

Diel habitat partitioning by bull charr and cutthroat trout during fall and winter in Rocky Mountain streams

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Synopsis

We used underwater observation to determine diel habitat partitioning between bull charr, *Salvelinus confluentus*, and cutthroat trout, *Oncorhynchus clarki*, during fall and winter (0.1–8.3°C) in two Rocky Mountain streams that differed in habitat availability. The majority (> 70%) of both species emerged from concealment cover at night, though bull charr exhibited a greater tendency for nocturnal behavior than cutthroat trout. Differences in day and night counts were most pronounced at temperatures < 3°C, when very few fish of either species were observed in the water column during the day, but both species were common at night. Both species used concealment cover of large woody debris and boulder substrate crevices in deep pools during the day. At night, fish emerged from cover and habitat use shifted to shallow water with low cover. Microhabitat partitioning among species and size classes occurred at night, cutthroat trout moving into shallower, faster water that was farther from cover compared to bull charr. Smaller fish of both species occupied focal positions in slower, shallower water closer to the substrate than larger fish. Large, mixed-species aggregations also were common in beaver ponds both day and night. High variation in diel and site-specific winter habitat use suggests the need for caution in developing habitat suitability criteria for salmonids based solely on daytime observations or on observations from a few sites. Our results support the need to incorporate nocturnal habitat use and partitioning in studies of salmonid ecology.

Introduction

Stream-dwelling salmonids undergo two prominent behavioral changes, migration and concealment, in response to declining temperatures and photoperiod at the onset of winter (Cunjak 1996). Fall migration to overwintering areas, ranging from < 1 to > 60 km, has been observed in salmonids occupying a broad range of winter habitats (e.g., Brown & Mackay 1995, Cunjak 1996, Jakober et al. 1998). Following fall migration, salmonids in small streams become strongly photonegative and ‘vanish from view’ during daytime (Rimmer et al. 1983), entering cover of substrate crevices,

large woody debris, and submerged vegetation (Cunjak 1988, McMahon & Hartman 1989, Contor & Griffith 1995, Thurow 1997).

Adoption of strong concealment behavior at low temperature led to the view that salmonids are largely dormant during the winter. However, concealed salmonids undergo a third behavioral shift, that of emergence from cover after sunset to feed in the water column (Campbell & Neuner 1985, Fraser et al. 1993, Heggenes et al. 1993, Contor & Griffith 1995), even at temperatures near 0°C (Thurow 1997). Heggenes et al. (1993), for example, counted five brown trout, *Salmo trutta*, in a Norwegian stream during winter days

compared to 753 during winter nights. Diurnal concealment and nocturnal emergence from cover during winter has now been widely documented among salmonids, including Atlantic salmon, *Salmo salar* (Cunjak 1988, Fraser et al. 1993, Valdimarsson et al. 1998), brown trout (Griffith & Smith 1993, Heggenes et al. 1993), bull charr, *Salvelinus confluentus* (Baxter & McPhail 1997, Thurow 1997, Bonneau & Scarnecchia 1998), cutthroat trout, *Oncorhynchus clarki* (Griffith & Smith 1993, Bonneau & Scarnecchia 1998), coho salmon, *O. kisutch* (Bradford et al. 1995), and rainbow trout, *O. mykiss* (Campbell & Neuner 1985, Contor & Griffith 1995).

Despite the prevalence of nocturnal activity among salmonids during winter, much remains to be learned about this unusual behavior. Little is known about how such factors as fish size, species interactions, and habitat availability influence diel behavior and habitat use. Intra- and interspecific interactions may be more severe in winter because of more restricted habitat requirements (Cunjak & Power 1986, Heggenes et al. 1993). Differences in day and night habitat use have important implications to assessing fish response to habitat manipulation (Bradford et al. 1995).

Native bull charr and cutthroat trout co-occur in Rocky Mountain streams that differ markedly in habitat availability and winter severity (Jakober et al. 1998). High elevation streams are characterized by diverse substrate, abundant large woody debris (LWD), and nearly complete surface ice cover from October to March. Midelevation streams are characterized by fluctuating surface and subsurface ice, less LWD, and abundant boulder/cobble substrate. In summer, bull charr and cutthroat trout are both diurnal and nocturnal, and show little evidence of diel habitat shifts (Thurow & Schill 1996, Bonneau & Scarnecchia 1998). Like other salmonids that evolved sympatrically, they appear to avoid direct competition for food or habitat by partitioning available resources: bull charr are primarily benthic foragers whereas cutthroat trout occupy mid-water positions and feed on surface drift (Nakano et al. 1992, Bonneau & Scarnecchia 1998). Both species become largely nocturnal during winter (Thurow 1997, Bonneau & Scarnecchia 1998), but information on habitat partitioning and timing of diel habitat shifts at low temperatures, particularly among different size classes, is limited. Our objective was to examine how habitat availability, temperature, fish size, and habitat partitioning influences diel habitat use by these two co-occurring species.

Study area

We conducted our study in two tributaries to the Bitterroot River in western Montana that differ in habitat availability and typify the range of stream habitat where both species co-occur. Meadow Creek is a high elevation (mean 1818 m), third-order tributary to the East Fork of the Bitterroot River near Sula, Montana. Wetted width averages 2–3 m at base flow ($0.3 \text{ m}^3 \text{ s}^{-1}$), and average gradient is 2.1% (Jakober 1995). Large woody debris (LWD > 10 cm in diameter and > 3 m in length) is abundant (116 pieces 100 m^{-1}), and substrate is primarily gravel and cobble with few boulders (23 pieces 100 m^{-1}). Pools and beaver ponds are common (36% and 40% of surface area, respectively). The stream is almost entirely covered with surface ice from early November through late March but anchor and frazil ice are rare. Daly Creek, located 33 km north of Meadow Creek, is a moderate-sized (5–7 m wide; discharge $0.7 \text{ m}^3 \text{ s}^{-1}$), fourth-order tributary, with an average gradient of 4.1%, and a mean elevation of 1424 m. Fast water habitats (riffles and glides) were the predominant habitat type (77% of surface area), and LWD was about 50% less abundant than Meadow Creek (67 pieces 100 m^{-1}). Beaver ponds were absent, and substrate was primarily boulders (250 pieces 100 m^{-1}) and cobble. Surface ice fluctuates markedly during the winter in response to frequent freezing and thawing events, and anchor and frazil ice are common. In both streams, slimy sculpin, *Cottus cognatus*, was the only other fish species present.

Materials and methods

Diel activity and habitat use were determined using snorkeling observations in a 2 km study section established in each stream. Study sections were established near the lower elevational limit of bull charr distribution where both species were common and representative habitat types were available. Fish counts occurred over two fall-winter periods (September to March, 1992–1993 and 1993–1994). A total of 12 counts (9 day, 3 night, 60 h of observations) were made in Meadow Creek, and 21 counts (10 day, 11 night, 85 h of observations) were made in Daly Creek. Day counts were conducted between 9:30 and 16:00 h and night counts between 19:30 and 4:00 h (1 h after sunset to 1 h before sunrise). Complete ice cover prevented counts in Meadow Creek beyond early winter, but surface

ice cover in Daly Creek was less extensive and more variable, and surveys were made from early fall to midwinter.

Study sections were divided into habitat types, as modified from the classification of Bisson et al. (1988), as riffle, glide, pool formed by LWD, pool formed by boulders, pocket water (small pools formed by boulders within riffles or glides), beaver pond, and pool lacking cover of LWD or boulders. We randomly selected 41 habitat units in Meadow Creek and 29 habitats in Daly Creek for underwater surveying. The number of sites selected was chosen to obtain a minimum of five replicates of each habitat type and to sample approximately equal areas of stream (Meadow Creek = 2621 m²; Daly Creek = 2975 m²; ca. 25% of available habitat).

We observed fish by entering the downstream end of a habitat unit and moving slowly upstream in a zigzag fashion. Because of strong concealment behavior by fish during our surveys, we used a diving light both day and night to carefully search areas beneath LWD, streambanks, rocks, and ice ledges. The majority of fish could be approached within 1 m and exhibited low fright response to the light. Upon encountering a fish, we marked focal positions with numbered and painted stones, determined fish species, size category, and dominant cover type, and estimated focal point elevation above the streambed. Data were relayed to an assistant on the bank. Size categories were 50–100, 101–200 mm, and > 200 mm total length, which corresponded to young-of-the-year, juvenile, and adult age-classes. Snorkelers estimated size of dummy fish underwater to insure accuracy (> 95% after practice) of fish size estimation. Dominant cover (cover type within 50 cm of focal position) was classified as none, cobble (diameter 64–256 mm), boulder (diameter > 256 mm), LWD, undercut bank, submerged aquatic vegetation, and surface ice. Groups of ≥ 5 fish in close proximity to each other were classified as aggregations (Cunjak & Power 1986). Focal positions for aggregations were determined as the mean of measurements at the anterior, posterior, and center of the group. Following survey completion, total depth, distance to nearest cover, and water velocity were measured at each marked focal point using an electromagnetic current meter, wading rod, and meter stick. Water temperatures during the study were measured every 4.8 h with electronic thermographs.

Microhabitat availability was measured at ten equally spaced points along transects set at 2.4 m intervals within each habitat unit sampled. At each point,

we measured depth, bottom (5 cm from substrate) and mean column velocity, and dominant cover, yielding 1500 to 2000 measurements per stream. Habitat availability was estimated in September 1993 for both streams. We assumed availability was the same for both years since base flows were similar.

Accuracy of day and night snorkeling was assessed by comparing underwater counts with electrofishing removal estimates. Randomly selected habitat units, representing one of each type (excluding beaver ponds), were sampled in October 1993 in each stream. Block nets were positioned at each end of a habitat unit, and day snorkel counts were followed by a 2-pass removal using a backpack electrofisher. Night counts were made within 5 d of electrofishing removal estimates.

To compare habitat partitioning and day and night microhabitat use between species and size classes, we used multifactor analysis of variance (ANOVA) and Tukey's multiple comparison test (Zar 1984). Data were pooled across year and stream since initial analyses of microhabitat use revealed little differences among these factors. Nonnormal microhabitat data were transformed ($\log(x+1)$) to meet ANOVA assumptions, but means reported in the text and figures are from pretransformed data. Chi-square goodness-of-fit tests and Bonferroni confidence intervals (Byers et al. 1984) were used to compare cover use with availability. Cover use was analyzed separately for each stream because of differences in habitat availability. Simple linear correlation (Zar 1984) was used to examine associations between diel behavior and temperature. Significance of tests was determined at $\alpha = 0.05$ level.

Results

Diel behavior

We observed 764 solitary bull charr, 2527 cutthroat trout, and 192 single- and mixed-species aggregations in the two study streams during the two fall-winter periods. Both bull charr and cutthroat trout were largely nocturnal at temperatures ranging from 0.1–8.3°C (Figure 1). Bull charr exhibited a significantly greater tendency for nocturnal behavior than cutthroat trout ($\chi^2 = 77.2$, $p < 0.001$). Overall, 84% of bull charr and 70% cutthroat trout were observed at night. In both species, the proportion of nocturnal

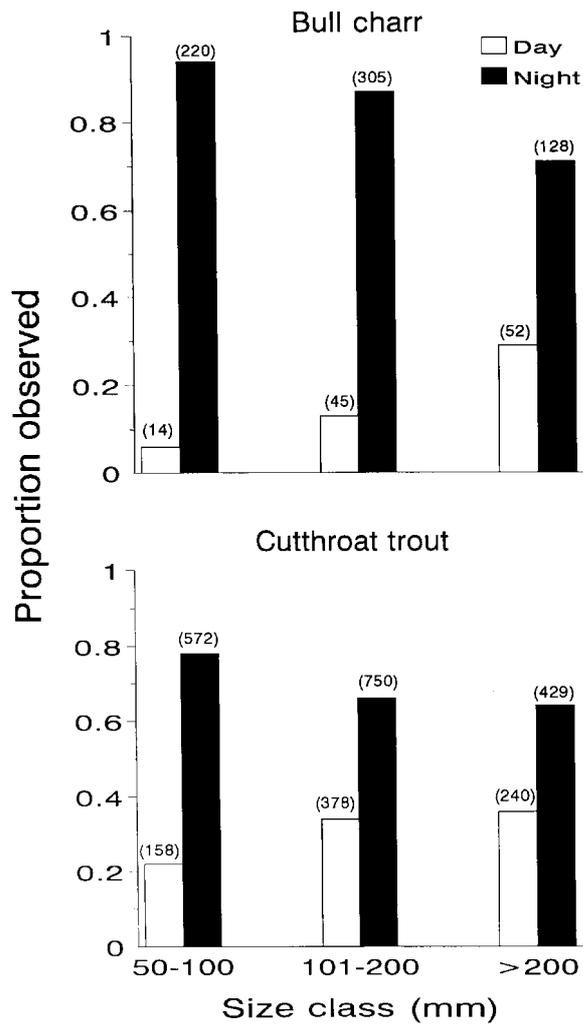


Figure 1. Proportion, by size class, of bull charr and cutthroat trout observed during day and night counts. Sample size shown in parentheses.

activity increased significantly (< 0.001) with decreasing fish size.

Comparisons of electrofishing estimates with day and night counts provided further confirmation of emergence of bull charr and cutthroat trout from concealment cover at night. Of the 37 bull charr and 104 cutthroat trout estimated by electrofishing, 2 (5.4%) bull charr and 34 (32.7%) cutthroat trout were observed during day counts, and 24 (64.9%) and 101 (97.1%), respectively, observed at night.

Water temperature influenced diurnal but not nocturnal behavior. In both streams, daytime counts of

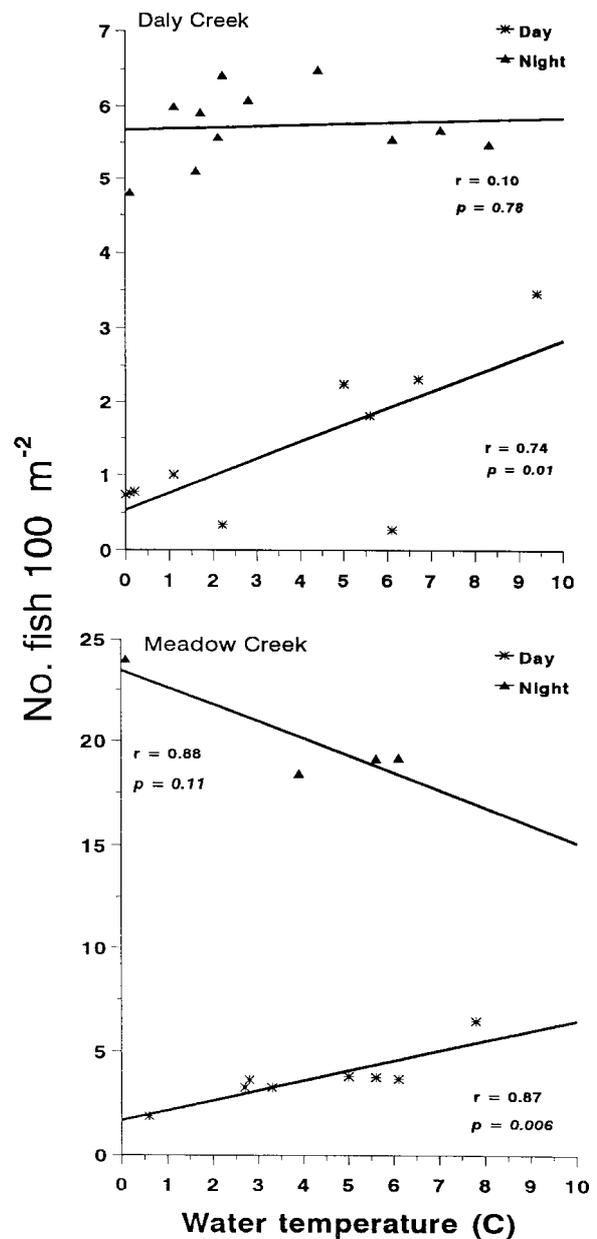


Figure 2. Relationship between mean daily water temperature and day and night density (bull charr and cutthroat trout combined) in study streams.

bull charr and cutthroat trout showed a positive linear association ($p \leq 0.01$) with temperature (Figure 2), and nearly all fish were concealed $< 3^\circ\text{C}$. In contrast, nighttime counts remained similar and did not change significantly over the range of $0.2\text{--}8^\circ\text{C}$ ($p > 0.11$).

Habitat use

Focal positions occupied by bull charr and cutthroat trout differed by species, size class, and diel period (Table 1). We observed very few fish during the day at temperatures $< 7^{\circ}\text{C}$ except in beaver ponds. The few bull charr we did observe in habitats other than beaver ponds occupied deep (40.9 ± 1.6 SE cm), slow (7.5 ± 0.2 cm s^{-1}) water in or near the substrate (2.8 ± 0.3 cm) (Figure 3). At night, bull charr were observed in significantly ($p < 0.003$) shallower (35.0 ± 0.5 cm) and slower (5.1 ± 0.2 cm s^{-1}) water but remained on or near (1.4 cm) the substrate. Cutthroat trout were also observed in shallower and slower water at night, but occupied focal positions higher in the water column and farther away from cover than bull charr ($p < 0.02$). We estimated about 25% of cutthroat trout occupied focal positions in the water column at night and the remainder rested on the substrate; all bull charr were observed resting on the substrate at night.

Small fish (< 100 mm) of both species occupied positions in slower, shallower water and were closer to the substrate and cover than larger fish both day and night (Figure 3). Bull charr and cutthroat trout of the same size class generally had high overlap of focal positions during the day ($p > 0.17$ for 9 of 12 size class by microhabitat use comparisons), but little overlap in focal positions at night ($p < 0.01$ for 9 of 12 comparisons). The most marked difference in microhabitat use between species and size classes occurred in focal point depth; cutthroat trout occupied focal depths $\sim 50\%$ shallower than bull charr at night.

Table 1. Three-way ANOVA for the effects of species, size class, and diel period (day vs. night) on microhabitat use of juvenile bull trout and cutthroat trout.

| Variable | Source of variation | F | df | p |
|-------------------|---------------------|---------|----|-----------|
| Focal depth | Species | 793.58 | 1 | < 0.001 |
| | Size class | 10.09 | 2 | < 0.001 |
| | Diel period | 1000.00 | 1 | < 0.001 |
| Focal elevation | Species | 293.78 | 1 | < 0.001 |
| | Size class | 65.86 | 2 | < 0.001 |
| | Diel period | 377.28 | 1 | < 0.001 |
| Distance to cover | Species | 7.97 | 1 | 0.005 |
| | Size class | 9.64 | 2 | < 0.001 |
| | Diel period | 21.15 | 1 | < 0.001 |
| Focal velocity | Species | 3.47 | 1 | 0.06 |
| | Size class | 57.28 | 2 | < 0.001 |
| | Diel period | 33.45 | 1 | < 0.001 |

Marked habitat shifts occurred in conjunction with changes in focal position from day to night. In Daly Creek, bull charr and cutthroat trout used pools with cover of boulders or LWD during the day (Figure 4). Pool habitats with cover remained important at night, but both species shifted to greater use of riffles and glides. In Meadow Creek, bull charr and cutthroat trout were most abundant in beaver ponds and in pools with LWD both day and night, but also shifted to use of glides and pools with low cover at night.

Bull charr and cutthroat trout generally occupied similar cover types but preferences varied with availability (Figure 5). Both species were closely associated with cover during the day ($> 75\%$) but decreased cover use at night. In Daly Creek, bull charr and cutthroat trout preferred boulder and LWD cover both day and night, despite LWD comprising a small proportion of available habitat. In lower-gradient Meadow Creek, where undercut banks were common and boulder and cobble substrate relatively rare, cutthroat trout preferred LWD and undercut banks during the day and night. Both species were observed resting on submerged vegetation at night in beaver ponds and glides, a cover type not used during the day and not available in Daly Creek.

Aggregations

A total of 59% of cutthroat trout and 16% of bull charr were observed in aggregations during fall and winter. Aggregations were comprised primarily of fish < 200 mm whereas larger fish of both species were more solitary (χ^2 tests, $p < 0.001$) particularly among bull charr (Figure 6).

Mean aggregation size was about twice as large during the day than at night (27.0 vs. 13.9, $t = 3.8$, $p < 0.001$). Aggregations were considerably larger (22.8 vs. 7.3 fish aggregation $^{-1}$) and more numerous (11.8 vs. 2.4 aggregations count $^{-1}$) in Meadow Creek, which had larger pool area and less large substrate than Daly Creek. Largest aggregations were observed in Meadow Creek beaver ponds, where mixed-species aggregations as large as 120 trout were observed. Unlike the decrease in daytime counts of solitary trout at low temperature (Figure 2), aggregation size increased both day ($r = 0.92$, $N = 8$; $p < 0.001$) and night ($r = 0.98$, $N = 4$; $p = 0.03$) as temperature declined. Daytime aggregation size varied from 15.8 ± 4.5 fish at 7.8°C to 73.2 ± 16.1 at 0.6°C , and nighttime aggregation size from 16.1 ± 3.1 fish at 6.1°C to 37.3 ± 7.9 at 0.1°C .

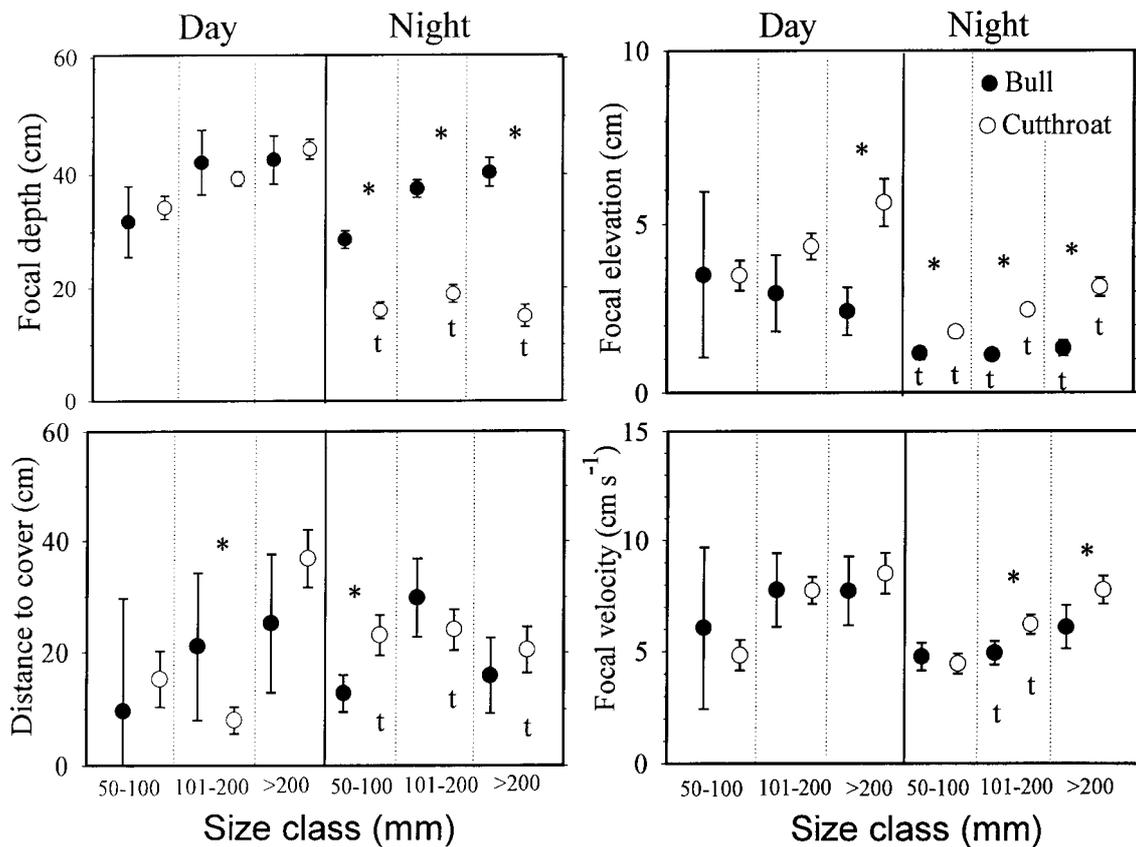


Figure 3. Focal positions (mean \pm SE) occupied by different size classes of bull charr and cutthroat trout during day and night. Significant ($p < 0.05$) differences in focal position between bull charr and cutthroat trout of the same size class indicated by asterisk, and between day and night by the same species and size class indicated by 't'.

Aggregations occupied significantly ($p < 0.01$) deeper water (> 60 cm) than solitary fish both day and night (Figure 7), occurring in the deepest sections of beaver ponds and other deep pools with slow ($< 5 \text{ cm s}^{-1}$) current velocity. Aggregations also showed significant diel microhabitat differences. During the day, aggregations occupied midwater locations (focal point elevation, 11.9 ± 0.9) in beaver ponds and near LWD in other pool types. At night, aggregations exhibited a similar habitat shift as did solitary fish, moving significantly ($p < 0.01$) closer to the substrate and farther away from cover.

Discussion

The majority of bull charr and cutthroat trout were nocturnal during fall and winter in our two study

streams, consistent with previous observations of stream salmonids at low temperature (Campbell & Neuner 1985, Fraser et al. 1993, Contor & Griffith 1995, Thurow 1997). Differences in day and night counts were most pronounced at temperatures $< 3^\circ\text{C}$, when very few fish were observed in the water column or on the substrate during the day, but large numbers were seen at night. In contrast, during summer at temperatures $> 10^\circ\text{C}$, bull charr and cutthroat trout have been observed in about equal numbers both day and night (Thurow & Schill 1996, Bonneau & Scarnecchia 1998). Declining temperature appeared to trigger decreased diurnal activity as we found a significant positive relationship between temperature and diurnal activity in both streams. At night, however, we observed similar numbers of bull charr and cutthroat trout over a wide range of temperatures (0.2 to 8°C , Figure 2). These results are consistent

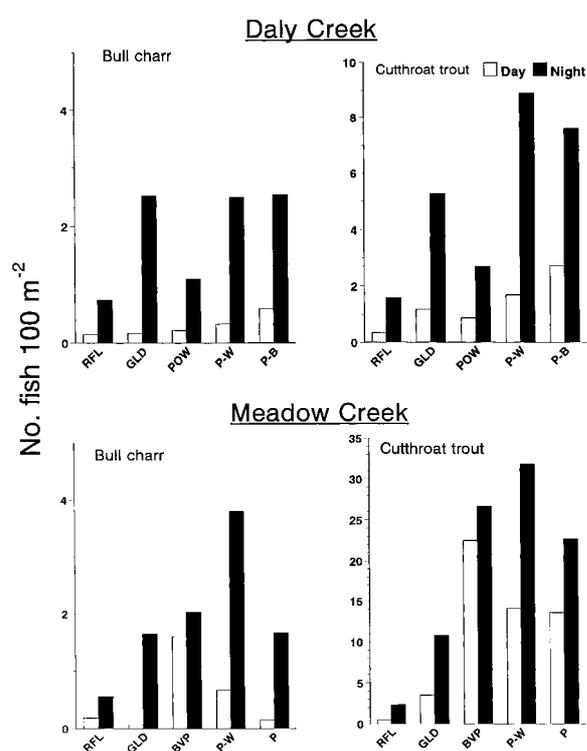


Figure 4. Mean density (no. fish 100 m^{-2}) of bull charr and cutthroat trout during day and night in the two study streams. Habitat types are: RFL = riffle; GLD = glide; POW = pocket water; P-W = pools with large woody debris; P-B = pools with boulders; P = pools lacking LWD or boulders; BVP = beaver ponds. Note differences in scale of y-axis.

with observations that diel shifts at low temperature are caused by increased daytime concealment rather than an increase in nocturnal activity (Fraser et al. 1993, 1995, Heggenes et al. 1993, Valdimarsson et al. 1997).

Increased daytime concealment is also accompanied by a switch to nocturnal foraging during winter (Fraser et al. 1993, 1995, Riehle & Griffith 1993, Contor & Griffith 1995, Metcalfe et al. 1999). During summer at warmer temperatures, cutthroat trout and other salmonids are typically observed resting on the substrate at night and feeding predominantly occurs during diurnal and crepuscular periods (Fraser et al. 1993, 1995, Riehle & Griffith 1993). Although we did not quantify feeding in our study, we commonly observed cutthroat trout at night occupying focal positions in the water column and capturing drifting insects. The benthic orientation of bull charr made definitive feeding observations difficult, but nocturnal feeding has been documented elsewhere (Thurow 1997,

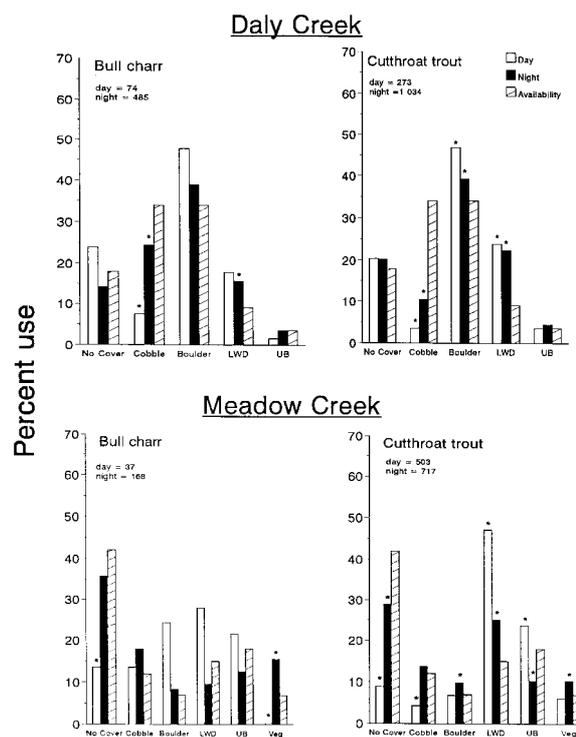


Figure 5. Percent day and night use of available cover by bull charr and cutthroat trout in the two study streams. Cover types are: LWD = large woody debris; UB = undercut bank; Veg = submerged aquatic vegetation. Asterisks denote significant ($p < 0.05$) preference or avoidance of each cover type.

Bonneau & Scarnecchia 1998). Bull charr are better able to feed in low light than cutthroat trout (Schutz & Northcote 1972), which could explain their greater tendency for nocturnal behavior.

Daytime predation risk has been suggested as the dominant factor influencing these marked seasonal shifts in diel behavior (Fraser et al. 1993, 1995, Metcalfe et al. 1999). Because of a substantially diminished predator avoidance capacity at low temperature (Graham et al. 1996), salmonids face considerable predation pressure from diurnally active, endothermic terrestrial and avian predators during fall and winter (Dolloff 1993, Metcalfe et al. 1999). In our study, the greater nocturnal activity of smaller size classes during winter, and the increase in concealment and in the size and number of aggregations during the day as temperature declined, lend support to the predation risk hypothesis.

Aggregation was another conspicuous response to low temperature. Winter aggregation is common

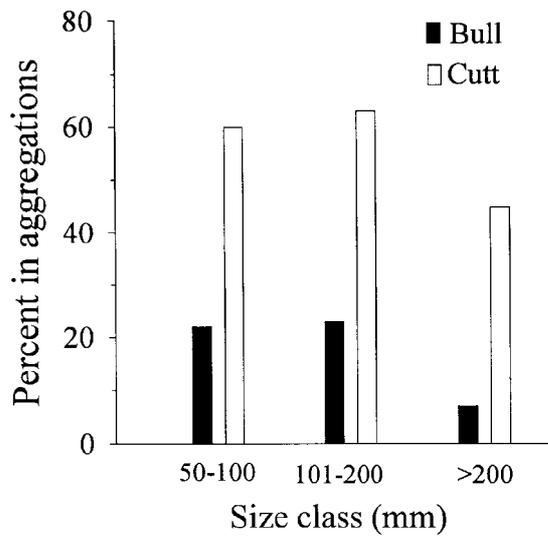


Figure 6. Percent, by size class, of bull charr and cutthroat trout observed in aggregations.

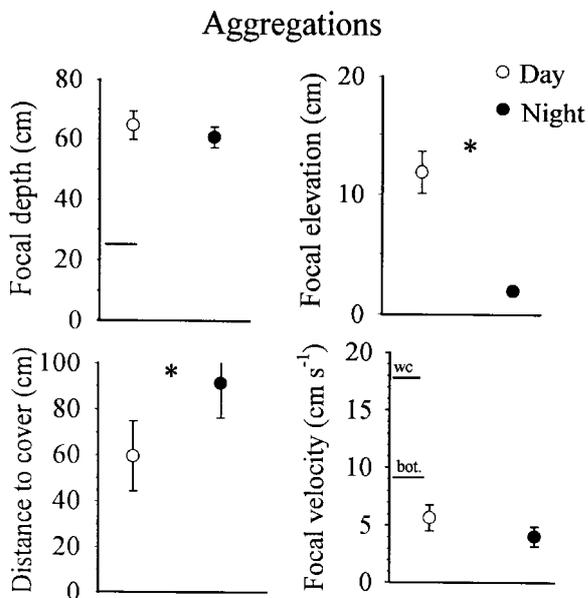


Figure 7. Day and night focal positions (mean \pm SE) occupied by aggregated bull charr and cutthroat trout. Horizontal lines indicate means of available water depths and bottom and water column velocities. Significant ($p < 0.05$) diel differences in focal position shown by asterisk.

among salmonids and other stream fishes, and is hypothesized to be a result of a relaxation of territoriality coupled with a 'squeezing effect' from ice exclusion or limited availability of pools and of

preferred concealment cover of substrate crevices and LWD (Cunjak & Power 1986, Brown & Mackay 1995, Cunjak 1996). The preponderance in aggregations of individuals too large (> 250 mm) to conceal in cover interstices is considered further support of the habitat limitation idea (Heggenes et al. 1993, Brown & Mackay 1995). However, we observed an opposite pattern that suggests aggregation is not solely due to limited concealment habitat: high aggregation (> 85%) in Meadow Creek where pools and LWD were abundant and habitat exclusion due to subsurface ice formation was rare (Jakober et al. 1998); low aggregation (< 15%) in Daly Creek where substrate crevices were abundant but pools were limited and ice exclusion common; and a preponderance of smaller sized (< 200 mm) individuals in aggregations in both streams. Moreover, we found considerable diel changes in aggregation formation among the two study streams. For example, in Meadow Creek beaver ponds the formation of large aggregations during the day and the breakdown into smaller, more numerous aggregations at night, parallels the diel changes in fish schools Helfman (1993) reported in response to changing predation pressure with varying light levels. The dynamic seasonal and diel changes in aggregation suggests this behavior is a complex response to both habitat availability and predation risk. Examination of survival differences between aggregated fish and concealed solitary fish would help determine the relative fitness of these alternative overwintering styles (e.g., Brown & Hartman 1988).

In summer, daytime intraspecific habitat partitioning by fish size is common among stream dwelling salmonids as a result of size-related differences in feeding efficiency and predation risk (Baltz et al. 1991, Mäki-Petäys et al. 1997). Interspecific habitat partitioning is also common as a result of interactive or selective partitioning of available resources (Dolloff & Reeves 1990, Baltz et al. 1991). Decreased daytime habitat partitioning during winter has been attributed to reduced aggression and energetic demands and similar requirements for concealment cover with declining temperature (Cunjak & Power 1986, Baltz et al. 1991). We also found a high degree of intraspecific and interspecific overlap in daytime microhabitat use between bull charr and cutthroat trout, as did Bonneau & Scarnecchia (1998), but we did observe clear evidence of intraspecific and interspecific habitat partitioning during winter nights. At night, both species moved away from cover into faster, shallower water, but cutthroat trout occurred farther from cover than bull charr and, in

both species, smaller fish occupied focal positions in slower, shallower water that were closer to the substrate than larger fish. Bonneau & Scarnecchia (1998) also observed microhabitat partitioning between juvenile cutthroat trout and bull charr on winter nights; a new finding of our study was evidence for microhabitat partitioning among size classes.

Nighttime winter habitat partitioning by bull charr and cutthroat trout mirrored the spatial habitat partitioning by these two species during summer days. Nakano et al. (1992) and Bonneau & Scarnecchia (1998) observed that cutthroat trout and bull charr differ in focal point depth, use of overhead cover, and feeding mode. During summer days, cutthroat trout are exclusively drift or surface feeders, occupying midwater positions away from cover, whereas bull charr are primarily benthic foragers, positioned on or near the substrate in close proximity to cover. Whether winter habitat partitioning is interactive or selective (Dolloff & Reeves 1990) could not be determined by our observational study. However, the degree of difference in feeding mode and microhabitat selection between the two species suggests such partitioning is likely a result of selection for mechanisms for co-existence (Nakano et al. 1992). Dolloff & Reeves (1990) provided experimental evidence that habitat partitioning by naturally sympatric juvenile Dolly Varden, *S. malma*, and coho salmon, species behaviorally and morphologically similar to bull charr and cutthroat trout, respectively, was due to innate differences in habitat preferences.

Our study was limited by the inability to locate a significant proportion of concealed fish during daytime underwater surveys. Daytime microhabitat measurements were therefore mostly based on the small proportion (< 25%) of fish that were unconcealed, a potential source of bias. Using electrofishing, Mäki-Petäys et al. (1997) found evidence of size-related habitat partitioning among juvenile Atlantic salmon. Thurow (1997) also found a relationship between fish size and home stone size among concealed juvenile bull charr. Results of these studies suggest that more detailed measurements of concealed fish may also reveal evidence for intra- and interspecific habitat partitioning among salmonids during winter days.

Both species used a diverse array of habitats during fall and winter. Our results substantiate previous work on the critical importance of pools, large woody debris, unembedded large substrate, and undercut banks as daytime concealment cover for overwintering salmonids (e.g., Cunjak & Power 1986,

McMahon & Hartman 1989, Brown & Mackay 1995, Cunjak 1996, Thurow 1997). Nighttime observations revealed that other habitat features are important as well. At night we observed both species using habitat types (low cover, faster water habitats of runs and riffles) and cover types (small patches of aquatic vegetation) that were not used during the day. Moreover, we found considerable site-specific differences in winter habitat use (see also Cunjak & Power 1986, Brown & Mackay 1995). Beaver ponds, a habitat type lacking in Daly Creek, formed a critical winter habitat component in Meadow Creek, where > 70% of fish were counted in five beaver ponds comprising 30% of the area sampled. Beaver ponds are important overwintering sites for salmonids occupying widely varying winter conditions (Chisholm et al. 1987, Brown & Hartman 1988), and further investigation of their value as winter habitat for fishes is needed (Cunjak 1996). The seven-fold difference in abundance we observed among the five Meadow Creek beaver ponds (Jakober 1995) suggests that examination of factors affecting their suitability as winter habitat would be a fruitful avenue for future research.

High diel and site-specific variation in winter habitat use calls for caution in developing habitat suitability criteria for salmonids based solely on daytime observations or from a few sites (Campbell & Neuner 1985, Bradford et al. 1995), and supports the recommendation that maintenance or enhancement of habitat complexity is vital to winter habitat management (Cunjak 1996). Reduction of LWD and deep pools, sedimentation of large substrate, and other habitat simplification processes will decrease winter carrying capacity (Hillman et al. 1987, McMahon & Hartman 1989), and increase susceptibility of overwintering salmonids to winter disturbances such as flooding and icing, which may be exacerbated by land management activities (Erman et al. 1988, Reeves et al. 1993, Cunjak 1996). For example, bull charr are rarer in catchments with a high level of land use disturbance (Rieman et al. 1997) and lacking LWD or pools (Rich 1996).

Principles of stream fish ecology have largely been derived from studies conducted during summer days. While studies of winter behavior and habitat use have been a focus of much research in recent years (Cunjak 1996), nocturnal activity of stream fishes remains largely unexplored (Metcalfe et al. 1999). Pronounced nocturnal activity and habitat partitioning among species and size-classes documented in ours and other recent studies conducted during both winter and summer (e.g., Fraser et al. 1995, Reebbs

et al. 1995, Gries et al. 1997, Bonneau & Scarnecchia 1998), suggest that nocturnal behavior and habitat use patterns likely influence the abundance and distribution of stream fishes to a larger degree than currently appreciated.

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