Seasonal and diel changes in habitat use by juvenile bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) in a mountain stream

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Abstract: Habitat use by juvenile bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) in Trestle Creek, Idaho, changed seasonally and dielly. Both cutthroat and bull trout selected pools over riffles in both summer and winter. Both species used a wide range of depths at night but were absent from shallow water (<15 cm) during the day in summer and winter. During summer, juveniles of both species occupied areas of lower velocity water at night than during the day. Both species also occupied lower velocity water during winter days than summer days. During winter days, juvenile bull trout were located below or directly on cobble substrate, whereas cutthroat trout often formed aggregations suspended in the water column of large pools. Both species were more closely associated with cover during the day, and made the greatest use of cover during winter days. Land management activities resulting in decreased pool habitat, instream cover, and stream-bed stability may be especially detrimental to bull trout and cutthroat trout in winter.

Résumé : L'utilisation de l'habitat fluctue en fonction de la saison et en fonction de la journée chez les individus immatures de l'Omble à tête plate (*Salvelinus confluentus*) et de la Truite fardée (*Oncorhynchus clarki*) de Trestle Creek, Idaho. Les poissons des deux espèces préfèrent les cuvettes aux rapides aussi bien en été qu'en hiver; ils se tiennent à diverses profondeurs durant la nuit, mais fuient les eaux peu profondes (<15 cm) durant la journée, tant en été qu'en hiver. Durant l'été, les poissons juvéniles des deux espèces se tiennent plus dans les eaux lentes la nuit que le jour. Les deux espèces choisissent également les eaux lentes plus volontiers en hiver qu'en été. Pendant les journées d'hiver, les jeunes ombles se tiennent en aval de substrats pierreux ou directement au-dessus, alors que les jeunes truites forment des bancs en suspension dans la colonne d'eau dans les grandes cuvettes. Les poissons des deux espèces sont associés plus étroitement aux zones protégées par la végétation au cours de la journée, et c'est en hiver qu'ils utilisent ces zones le plus fréquemment. Les activités d'aménagement susceptibles d'entraîner la réduction des zones à cuvettes et la dégradation de la couverture de végétation au-dessus des ruisseaux ou de perturber la stabilité du substrat peuvent être particulièrement dommageables aux Ombles à tête plate et aux Truites fardées en hiver.
[Traduit par la Rédaction]

Introduction

Bull trout (*Salvelinus confluentus*) and west-slope cutthroat trout (*Oncorhynchus clarki*) have sustained significant reductions in distribution and abundance in this century. Several factors have contributed to the decline of both species, including loss of essential habitats and competition and hybridization with introduced species (Liknes and Graham 1988; Goetz 1989).

Bull trout, a recently recognized species of charr closely related to Dolly Varden (*Salvelinus malma*; Cavender 1978), was historically distributed mainly in interior streams and rivers from the upper Sacramento River in California (Goetz 1989) northward to the upper Yukon River in Canada (Haas and McPhail 1991). The most serious population declines have occurred in southern portions of its range (Goetz 1989), including California, where it has been extirpated, Oregon, where two-thirds of the 65 populations are at risk of extinction (Ratliff and Howell 1992), and Idaho (Elle 1995). The species is classified as of “special concern” by the American Fisheries Society (Williams et al. 1989) and is listed as a Category 1 species under the Endangered Species Act (Office of the Federal Register (June 10, 1994): 30254).

West-slope cutthroat trout were historically distributed throughout portions of Idaho, Montana, Wyoming, and three Canadian provinces (Behnke 1988; Liknes and Graham 1988). The primary cause of population declines has been hybridization with rainbow trout (*O. mykiss*), golden trout (*O. aguabonita*), and Yellowstone cutthroat trout (Liknes and Graham 1988). Genetically pure populations of west-slope cutthroat trout remain in only 2.5% of their historic range (Liknes 1984).

Unlike those of many salmonids, the specific habitat

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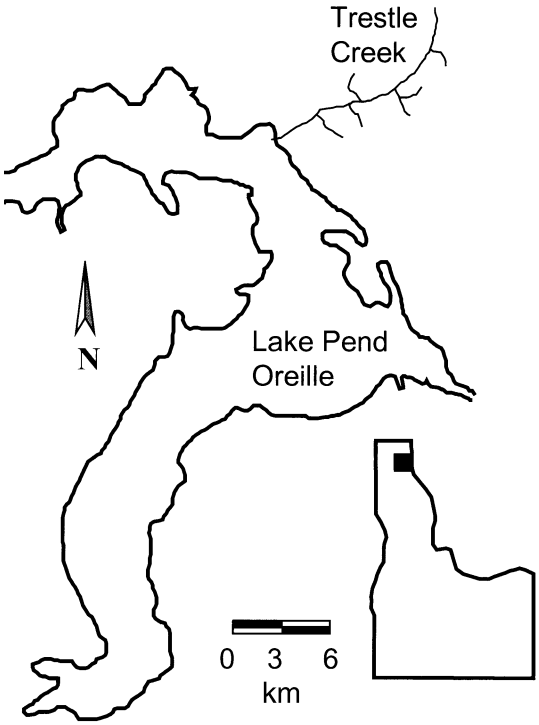


Fig. 1. Location of Trestle Creek, a tributary of Lake Pend Oreille, Idaho.

requirements of juvenile bull trout are not well understood. In many streams, bull trout and cutthroat trout coexist, which complicates evaluations of the habitat preferences of both species. Pratt (1984), Martin et al. (1992), Adams (1994), Goetz (1994), Jakober (1995), and Saffel and Scarnecchia (1995) reported on habitat use of bull trout or bull trout and cutthroat trout in Montana, Washington, Oregon, and Idaho. All of these studies except Jakober (1995) were conducted during summer; all studies except Goetz (1994), Jakober (1995), and Saffel and Scarnecchia (1995) were conducted by sampling only during the day. Because macro- and micro-habitat use by salmon and trout varies seasonally (Baltz et al. 1991) and dielly (Campbell and Neuner 1985), however, knowledge of both seasonal and diel variation in habitat use is necessary to adequately characterize a species' habitat requirements. Habitat use during summer may not, for example, reveal limitations on carrying capacity resulting from insufficient winter habitat. Habitat use may also differ between day and night. Bonneau et al. (1995) reported that bull trout were more easily enumerated by snorkelers at night; such day and night differences in observability may indicate diel shifts in habitat use.

Comprehensive knowledge of the habitat requirements of both species is essential because in many cases adults spawn and juveniles are reared in streams influenced by timber harvest and associated road construction. The objective of this study was to identify and characterize seasonal and diel changes in stream macrohabitat (pool and riffle) and microhabitat use by sympatric juvenile bull trout and cutthroat trout.

Study area

Trestle Creek is a small ($0.25\ m \cdot s^{-1}$ discharge in January and July 1992) high-gradient (3–8%), low-conductivity (<50 μmhos $\cdot\ cm^{-1}$) stream draining directly into Lake Pend Oreille, a large natural lake (area 38 200 ha) in northern Idaho (Fig. 1). Area geology is glaciated Belt (Etienne 1987), resulting in a stream bed consisting mainly of rounded cobbles. Large conifers shade nearly 100% of the channel. Numerous small springs feed into the stream from the hillsides, which reduces the incidence of freezing during winter.

The study section was 3 km long; its lower end was located 6 km upstream of the lake. Water temperatures ranged from 0–2°C in January to 9–11°C in July. The section was ice-free in winter. No aquatic macrophytes were present.

The only fish species present in the section were bull trout and cutthroat trout. The bull trout were adfluvial, being reared for 2–3 years in the stream before migrating into the lake to grow and mature as 4-, 5-, and 6-year-old fish (Pratt 1985). Cutthroat trout were both resident and adfluvial.

Materials and methods

Macrohabitat (pool and riffle) use

From the study section, three evenly spaced reaches (200 m in length) were selected. Habitat units within the three reaches were classified as pools or riffles (4 pools and 3 riffles in reach 1, 3 pools and 6 riffles in reach 2, and 5 pools and 1 riffle in reach 3). Flagging visible to a streamside observer at night marked the beginning and end of each habitat unit. The length and width of each habitat unit were measured to the nearest 0.5 m; mean width was estimated as the mean of widths at one-fourth, one-half, and three-fourths of the distance along a habitat unit. From length and mean width, the area of each habitat unit was calculated and areas were summed by type (pool or riffle).

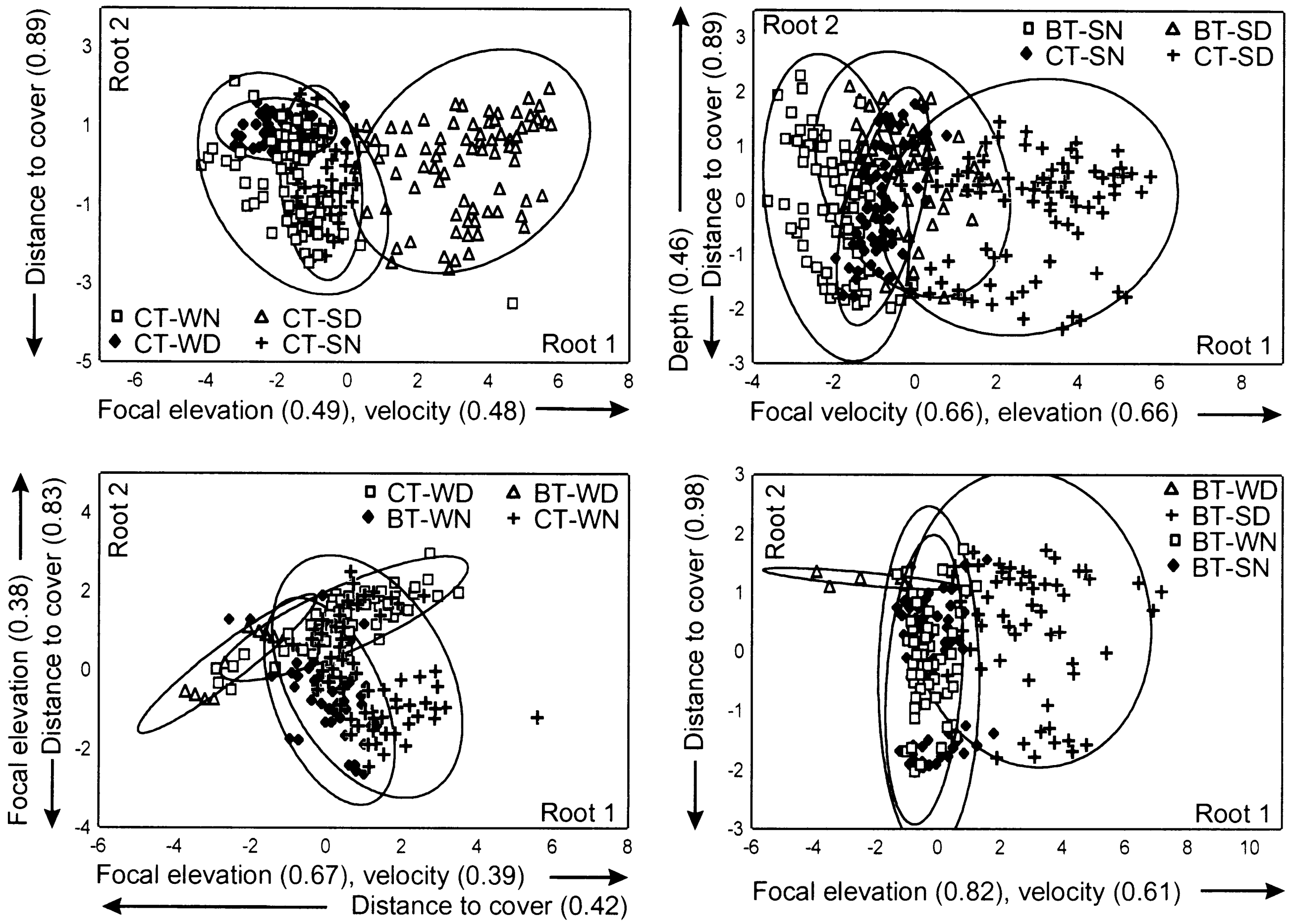
Juvenile bull trout and cutthroat trout in the three reaches were counted at night by a snorkeler and a bank observer (both carrying flashlights) in January and again in July, 1992. A bank observer walked parallel to the snorkeler and searched for fish in small back-waters and areas too shallow (<10 cm) to snorkel. Only night counts were conducted for the macrohabitat assessment; most bull trout remained hidden below the substrate during the day in both summer and winter (Bonneau et al. 1995). Data from fish counts were summed by habitat type and pooled for the three reaches. Percent use of pools for each species was calculated separately for summer and winter. Young-of-the-year fish (age-0) of both species were excluded from counts in summer but were included in counts the following January as age-1 fish. Observed use of pools was compared with expected use (based on percentage of pool habitat present) with a χ^2 test.

Microhabitat use

Microhabitat use by both species during day and night, summer and winter, was characterized by identifying specific locations where individual fish were observed (called focal points) and quantifying the physical features of these focal points. Juvenile bull trout and cutthroat trout were located by a snorkeler and a bank observer working upstream from the lower end of the reach as described above. During the day, it was necessary to actively search for fish within the substrate by lifting cobbles. Both the bank observer and the snorkeler used a flashlight during the day and night to help locate hidden fish.

Lengths of fish were estimated using measurements of objects near the fish when they were observed. Ages were determined with otoliths and length frequencies. Bull trout less than 70 mm total length (TL) and cutthroat trout less than 65 mm TL were considered to be age 0 in July. All cutthroat trout in the study area were less than 200 mm TL and all bull trout were less than 170 mm TL (except for six adult bull trout of 500–600 mm TL). These six fish were all

Fig. 2. Scatter plots of canonical scores with 95% ellipses. Factor loadings (those greater than 0.3) are given in parentheses following axis legends. Higher loadings indicate larger contributions to discrimination among groups (BT, bull trout; CT, cutthroat trout; SD, summer day; SN, summer night; WD, winter day; WN, winter night). All groups in each comparison were significantly different (*P* < 0.05), except BT-SN and BT-WN.



observed in only two pools and were not considered. When a fish was located, a numbered marker was placed on the substrate directly below it and the focal elevation was recorded.

Five microhabitat characteristics were measured at each focal point: (1) vertical distance of the fish above the substrate (focal-point elevation; cm), (2) total water depth (cm), (3) water velocity at the focal point ($m \cdot s^{-1}$), (4) distance (cm) to nearest cover (within 1 m of the fish), and (5) type of cover. Velocity at the focal point was measured with a Marsh–McBirney flowmeter to the nearest 0.01 $m \cdot s^{-1}$. Cover was classified as cobble/boulder, woody debris, turbulence, or rootwad/undercut bank. Rootwads and undercut banks were combined because they always occurred together in the study reaches. Depth was not considered cover because determination of depths suitable for cover would be arbitrary and the study area was shallow (maximum depth 0.9 m). For fish uncovered in the substrate, depth within the substrate was estimated and focal-point velocity and distance to nearest cover were recorded as zero. The assumption that water velocity was very near zero at focal points within the substrate was supported by frequent observations of fine organic matter under the cobbles, which was washed away when cobbles were lifted.

Data on fish and habitat characteristics were collected in summer and winter during periods of similar stream discharge. We assumed that habitat availability was similar between summer and winter. No noticeable change in discharge occurred between day and night in either season.

Discriminant function analysis was used to evaluate diel and seasonal segregation between and within species. This multivariate approach allows determination of the relative contribution of each variable (focal-point velocity, depth, focal-point elevation, distance to cover) to the separation among groups (i.e., by species, season, and diel period). MANOVA and Duncan's multiple-range test of the first and second canonical scores were used to determine the significance of group separation and differences in microhabitat characteristics.

Results

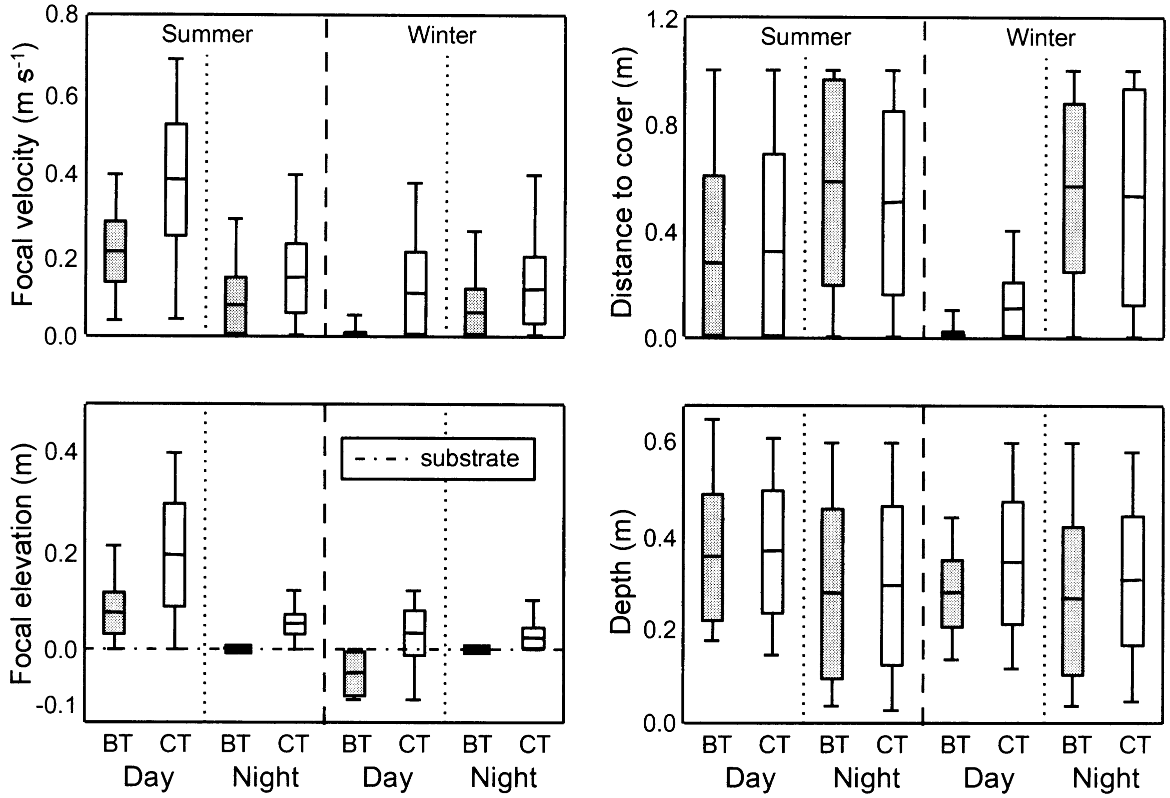
Macrohabitat use (night)

Both bull trout and cutthroat trout used pools significantly more often than expected on the basis of availability in summer and winter. Although pools constituted only 15% of available habitat, 44% of bull trout ($\chi^2_{[0.05,2]}$ = 73.9, P < 0.001) and 33% of cutthroat trout ($\chi^2_{[0.05,2]}$ = 45.8, P < 0.001) were observed in pools in summer; 55% of bull trout ($\chi^2_{[0.05,2]}$ = 133.2, P < 0.001) and 65% of cutthroat trout ($\chi^2_{[0.05,2]}$ = 65, P < 0.001) were observed in pools in winter.

Microhabitat use (day and night)

The discriminant function analysis produced two significant roots (χ^2 < 0.05) in all comparisons (Fig. 2). Focal-point velocity and focal-point elevation were the primary compo-

Fig. 3. Box plots of microhabitat variables (mean, standard deviation, and range) at focal points for juvenile bull trout (BT) and cutthroat trout (CT) during day and night, summer and winter.



nents (i.e., contributed the most to the separation among groups) of the first discriminant axis (root 1) and distance to cover was the primary component of the second discriminant axis (root 2). Depth contributed the least to discrimination among groups. All groups in each of the four comparisons were significantly different ($P < 0.05$), except for bull trout during winter and summer nights ($P > 0.05$).

Focal-point elevation

Bull trout

During summer days, bull trout locations were, on average, 7 cm above the substrate. During winter days, however, more than 90% of the bull trout were found within the substrate (mean depth –5.0 cm, $P < 0.001$); the remaining fish were resting on the substrate. At night, all bull trout observed were resting on the substrate in both summer and winter (mean depth 0 cm, $P > 0.05$). Focal-point elevations were significantly higher during summer days than summer nights ($P < 0.001$) and significantly lower during winter days than winter nights ($P < 0.001$). Figure 3 summarizes the measured microhabitat variables at the focal points where bull trout and cutthroat trout were observed).

Cutthroat trout

During summer days, cutthroat trout were located, on average, 19 cm above the substrate. During winter days, however, they were significantly lower in the water (mean 3 cm above the substrate, $P < 0.001$). At night they were, on average, closer to the substrate during winter (mean 2 cm above) than during summer (mean 5 cm above, $P < 0.001$). Cutthroat trout were located significantly higher in the water than bull trout during winter days ($P < 0.001$); at that time, bull trout were always on or below the substrate. Cutthroat trout were also higher in the water column than bull trout on summer days ($P < 0.001$), summer nights ($P < 0.001$), and winter nights ($P < 0.01$).

Depth

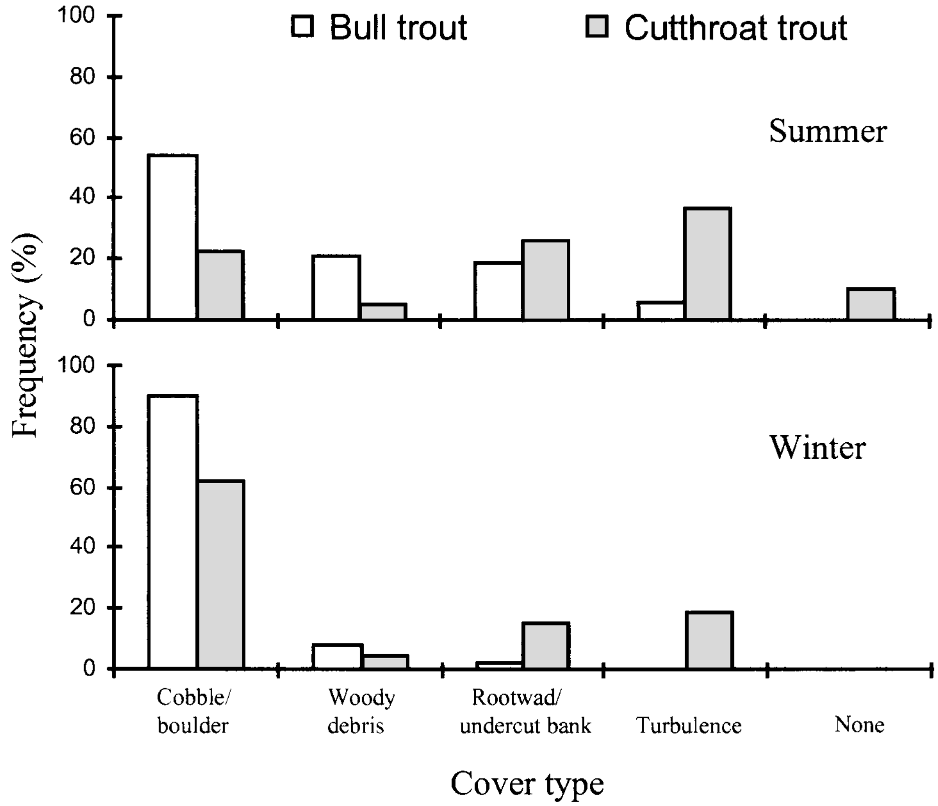
Bull trout

During summer, bull trout occupied shallower water at night (mean 28 cm deep) than during the day (mean 36 cm deep, $P < 0.01$), but there was no significant difference during winter (mean 28 cm deep during the day and 26 cm at night; $P > 0.5$). At night, bull trout occupied water of similar depths in summer and winter ($P > 0.5$), but during the day occupied deeper water during summer than winter ($P < 0.01$).

Cutthroat trout

In summer, cutthroat trout were found in significantly shallower water at night (mean depth 29 cm) than during the day (mean depth 36 cm, $P < 0.01$), but in winter the difference was not significant (mean depth 26 cm at night and 34 cm in the day; $P = 0.098$). Cutthroat trout did not occupy significantly different depths between summer and winter days ($P > 0.3$) or between summer and winter nights ($P > 0.6$). Cutthroat trout occupied significantly deeper water than bull trout during winter days ($P < 0.01$).

Fig. 4. Percentages of observed juvenile bull trout and cutthroat trout using specific cover types during summer and winter days.



Focal-point velocity

Bull trout

In summer, bull trout occupied significantly faster water during the day (mean velocity 0.21 $m \cdot s^{-1}$) than at night (mean velocity 0.07 $m \cdot s^{-1}$, $P < 0.001$), but in winter they occupied significantly slower water during the day (mean velocity 0 $m \cdot s^{-1}$) than at night (mean velocity 0.06 $m \cdot s^{-1}$, $P < 0.001$). These results are based on the assumption that water velocities were near zero below the substrate. Focal-point velocities did not differ significantly between summer and winter nights ($P > 0.2$) but were significantly higher during summer days than winter days ($P < 0.001$).

Cutthroat trout

Cutthroat trout occupied significantly faster water during summer days (mean velocity 0.39 $m \cdot s^{-1}$) than summer nights (mean velocity 0.14 $m \cdot s^{-1}$, $P < 0.001$) or winter days (mean velocity 0.10 $m \cdot s^{-1}$, $P < 0.001$). Focal-point velocities were not significantly different between winter days and winter nights ($P > 0.5$), but were higher during summer nights than winter nights ($P < 0.05$). Cutthroat trout occupied faster water than bull trout during summer and winter, day and night ($P < 0.001$).

Distance to nearest cover

Bull trout

Bull trout maintained positions closer to cover during the day than during the night in both summer ($P < 0.001$) and winter ($P < 0.001$). Bull trout related more closely to cover during winter days (mean distance 0.0 cm) than during summer days (mean distance 28 cm, $P < 0.001$), but exhibited no differences in proximity to cover between winter nights and summer nights ($P > 0.7$).

Cutthroat trout

Cutthroat trout also associated more closely with cover during the day than during the night in both seasons ($P < 0.001$). Like bull trout, cutthroat trout were found closer to cover during winter days (mean distance 10 cm) than during summer days (mean distance 31 cm, $P < 0.001$). Their proximity to cover did not differ between summer and winter nights ($P > 0.6$).

Cover type

Bull trout

Since cutthroat trout and bull trout did not appear to associate with any cover at night (except perhaps the stream bottom or darkness itself), only cover types used during the day are considered here. During summer days, bull trout used cobbles as cover during 54% of the observations, more than twice as often as woody debris and rootwad/undercut banks. During winter days, bull trout used unembedded cobbles as cover in 90% of observations.

Cutthroat trout

During summer days, cutthroat trout used turbulence as cover in 37% of the observations, followed by rootwad/undercut banks and cobbles. During winter days, unembedded cobbles were the most utilized cover (62%; Fig. 4). For both species, a wide range of cover types was used during summer days, but during winter days, unembedded cobbles served as the main cover.

Discussion

Our finding that juvenile bull trout and cutthroat trout used pools more than riffles is in agreement with other reports (McPhail and Murray 1979; Liknes and Graham 1988; Saffel and Scarnecchia 1995). Both species, especially cutthroat trout, made greater use of pools in winter. An increase in use of pools during winter was reported for brook trout (*S. fontinalis*) and brown trout (*Salmo trutta*) by Cunjak and Power (1986), for coho salmon (*O. kisutch*), Dolly Varden, and steelhead trout by Heifetz et al. (1986), and for coho salmon by Tschaplinski and Hartman (1983). In our study, increased winter use of pools by cutthroat trout was associated with their tendency to spend winter nights suspended midwater in the pools. Bull trout, which used pools less frequently than cutthroat trout in summer and winter, used areas on or near the substrate, often behind cobbles or boulders, which allowed them to inhabit low-velocity areas, even riffles.

Species that select pools over riffles, such as cutthroat trout and bull trout, may be especially affected by loss of pool habitat. Removal of vegetation in watersheds has been shown to result in increased peak discharges, destabilization of slopes, widened and braided channels, and loss of pools (Everest et al. 1985; Lyons and Beschta 1983). In the Belt geology of Trestle Creek and other portions of northern Idaho, rain on snow events on excessively logged watersheds can lead to slope failure and input of cobble/boulder-sized material into streams (Etienne 1987; Cacek 1989), resulting in the filling of pools and the creation of long stretches of unbroken, braided riffle habitat. The loss of pools (and overall habitat complexity) would decrease the amount of living space available for these species.

During summer, both species occupied slower moving water at night than during the day. Campbell and Neuner (1985) reported a shift to slower water at night for rainbow trout and attributed it to movement from feeding positions during the day to resting positions at night. Their conclusion is supported by Schutz and Northcote (1972), who reported that cutthroat trout fed much less efficiently as available light decreased. By night, cutthroat trout in Trestle Creek did not occupy feeding positions near current shear lines, but often rested in slack water away from the drift.

In contrast to cutthroat trout, bull trout did not occupy feeding positions during summer days, but were often observed roaming slack-water areas and picking prey items from the bottom. Many other bull trout were found beneath the substrate or resting on the bottom, evidently not feeding. By means of retinal and behavioral studies, Henderson and Northcote (1985, 1988) determined that the Dolly Varden (a close relative of the bull trout) is better adapted for feeding under low-light conditions than is the cutthroat trout. Although ours was not a study of feeding ecology, we did observe caudal fins protruding from the mouths of bull trout several hours after dark, indicating that they were feeding, at least to some extent, at dusk or at night. Bull trout are often piscivorous (Shepard et al. 1984; Boag 1987), and juvenile bull trout and young-of-the-year cutthroat trout, a potential prey, often occupy similar habitats (shallow stream margins) in Trestle Creek as well as other locations (e.g., Pratt 1984).

During winter days, we observed little feeding activity by juveniles of either species; fish were usually hidden beneath the substrate or in low-velocity areas above the substrate. Other researchers have reported an affinity of salmonids for residing in the interstices of unembedded substrate or resting in low-velocity areas in winter (Bustard and Narver 1975; Campbell and Neuner 1985; Cunjak and Power 1986; Hillman et al. 1987). Habitat use is often a compromise between potential profits (food abundance) and the risks of predation, depletion of energy, and injury (Bustard and Narver 1975; Bachman 1984; Fausch 1984; Cunjak and Power 1986). Our results support this idea. In winter, when salmonids' demand for food is lower (Reimers 1957), we found that fish were seldom in locations where energy expenditure or risk of predation was high. Those cutthroat trout not seeking cover during winter days formed aggregations in pools, perhaps thereby obtaining protection from predators (Shaw 1962).

Except for the absence of bull trout and cutthroat trout in shallow water (<15 cm) during the day, both species occupied a wide range of depths day and night, summer and winter. Cunjak and Power (1986) also reported a wide range of depth use in winter by brook trout and brown trout and suggested that water depth was not as important in determining fish distribution as velocity and cover. The presence of bull trout in shallow stream margins at night but not during the day was consistent with the results obtained by Campbell and Neuner (1985) and Riehle and Griffith (1993), who reported that juvenile rainbow trout avoided shallow water during summer and winter days but not at night. Although detailed information on habitat use by young of the year in Trestle Creek was not collected, we observed that young of the year of both species used shallow stream margins almost exclusively both day and night. Occupancy of low-velocity stream margins would allow young of the year to avoid larger fish during the day and to conserve energy.

In contrast to streams associated with other geological types in Idaho, such as the batholith, where intrusion of fine sediments and cobble embeddedness are often detrimental to salmonids (Bjornn 1971; Klamt 1976), streams associated with Belt geology are often dominated by cobbles (Etienne 1987). In such streams the presence of stable, unembedded cobbles and pools can be particularly important for salmonids, especially in winter. A scarcity of nocturnal or overwintering habitats can limit the carrying capacity for salmonids. For example, Lestelle and Cederholm (1984) reported that a stream cleaned of woody debris did not suffer a decrease in cutthroat trout numbers until winter. Cunjak and Power (1986) postulated that a bottleneck may occur in winter, since salmonids of different species are trying to use the same or nearly the same habitats. This bottleneck may become more pronounced when overwintering habitat is scarce.

In disturbed watersheds dominated by large stretches of unstable, unembedded cobbles, stream-bed stability may limit the success of bull trout and cutthroat trout. In the Coeur d'Alene River watershed of northern Idaho, for example, most of the bed materials are transported during normal bankful flows from heavily logged watersheds (Cross and Everest 1995). Since cutthroat trout, and more particlarly bull trout, overwinter within the substrate, high winter flows and resulting unstable substrates may result in low survival rates of eggs and fry (Elwood and Waters 1969; Seegrist and Gard 1972; Erman et al. 1988), washouts of fish from sections of streams (Pearsons et al. 1992), and direct crushing of fish (Erman et al. 1988). Similarly, in some areas the abundance of Dolly Varden has been positively linked to channel stability (Murphy et al. 1986).

Trestle Creek, like many streams containing bull trout, is groundwater fed and does not experience frazil and anchor ice formation. Fish in streams with less groundwater influence may behave differently, especially in winter (Brown and Mackay 1995). The main biases we are aware of in this study are associated with our inability to see fish during the day. Because juvenile fish, especially bull trout, often hid below the substrate by day, it was necessary to carefully lift cobbles and look for fish. Still, fewer fish were found during the day.

Acknowledgments

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