fredenberg 2002; Meeuwig et al. 2008; Martinez et al. 2009) of bull trout; although the specific mechanism resulting in these trends is unknown.

Bull trout and lake trout are generalist and opportunistic predators that may prey on a variety of fishes (Rawson 1961; Martin 1966; Donald and Alger 1993; Beauchamp and Van Tassel 2001; Clarke et al. 2005). Although published data are not available to show symmetrical or asymmetrical predation by these species, the generalist and cannibalistic (e.g., Beauchamp and Van Tassel 2001) predatory characteristics of these species suggest that either species may act as an intraguild predator (Polis et al. 1989). However, little is known about competitive interactions between these species. Competitive interactions between bull trout and lake trout may occur at or among different ontogenetic stages and for different resources. For example, it has been suggested that similarities in food habits between these species may result in competitive exclusion of bull trout by lake trout (Donald and Alger 1993). However, stable isotope analyses show that there is incomplete overlap in the source of energy that is assimilated between bull trout and lake trout (≥200 mm) for lakes in Glacier National Park, Montana (Meeuwig 2008). Alternatively, competition between bull trout and lake trout during juvenile life-history stages may have population level effects.

Juvenile bull trout often spend one to three years of their life in spawning and rearing streams prior to migrating to lake systems (see Pratt 1992 for review). However, in some systems bull trout migrate to lakes at early ages (e.g., ages 0 and 1; McPhail and Murray 1979; Fraley and Shepard 1989; Downs et al. 2006) and small sizes (e.g., <150 mm total length; Meeuwig and Guy 2007; Meeuwig et al. 2008). Migration to lake environments by juvenile bull trout may offer benefits in areas that exhibit environmental variability. For example, streams that exhibit high summer temperatures may be physiologically stressful (Selong et al. 2001; Dunham et al. 2003). Additionally, exclusion from upstream habitat as a result of water supercooling, anchor ice, and frazil ice during winter months can result in downstream movement of bull trout (Jakober et al. 1998). Therefore, movement of bull trout into lacustrine environments prior to age 2 could decrease exposure to physiologically stressful stream temperatures in the summer and mitigate movement associated with winter stream conditions.

Juvenile bull trout entering lacustrine environments would be exposed to both native and nonnative predators and competitors. Therefore, cover habitat (e.g., boulders, logs, aquatic vegetation, water turbulence, and concealing water depths; Armantrout 1998 *in* Stevenson and Bain 1999) would be important for juvenile bull trout entering lacustrine environments. Cover habitat conceals fish from predators and competitors (Orth and White 1999), and cover habitat is often defended or competed for through agonistic behavior (Moyle and Cech 1996). Cover habitat has been shown to be selected for by fishes [e.g., smallmouth bass, *Micropterus dolomieui* (Sechnick et al. 1986), Atlantic salmon, *Salmo salar* (Heggenes and Traaen 1988), bull trout (see Al-Chokhachy et al. 2010 for review)], and use of cover habitat can reduce predation risk. For example, predation on small (i.e., 35 to 44 mm total length) bluegills, *Lepomis macrochirus*, by largemouth bass, *M. salmoides*, (330 to 370 mm total length) decreased in areas of high structural complexity (Savino and Stein 1982).

Little is know about habitat use by juvenile lake trout; however, based on available data and the evolutionary association of lake trout with other predatory fishes (Martin and Olver 1980), it is plausible that juvenile lake trout use cover for protection, such as interstitial spaces along lake shorelines. For example, lake trout eleutheroembryos have been observed near spawning grounds within the interstices of rocks (Greeley 1936 *in* Martin and Olver 1980), and lake trout varying in length from 24 to 36 mm have been observed in association with a mixture of cobble, boulder, and sand substrate (Wagner 1981). If cover is an important resource for juvenile bull trout and lake trout in lacustrine environments, exclusion of bull trout from cover by lake trout through preemptive, territorial, or encounter competition (Schoener 1983) could result in bull trout being exposed to predators or being restricted to less productive or efficient foraging habitats. Therefore, exclusion of bull trout from cover may help explain declining trends in bull trout populations following the establishment of lake trout (e.g., Donald and Alger 1993; Fredenberg 2002).

A laboratory experiment was performed to evaluate habitat use and interactions between juvenile bull trout and lake trout (i.e., less than 80 mm total length). The aim of this study was to evaluate one aspect of a hypothesized intraguild predation relationship; specifically, competitive interactions for cover. Treatments evaluated the influences of fish density and species composition on use of cover, bottom, and water column habitats during daylight observations. Additionally, fish were allowed to emigrate from experimental tanks in the event that experimental conditions were unsuitable (e.g., Matter et al. 1989; McMahon and Hartman 1989). Specific predictions were made that: 1) a greater percent of bull trout and lake trout would emigrate from experimental tanks in the absence of cover habitat, 2) bull trout and lake trout habitat use would not differ in the presence of conspecific competitors compared to the absence of competitors, 3) in the presence of competitors, bull trout and lake trout habitat use would differ depending on whether the potential competitor was conspecific or heterospecific, and 4) in the presence of heterospecifics, lake trout would displace bull trout from cover habitat. Additionally, habitat selection by bull trout and lake trout was evaluated and agonistic interactions were recorded.

Materials and methods

Fish source and rearing conditions

Rearing and experimentation were conducted at Creston National Fish Hatchery, Montana, in an isolation room maintained for experimental use (i.e., not used for routine hatchery operation). Water used during rearing and experimentation was supplied from an artesian spring with an average annual temperature of about 8.3°C. Bull trout used in the experiment were second-generation progeny spawned in September 2006 from an experimental bull trout broodstock maintained at Creston National Fish Hatchery (Fredenberg et al. 1995). Lake trout used were obtained as eggs in November of 2006 from Saratoga National Fish Hatchery, Wyoming.

Bull trout and lake trout were incubated separately in eight tray Heath stack-type incubators. Once alevins neared swim-up, bull trout and lake trout were transferred to separate light blue fiberglass rearing tanks (3.0 m long×0.6 m wide×0.3 m deep; 0.2 m water depth) where they were held until they reached the target experimental size of about 60 to 80 mm. Artificial cover was provided by two sheets of corrugated fiberglass, each measuring 0.4 m long×0.2 m wide and suspended 5 cm off the bottom of the tank. Bull trout and lake trout were fed ad libitum by hand a diet composed of Silver Cup Fish Feed (Nelson & Sons, Inc., Murray, Utah). It was assumed that the feeding rates were sufficient due to the presence of uneaten food in the rearing tanks. Uneaten food was removed periodically to maintain water quality. Natural, ambient light was provided through a window in the isolation room during the rearing period.

Experimental tanks

Experimental tanks were constructed from particle board (bottom and three sides) sealed with light blue epoxy paint (Sweetwater epoxy paint, distributed by Aquatic Eco-Systems, Inc., Apopka, Florida) and plexiglas (one side, to allow observations). Tanks were a flow-through design with water entering the back-center of the tank near the top. Water exited the tank through a 5 cm inside diameter pipe located at the side of the tank that was designed to provide a shallow water exit for fish to emigrate from unsuitable experimental conditions (Matter et al. 1989). This pipe had a removable screen that was left in place during acclimation to experimental conditions and removed following acclimation. Tanks were arranged in two rows of four. A black plastic sheet was used to obscure the presence of the observer; a small slit was placed in the plastic sheeting to allow observations to be made. Each row of tanks was indirectly illuminated from above with one 100 w compact fluorescent light that produced a photoperiod of 14 h light and 10 h dark; light phase beginning at 07:00.

Research design

Once target fish length was achieved (June 2007), bull trout and lake trout were assigned to one of nine treatments (Table 1). Length (total length, mm) and mass (wet mass, g) were measured on all fish prior to experiments and individuals were assigned to treatments to minimize size differences within treatments. Bull trout varied from (mean±standard deviation) 67±4 to 70±2 mm and 2.4±0.5 to 2.9±0.4 g, and lake trout varied from 68±3 to 74±3 mm and 1.8±0.5 to 2.8±1.0 g among groups and treatments.

No individual fish were used in more than one treatment×replicate combination. Treatments varied in the presence of cover habitat (present or absent), fish density (one or two fish per tank), and species composition (bull trout, lake trout, or bull trout and lake trout) (Table 1). Fish densities were at least as great as those observed for these species in field studies (e.g., Peck 1982; Fraley and Shepard 1989; Hagen and Taylor 2001; Polacek and James 2003; Banish et al. 2008; Meeuwig et al. 2008). Cover consisted of one 85 mm long by 98 mm inside diameter section of PVC pipe, which was cut in half (internal volume=0.32 l). Treatments were placed into three 'groups' based on subsequent comparisons (Table 1).

Treatments were randomly assigned to the eight experimental tanks. The number of replicates varied from 4 to 6 among treatments (Table 1). Freshwater inflow ($\mathrm{l\,min^{-1}}$), temperature (°C), and dissolved oxygen ($\mathrm{mg\,l^{-1}}$) were measured immediately prior to the acclimation period and following the experiment. Freshwater inflow varied from (mean±standard deviation) 1.8±0.4 to 2.0±0.2 $\mathrm{l\,min^{-1}}$, temperature varied from 8.8±0.1 to 9.0±0.2 ° C, and dissolved oxygen varied from 7.78±0.23 to 8.38 ± 0.51 $\mathrm{mg\,l^{-1}}$ among all treatments and between the beginning of acclimation and the end of the experiment.

Fish were allowed to acclimate to experimental conditions for about 36 to 38 h prior to observation. The acclimation period began at about 18:00 so that the first observations could be conducted at 08:00. A small amount of food was added to each tank every morning prior to the beginning of the light phase of the photoperiod. Fish were observed feeding during the experiment, but uneaten food was always present in the tanks following the experiment. The screen blocking the tank exit was removed immediately prior to the beginning of the light phase of the photoperiod following the 36 to 38 h acclimation. For groups I and II, each tank was observed for six observation periods. Observation periods occurred at 08:00, 12:00, and 16:00 on the first and second day of the experiment and lasted 15 min. Observations were not made during the night in order to avoid potential behavioral artefacts associated with use of handheld lights or invasive marking techniques.

Fish presence (i.e., whether fish emigrated from experimental tanks) and habitat use in the tank was recorded once every 30 s during the 15 min observation. Habitat use included a) if fish were using cover (when available), b) if fish were using the tank bottom, and c) if fish were using the water column (i.e., not in contact with the bottom of the tank). Cover habitat occupied 1% of the tank volume, bottom habitat occupied 10% of the tank volume and consisted of the lowermost 2 cm of the water

Table 1 Group, treatment, number of replicates, cover present, fish density, and species composition for experimental treatments. Group III consisted of one bull trout for two days of observation (treatment III.a) followed by the addition of one lake trout for an additional two days of observation (treatment III.b)

Group	Treatment	Replicates	Cover present	Fish density	Species composition
I	I.a	5	No	1	Bull trout
	I.b	4	No	1	Lake trout
II	II.a	6	Yes	1	Bull trout
	II.b	5	Yes	1	Lake trout
	II.c	5	Yes	2	Bull trout
	II.d	5	Yes	2	Lake trout
	II.e	5	Yes	2	Bull trout and lake trout
III	III.a	4	Yes	1	Bull trout
	III.b	4	Yes	2	Bull trout and lake trout

column (approximate body depth of bull trout and lake trout used) of the tank minus the portion occupied by cover, and water column habitat occupied the remaining 89% of the tank volume. When two fish were present in a tank, chasing and nipping behaviors were recorded continuously throughout each 15 min observation period. For group III, procedures were as above with the exception that following observations on the second day the tank exit was blocked, a lake trout was added to the tank, and observations were resumed the next day for two additional days with the exit to the tank open.

Data analysis

All analyses were performed at $\alpha=0.05$ using SAS software (SAS version 9.1; SAS Institute Inc., Cary, North Carolina). Repeated measures analysis of variance (PROC MIXED; SAS Institute 1989) was used for all habitat use comparisons because observations were made repeatedly on the same experimental unit (tank) over a 32 h (groups I and II) to 80 h (group III) time period. All statistical models initially included a treatment effect, a time effect (continuous time effect; groups I and II: 0 to 32 h; group III: 0 to 80 h), and an interaction term to test for treatment× time effects. If the interaction term was not significant the model was fit including only treatment and time effects and if the time effect was not significant the model was fit including only the treatment effect. Unless otherwise noted, interaction terms and time effects were not significant.

For group I, comparisons were made between treatments in the proportion of time using the tank bottom and the proportion of time using the water column. In the absence of significant interaction and time effects, the treatment effect was used to test for differences in habitat use between bull trout and lake trout.

For group II, comparisons were made among treatments in 1) the proportion of time using cover, 2) the proportion of time using the tank bottom, and 3) the proportion of time using the water column. For treatments II.c and II.d, two conspecifics were present in the tank; however, individuals could not be uniquely identified. Therefore, the behavior of both individuals were recorded at 30 s intervals during each observation period (as above), but a post-hoc randomization procedure was used to randomly select one of those observations per 30 s interval for analysis. In the absence of significant interaction and time effects, preplanned comparisons using CONTRAST statements were used to compare between: 1) treatments II.a and II.c to test for differences in habitat use by bull trout at densities of one and two bull trout per tank, 2) treatments II.b and II.d to test for differences in habitat use by lake trout at densities of one and two lake trout per tank, 3) treatment II.c and the bull trout in treatment II.e to test for differences in habitat use by bull trout in the presence of a conspecific and a heterospecific, and 4) treatment II.d and the lake trout in treatment II.c to test for differences in habitat use by lake trout in the presence of a conspecific and a heterospecific. If no density effects (CONTRAST 1 and 2) and no species composition effects (CONTRAST 3 and 4) were observed, a fifth CONTRAST was performed to examine differences in habitat use between bull trout and lake trout among all treatments in group II.

For group III, differences in bull trout habitat use between the first two days of observation (treatment III.a) and the second two days of observation (treatment III.b) were evaluated. Habitat use comparisons included 1) the proportion of time using cover, 2) the proportion of time using the tank bottom, and 3) the proportion of time using the water column. In the absence of significant interaction and time effects, the treatment effect was used to test for differences in bull trout habitat use before and after the addition of a lake trout.

A chi-square procedure was used to evaluate whether bull trout and lake trout were using habitats in proportion to their availability. For this analysis, available habitats considered were cover, bottom, and water column habitats. Separate analyses were performed for treatments in which individual fish could be identified (i.e., treatment II.a, treatment II.b, and treatment II.e). For treatment II.e separate analyses were performed for bull trout and lake trout. Each chi-square test was performed following the methods summarized by Rogers and White (2007) in which individual fish are treated as the primary sampling unit. Three chi-square statistics were calculated that evaluate if individual fish within a treatment were using habitat differently (x^2_{L1}), if at least one of the fish within a treatment was selecting a specific habitat (x^2_{L2}), and if the fish within a treatment were using the habitat types in proportion to their availability ($x^2_{L1} - x^2_{L2}$), on average.

Population based selection ratios and Bonferonni-adjusted 95% confidence intervals were calculated to examine selection or avoidance of particular habitats (Rogers and White 2007). For these ratios, values greater than 1.00 indicate selection and values less than 1.00 indicate avoidance of a particular habitat. The 95% confidence intervals calculated for these ratios include information on variability among individual fish, and selection or avoidance of a particular habitat could only be inferred if the 95% confidence interval did not overlap 1.00.

Agonistic interactions were infrequent and variable among replicates within treatments. Therefore, data were summed over all replicates by treatment and presented as interactions per minute of observation to provide a qualitative assessment of agonistic interactions.

Results

Emigration from experimental tanks varied among treatments and between species (Table 2). By species, the greatest emigration occurred when cover was present and fish density was one fish per tank and the lowest emigration occurred when cover was present and fish density was two fish per tank (Table 2).

Table 2 Treatment and percent of bull trout and lake trout emigrating from experimental tanks. Treatments II.c and II.d had a density of two conspecific fish per tank; therefore, one fish could leave or both fish could leave

		Percent emigrating	
Treatment		Bull trout	Lake trout
I.a		20	
I.b			50
II.a		43	
II.b			60
II.c	One leaving	20	
	Both leaving	0	
II.d	One leaving		20
	Both leaving		0
II.e		0	20
III.a		20	
III.b			40

For group I, the proportion of time using the tank bottom differed significantly with time ($F_{1,38.4}$=5.02, P=0.031) and between treatments ($F_{1,7.8}$=20.21, P=0.002). The proportion of time using the tank bottom decreased with time, and varied from 0.33 to 0.90 among observation periods for bull trout and from 0.00 to 0.03 among observation periods for lake trout. Additional evaluation of these trends indicated that the effect of time was the result of one influential observation period (i.e., the first observation period). After removal of the first observation period, treatments I.a and I.b differed significantly for the proportion of time using the tank bottom ($F_{1,7.63}$=10.89, P=0.012); bull trout used the tank bottom more than lake trout and lake trout used the water column more than bull trout (Table 3).

For group II, treatments II.a and II.c did not differ for the proportion of time using cover ($F_{1,22.1}$=1.11, P=0.303) and using the tank bottom ($F_{1,23.1}$=2.53, P=0.126). However, treatments II.a and II.c differed significantly for the proportion of time using the water column ($F_{1,23.6}$=6.60, P=0.017), with a greater proportion of the time spent using the water column at a fish density of one compared to two bull trout per tank (Table 3). Treatments II.b and II.e did not differ for the proportion of time using cover ($F_{1,24.1}$<0.01, P=0.980), using the tank bottom ($F_{1,25.6}$=0.01, P=0.911), and using the water column ($F_{1,25.9}$<0.01, P=0.950) (Table 3).

Bull trout in treatments II.c and II.e did not differ for the proportion of time using cover ($F_{1,21.5}$<0.01, P=0.976), using the tank bottom ($F_{1,22.4}$=0.14, P= 0.709), and using the water column ($F_{1,23.0}$=0.08, P= 0.779) (Table 3). Lake trout in treatments II.d and II.e did not differ for the proportion of time using cover ($F_{1,21.5}$<0.01, P=0.991), using the tank bottom ($F_{1,22.4}$<0.01, P=0.989), and using the water column ($F_{1,23.0}$=< 0.01, P=0.984) (Table 3). Because no density effects and no species composition effects were observed for bull trout and lake trout for the proportion of time using cover and the tank bottom, use of these habitats were compared between bull trout and lake trout among all treatments in group II. Bull trout and lake trout differed significantly in the proportion of time using cover ($F_{1,22.6}$=20.08, P<0.001) and using the tank bottom ($F_{1,23.7}$=37.01, P<0.001). Bull trout spent a greater proportion of time using cover and the tank bottom than lake trout (Fig. 1).

Table 3 Proportion of time spent by bull trout and lake trout using cover, bottom, and water column habitats by treatment. Fish density is the density of fish in individual treatments

Treatment	Fish density	Bull trout (mean±95% CI)			Lake trout (mean±95% CI)		
		Cover	Bottom	Water column	Cover	Bottom	Water column
I.a	1		0.46±0.13	0.54±0.13			
I.b	1					0.01[a]±0.01	0.99±0.01
II.a	1	0.23±0.15	021±0.09	0.55±0.14			
II.b	1				0.02±0.02	0.01±0.02	0.96±0.02
II.c	2	0.39±0.11	0.35±0.11	0.26±0.10			
II.d	2				0.02±0.02	0.01[a]±0.01[a]	0.98±0.02
II.e	2	0.37±0.17	0.33±0.12	0.30±0.13	0.03±0.04	0.00±0.00	0.97±0.04
III.a	1	0.16±0.12	0.36±0.14	0.48±0.16			
III.b	2	0.16±0.15	0.41±0.15	0.43±0.14			

[a] Value < 0.005

For group III, treatments did not differ for the proportion of time using cover ($F_{1,43}$=0.29, P=0.591), using the tank bottom ($F_{1,42.8}$=0.45, P=0.506), and using the water column ($F_{1,42.7}$=0.04, P=0.837). The proportion of time that bull trout used the different habitats was similar prior to the addition of a lake trout and after the addition of a lake trout (Table 3).

Within treatments II.a, II.b, and II.e, fish were variable in the types of habitats that they used (Table 4; x^2_{L1}) and at least one of the fish within each treatment selected a specific habitat type (Table 4; x^2_{L2}). On average, fish within treatments were using habitats in disproportion to their availability (Table 4; x^2_{L1}–x^2_{L2}). Bull trout avoided water column habitat in the presence of lake trout, but not in the absence of lake trout and did not select or avoid cover or bottom habitats (Fig. 2). Lake trout avoided bottom habitat in the presence and absence of bull trout, but did not select or avoid cover or water column habitats (Fig. 2). Intraspecific and interspecific agonistic interactions varied from 0.000 to 0.007 interactions per min (14 total agonistic interactions among treatments) with the exception of lake trout chasing lake trout, for which 0.116 interactions per min (52 total agonistic interactions) were observed.

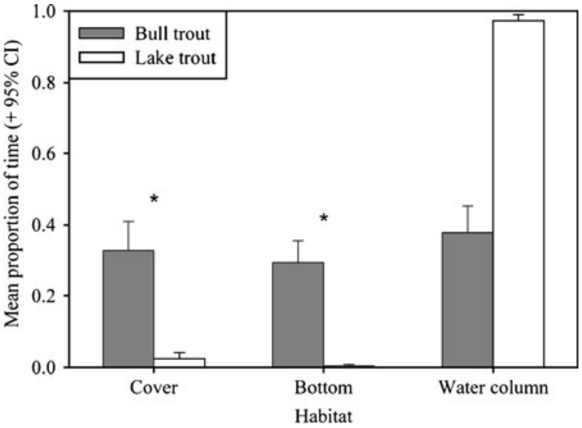

Fig. 1 Proportion of time (mean+95% CI) using cover and tank bottom habitats by bull trout and lake trout. Bull trout and lake trout differed significantly (*) for the proportion of time spent using cover and bottom habitats. Statistical comparisons were not made between bull trout and lake trout in the proportion of time spent using the water column because bull trout use of the water column was dependent on fish density; however, mean values (+ 95% CI) are provided for descriptive purposes

Discussion

Studies have shown that juvenile bull trout in natural and artificial stream environments are positively associated with cover habitat (Polacek and James 2003; Al-Chokhachy and Budy 2007), but that use of cover habitat may change over a diel period (Baxter and McPhail 1997; Thurow 1997). Additionally, stream dwelling bull trout are generally located within the lowermost portion of the water column (Polacek and James 2003; Al-Chokhachy and Budy 2007). Results from this laboratory study indicate that bull trout in standing waters do use cover and bottom habitat, but they also used water column habitat. Additionally, there was a lack of selection for cover and bottom habitat. This lack of selection may be the result of variability in habitat use among individual

Table 4 Treatment, chi-square analysis, degrees of freedom (df), chi-square value, and probability value for tests for habitat use in proportion to its availability. The x^2_{L1} analysis tests for differences among fish within treatments. The x^2_{L2} analysis tests if at least one of the fish within each treatment selected a specific habitat type. The x^2_{L1}–x^2_{L2} analysis test whether, on average, fish within treatments were using habitats in disproportion to their availability (Rogers and White 2007)

Treatment	Chi-square analysis	df	Value	Probability
II.a	x^2_{L1}	10	624.22	<0.001
	x^2_{L2}	12	872.50	<0.001
	x^2_{L1}–x^2_{L2}	2	248.28	<0.001
II.b	x^2_{L1}	8	17.62	0.024
	x^2_{L2}	10	48.47	<0.001
	x^2_{L1}–x^2_{L2}	2	30.85	<0.001
II.e – bull trout	x^2_{L1}	8	160.05	<0.001
	x^2_{L2}	10	1222.58	<0.001
	x^2_{L1}–x^2_{L2}	2	1062.53	<0.001
II.e – lake trout	x^2_{L1}	4	68.38	<0.001
	x^2_{L2}	10	123.37	<0.001
	x^2_{L1}–x^2_{L2}	6	54.99	<0.001

bull trout. Individual bull trout were using habitats in disproportion to their availability. Bull trout were observed using cover and bottom habitat about as often as using water column habitat; although, water column habitat made up a greater proportion of the tank volume (89% of tank volume). However, analyses of selection included information on variability among individuals and because some bull trout generally used cover habitat and some bull trout generally used bottom habitat no selection for these habitats among all bull trout could be inferred.

Although there is little quantitative, published data related to habitat use by juvenile lake trout, some studies have indicated that juvenile lake trout may be found associated with coarse substrates (Greeley 1936 in Martin and Olver 1980; Martin and Olver 1980; Wagner 1981; Peck 1982). In this study, lake trout spent the greatest proportion of time in the water column and rarely used cover or bottom habitats. In an artificial stream environment, lake trout (27.8± 1.9 mm; mean±std. dev.) were generally present in the water column except at high temperatures (i.e., 12.4 to 19.2°C), where they showed a weak preference for cover habitat (Heggenes and Traaen 1988). In this study, there was a lack of significant selection for cover habitat by lake trout, and lake trout avoided bottom habitat, unlike bull trout.

The prediction that bull trout and lake trout habitat use would not differ in the presence of conspecific competitors compared to the absence of competitors was supported, with the exception that bull trout used the water column more in the absence of conspecifics. However, there was a lack of support for the prediction that habitat use by bull trout and lake trout in the presence of potential competitors would differ

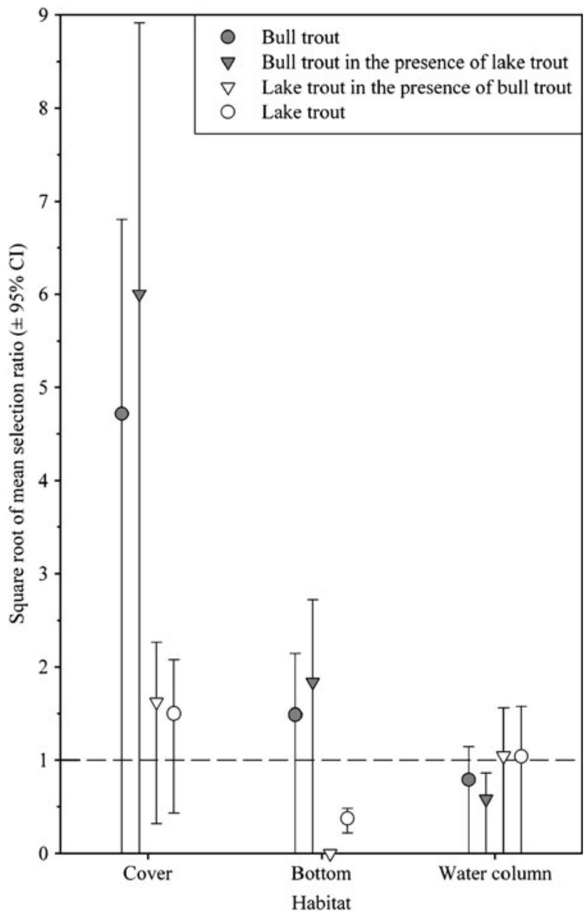

Fig. 2 Square root of mean selection ratios (± 95% CI) for cover, tank bottom, and water column habitats for bull trout (*filled circles*), bull trout in the presence of lake trout (*filled triangles*), lake trout in the presence of bull trout (*open triangles*), and lake trout (*open circles*). A reference line (*dashed line*) is placed at a selection ratio value of one. Selection for a habitat is represented by selection ratios greater than one and avoidance is represented by selection ratios less than one. Confidence intervals that overlap the reference line indicate a lack of selection or avoidance. A square root transformation was performed for presentation purposes only and does not affect the interpretation of selection or avoidance

depending on whether the potential competitor was conspecific or heterospecific. Had this prediction been supported, it would have provided evidence for habitat shifts associated with species composition, as fish density generally did not have an effect. Additionally, no change in habitat use was observed for bull trout previously acclimated to experimental conditions following the addition of a lake trout. Therefore, the prediction that lake trout would displace bull trout from cover habitat was not supported.

If habitat preferences of these species differ substantially, habitat shifts would not be anticipated. For example, there were no changes in cover use, foraging rate, or foraging distance of bull trout following the removal of westslope cutthroat trout, *Oncorhynchus clarkii lewisi*, from pools in a northwest Montana stream, and it was speculated that bull trout and cutthroat trout have little niche overlap (Nakano et al. 1998). In the same study, removal of brook trout, *Salvelinus fontinalis*, resulted in decreased cover use, increased foraging rate, and increased foraging distance by bull trout; suggesting greater niche overlap between bull trout and brook trout than between bull trout and westslope cutthroat trout. Conversely, no shift in resource use (i.e., microhabitat use, focal point height, and surface feeding frequency) by bull trout associated with the presence of brook trout was observed in eastern Oregon streams (Gunckel et al. 2002); however, based on faster growth rates and aggressive behavior observed for brook trout, Gunckel et al. (2002) suggested that over longer time intervals than their study, or under conditions of resource limitation, brook trout may displace bull trout.

Agonistic interactions in this study were generally similar among treatments (<0.007 interactions per minute). Interestingly, incidents of lake trout chasing lake trout were approximately 10 times higher than other agonistic interactions within treatments. Bull trout used the various habitats in about equal proportions; therefore, they may have partitioned these resources resulting in fewer intraspecific interactions. Conversely, lake trout spent a much greater proportion of time in the water column and rarely used the cover or bottom habitats, and likely had a greater probability of encountering conspecifics in close proximity resulting in an increased frequency of agonistic interactions. The avoidance of water column habitat by bull trout in the presence of lake trout may have been a strategy to avoid interspecific agonistic interactions by bull trout.

Although general differences in habitat use and agonistic interactions (to a lesser degree) were observed in this study, certain limitations existed that may have influenced the results. It was predicted that a greater percent of bull trout and lake trout would emigrate from the experimental tanks when cover habitat was absent than when present. A greater percent of emigration in the absence of cover would have provided evidence that cover was an important resource for these species (Matter et al. 1989). However, the greatest percent of both species emigrated when cover was present and fish density was one fish per tank, with a lower percent of emigration observed at densities of two fish per tank. Therefore, no clear trends with respect to cover presence or absence were observed, and emigration was likely the result of exploratory movements by bull trout and lake trout associated with increased territory size in the absence of potential competitors (e.g., Keeley 2000).

Cover is often associated with reduced predation risk, and the study design of this experiment did not include predation risk. It is possible that inclusion of predation risk (e.g., introduction of a potential predator into the experimental tanks) may have resulted in greater use of cover and competition for cover by bull trout and lake trout. For example, predation risk by northern pike resulted in changes in habitat use and foraging rate by brown trout, *Salmo trutta*, in artificial streams (Greenberg et al. 1997).

In this study, observations were made only during daylight portions of the photoperiod. Diel differences in habitat use have been observed for bull trout in some studies; however, a meta-analysis of bull trout habitat associations suggests that this trend is not pervasive (Al-Chokhachy et al. 2010). Bull trout moved from cover during the day to shallow water habitats with low cover at night in two tributaries to the Bitterroot River, Montana (Jakober et al. 2000). Age 0 bull trout moved from deeper water habitats during the day to shallower habitats at night in Indian Creek, Washington (Polacek and James 2003). Juvenile bull trout used cover more during the day than at night in artificial and natural streams (Baxter and McPhail 1997; Thurow 1997). Bull trout may have used cover to a lesser degree had observations been made during the night in this study; however, bull trout would have likely increased their use of bottom habitat as opposed to water column habitat based on trends from field studies (see Al-Chokhachy et al. 2010 for review). Additionally, a greater degree of interspecific agonistic interactions may have been observed had bull trout moved out of cover or used shallower portions of the water column in this study.

Habitat use may change and interspecific, agonistic interactions may increase when feeding territories are established for salmonids (e.g., Glova 1986). However, a small amount of food was added to the experimental tanks each morning prior to the light phase of the photoperiod. It was assumed that the amount of food was sufficient to meet energetic requirements of the experimental bull trout and lake trout as uneaten food was always present. Therefore, territorial behavior and resultant agonistic interactions may have been unnecessary under the experimental conditions; under conditions of limited food availability both intraspecific and interspecific agonistic interactions may have been more abundant.

Results from this study provide little evidence that bull trout and lake trout compete for cover. Differences in habitat use between these species were observed and there was some degree of selection and avoidance for different habitats. Additionally, few agonistic interactions were observed between these species during the study. Future research should examine the influence of predators on habitat use by and competition between juvenile bull trout and lake trout as well changes in diel habitat use by these species in lentic environments. In the absence of competitive interactions between juvenile bull trout and lake trout, other ecological interactions between these species should be evaluated to help elucidate factors responsible for bull trout declines following the introduction of lake trout. For example, dietary overlap between bull trout and lake trout was observed in some Canadian lakes (e.g., Donald and Alger 1993), but stable isotope data show that there is incomplete overlap between these species in their sources of energy for lakes in Glacier National Park (Meeuwig 2008). However, studies have not evaluated food habitats of juvenile bull trout and lake trout, and differences in habitat use may confer a growth advantage to one species during juvenile life stages. Additionally, the effect of lake trout predation on bull trout is unknown, but potentially important given the ability of lake trout to consume prey up to 50% of their own length (Ruzycki 2004). Therefore, additional research that simultaneously evaluates the effects of multiple ecological interactions (e.g., intraguild predation; Polis et al. 1989) and various life-history stages may be most useful for elucidating the effects of lake trout introductions on bull trout populations.

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