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Resource Utilization by Bull Char and Cutthroat Trout in a Mountain Stream in Montana, U.S.A.

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Abstract Resource utilization of sympatric populations of bull char, *Salvelinus confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, were studied by underwater observations of foraging behaviour and microhabitat use, and dietary analysis in a mountain stream of the Flathead River Basin, northwest Montana, U.S.A. Nearly 70% of bull char were categorized as benthic foragers, which moved constantly and captured prey primarily from the streambed, while all cutthroat trout were drift foragers, which held relatively fixed focal points in the midwater layers of pools during foraging. The composition of stomach contents was markedly different between the two species. Bull char fed primarily on baetid mayflies captured from the benthos or drift, whereas cutthroat trout ate primarily terrestrial invertebrates. The species also used different microhabitats. Bull char held positions close to the streambed and rarely strayed far from overhead cover, whereas cutthroat trout held focal points farther above the bed and far from overhead cover. Dietary segregation between these two salmonids appeared to result not only from differences in foraging tactics but also in the foraging microhabitats. Resource partitioning is considered to be one of important mechanisms allowing coexistence of these two stream salmonids.

In freshwater fish communities, resource partitioning is thought to be one of major mechanisms permitting similar species to coexist (see Ross, 1986 for a review). It generally occurs along the niche dimensions of microhabitat, food, or time, and is thought to form interspecific interactions, either at present or in the past (Larkin, 1956; Werner and Hall, 1977; Ross, 1986). Many studies have been carried out on competitive relationships between various sympatric species of salmonids (see Fausch, 1988 for a review). These studies have demonstrated that salmonids often undergo niche shifts in microhabitat and/or food in the presence of interacting species (Hartman, 1965; Nilsson, 1965; Ishigaki, 1969; Andrusak and Northcote, 1971; Fausch and White, 1981, 1986; Hindar et al., 1988).

Two native salmonid fishes, bull char, *Salvelinus confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, commonly occur in sympatric populations in the Flathead Lake and River system in Montana, U.S.A. (Liknes and Graham, 1988; Fraley and Shepard, 1989). Any articles, however, have not dealt with their interactions in sympatry in lotic systems. The purpose of our research was to make a preliminary investigation of the mechanisms by which this pair of salmonids coexists in streams. In this paper, we examine the foraging behaviour, microhabitat use, and diet of each species in order to evaluate how these stream salmonids partition resources.

Methods and Materials

Study area. The upper Flathead River basin of northwestern Montana, which is a headwater drainage of the Columbia River Basin, consists of Flathead Lake and its inlet river system. The study was performed in Red Meadow Creek (48°48′N, 114°28′W), a tributary of the North Fork of the Flathead River. The study area was located approximately 17 km upstream from the confluence with the North Fork, at an altitude of 1,460 m. Here the stream averaged 4 m wide and had 2.5% gradient (estimated from a map). Water temperature in the study area ranged from 5.9 to 9.5°C in early August.

In addition to bull char and cutthroat trout, Red Meadow Creek was also inhabited by sculpin, *Cottus* sp., mountain whitefish, *Prosopium williamsoni*, and arctic grayling, *Thymallus arcticus*, but these were rarely observed. The last species is not native to this drainage, but was introduced into a lake in the headwaters.

General biology. Bull char, which inhabits the inland waters of northwestern North America, is a distinct species from Dolly Varden, *Salvelinus malma* (Cavender, 1978; Haas and McPhail, 1991). The population in the Flathead River system is largely adfluvial. Most of the fish migrate downstream after 1 to 4 years of stream residence, grow to maturity in Flathead Lake, and later migrate upstream to spawn in tributaries (Fraley and Shepard, 1989). Bull char first attain sexual maturity at age 5 or older in the Flathead system.

Fourteen subspecies of cutthroat trout occur in different regions of western North America (Behnke, 1988). Westslope cutthroat trout, one of these subspecies, is primarily distributed west of the Continental Divide in Montana, Idaho, and British Columbia. Three life history forms are known to occur: lacustrine-adfluvial migrating between lakes and main rivers; fluvial-adfluvial moving between main rivers and tributaries; and fluvial fish resident in small tributaries throughout their entire lives (Liknes and Graham, 1988). Juveniles of the first two forms emigrate downstream primarily at ages 2 and 3, and most spawners were age 4 and older in the Flathead system.

Underwater observation of fish. After preliminary snorkeling on August 6, 1991 to locate the study area, bull char and cutthroat trout were observed in Red Meadow Creek in the daytime on August 8. Focal animal observations (Altman, 1974) of fishes were made underwater by snorkeling in an upstream direction, which causes minimal disturbance. Each individual was observed for 5 min or more and all foraging acts were recorded. Foraging acts were defined as any feeding attempts, whether successful or not, and were classified as benthic or drift foraging. If the snout of the fish touched the bottom during the feeding attempt, this was recorded as benthic foraging. All other feeding attempts were recorded as drift foraging. Focal fish were classified as either drift foragers, if they typically held focal points (sensu Griffith, 1972) in the stream flow and intercepted food items in the drift, making occasional feeding attempts on the bottom, or benthic foragers, if they primarily cruised around and beneath cobbles on the streambed, picking at benthic invertebrates and rarely made forays into the water column to intercept drift. The fork length of each focal fish was estimated to the nearest 0.5 cm by comparing it to stones on the bottom which were later measured. Body size was also measured for some fish captured after the observations. The distance between the snout of the fish holding a focal point and the bottom (termed focal point depth) was estimated, and the presence of overhead cover was recorded for all focal individuals and some other fish which were observed for shorter periods.

Scan observations (Altman, 1974) were also made in the two pools. Prior to scan observations, topographic maps of the observed pools were drawn on a scale of about 1 : 20. The positions of individuals of both species, which were individually identified by body size and spotting pattern, were recorded on the maps once each 10 to 50 min.

Sampling macrobenthic/drifting invertebrates and fish. Macrobenthic invertebrates were sampled using a 25×25 cm Surber net sampler with 0.3-mm mesh in the study area on August 8, 1991. One sample was taken from each of three different habitat types: the stream margin, the center of a riffle (substrate of loose cobble), and in a pool (pebble and sand).

Drifting invertebrates were sampled with a drift net having 0.3-mm mesh and a mouth opening of 25 ×25 cm. The net was set with its bottom edge touching the stream bed and top just above the water surface for 30 min during the afternoon (1340–1730). Three samples were taken from sites with different riparian vegetation: two from an open area with low shrubs and one from beneath branches of riparian coniferous forest. No measurement of current velocity at the mouth of the net was made, however.

Ten bull char and 26 cutthroat trout were collected either by angling or using cast and hand nets in the daytime on August 6 and 8, 1991. Of these, 5 bull char and 17 cutthroat trout were captured after focal animal observation by hand nets or angling while snorkeling. All fish captured were immediately preserved in 10% formalin.

Invertebrates in the benthos, drift and the diet of fishes were classified as terrestrial or aquatic, and the aquatic invertebrates were identified to family or order.

Results

Foraging behaviour. Frequency of individuals employing each foraging mode was significantly different between bull char and cutthroat trout ($\chi^2=24.3$, df$=1$, $P<0.001$). Thirteen of 19 (68.4%) bull char observed were benthic foragers, whereas all cutthroat trout fed almost exclusively on drift (Table 1). For bull char, fork length of drift foragers was significantly larger than benthic foragers (Mann-Whitney U-test, $U=13.5$, $P<0.05$).

Among bull char, benthic foragers had higher total foraging rates than drift foragers (Mann-Whitney U-test, $U=13.5$, $P<0.05$). Foraging rates of drift foragers were far higher for cutthroat trout than in bull char ($z=3.00$, $P<0.01$), but were not significantly different between two species when drift and benthic foragers were combined ($z=0.50$, $P>0.05$).

Habitat use. Twelve of 28 (42.9%) bull char and all 37 cutthroat trout observed held focal points (Table 2). All but one of the bull char that held focal points were beneath overhead cover whereas only 10 of 37 (27.0%) of cutthroat were. The proportions were significantly different ($\chi^2=15.5$, df$=1$, $P<0.001$). The focal point depth was also significantly different between the two species, with bull char holding positions closer to the streambed ($N=12$, $\bar{x}\pm SD=4.1\pm3.1$ cm) than cutthroat trout ($N=37$, $\bar{x}\pm SD=11.9\pm5.9$ cm; Mann-Whitney U-test, $z=4.15$, $P<0.01$).

We examined the distribution of individual fish in the two sympatric pools (Fig. 1). In both pools, most of cutthroat trout held focal points in the midwater layer beneath the principal surface currents near the center of the pool. The smallest cutthroat in each pool (AC7 and BC5) used focal points at the margins of the pools, away from the principal currents.

Among bull char, one of four individuals in pool A (AB2) and one of three in pool B (BB1) usually held focal points near the streambed. These individuals were classified as drift foragers. Of the other five individuals, which were benthic foragers, three (AB1, BB2 and BB3) occasionally held focal points but frequently cruised around large areas of streambed. The other two (AB3 and AB4) moved continuously over large area and did not hold focal points.

Potential prey and diets. The most numerically abundant macrobenthic invertebrates collected were Heptageniidae (Ephemeroptera), followed by Plecoptera, Baetidae (Ephemeroptera), Ryacophilidae (Trichoptera) and Chironomidae (Diptera; Table 3). The drifting invertebrates were composed of both macrobenthic and terrestrial invertebrates (Table 3). Baetidae were most abundant in the drift, followed by terrestrial invertebrates, Chironomidae, Simuliidae (Diptera) and Heptageniidae. Among the invertebrates accounting for fairly large proportions of both the benthos and drift samples, the numerical proportions for Chironomidae and Baetidae in the drift samples were far larger than those in the benthos. In contrast, the reverse was true for Heptageniidae and Plecoptera.

Stomach contents were compared between the two species (Fig. 2). Foraging behaviour had been observed for five of the bull char and 17 cutthroat trout just before capture. However, since all cutthroat trout observed, including these 17 individuals, were classified as drift foragers, all samples for this species

Table 1. Frequency of foraging attempts on drift and benthos by bull char and cutthroat trout, based on focal animal observations in Red Meadow Creek, Montana on August 8, 1991. FL, fork length

Species	Foraging mode	No. of fish observed	Range of FL (mm)	Frequency of foraging acts (mean±*SD)/5 min*		
				Drift	Benthic	Total
Bull char	Drift forager	6	100–155	3.83±1.33	0.67± 0.82	4.50± 1.97
	Benthic forager	13	40–125	0.92±2.02	14.23±11.11	15.15±10.94
	Total	19	40–155	1.85±2.27	9.95±11.16	11.79±10.33
Cutthroat trout	Drift forager	25	40–230	12.12±7.84	0.28± 0.46	12.40± 7.93
	Benthic forager	0	—	—	—	—
	Total	25	40–230	12.12±7.84	0.28± 0.46	12.40± 7.93

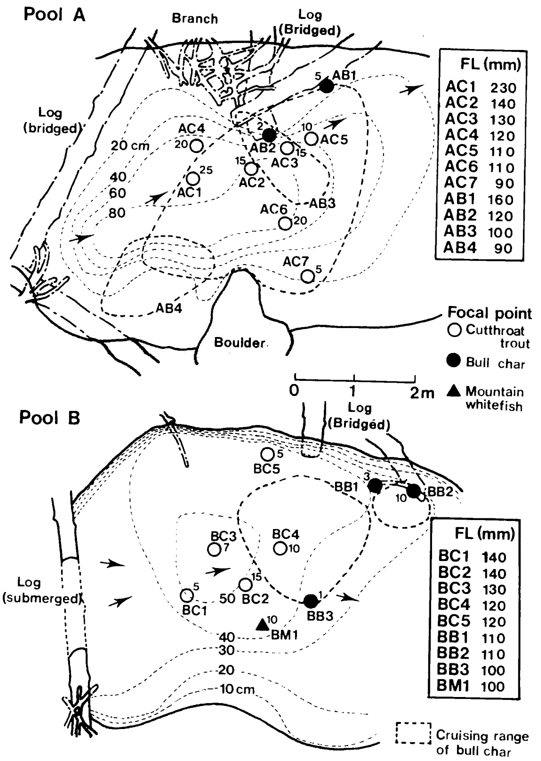

Fig. 1. Maps of two pools in Red Meadow Creek, Montana showing fish distributions on August 8, 1991. Scan observations of fishes were carried out eight times during 1407–1735 hours in pool-A (upper) and five times during 1300–1425 hours in pool-B (lower). The focal point used most frequently by each individual is shown for cutthroat trout (open circles), bull char (solid circles), and mountain whitefish (solid triangle). Numbers by focal points indicate focal point depth. Thick broken lines show outlines of cruising range of bull char. Fine broken lines show isoplethes of water depth. Arrows indicates the principal surface current in the pools. Logs denoted as bridged were above the water surface. FL, fork length.

Table 2. Numbers of bull char and cutthroat trout holding focal points with and without overhead cover in Red Meadow Creek, Montana on August 8, 1991

Species	Holding focal point			Holding no focal point
	Beneath cover	Without cover	Total	
Bull char	11	1	12	16
Cutthroat trout	10	27	37	0

were combined. Fork length of the cutthroat trout examined ($N=26$, $\bar{x} \pm SD = 122.9 \pm 36.3$ mm) was significantly larger than that of bull char ($N=10$, $\bar{x} \pm SD = 75.0 \pm 38.6$ mm; Mann-Whitney U-test, $z=3.06$, $P<0.01$).

The composition by number of invertebrates in the diet was significantly different between the two species ($\chi^2=317.2$, df$=5$, $P<0.001$). A very small proportion of the diet of bull char was made up of terrestrial invertebrates, whereas this made up 61.6% of the diet of cutthroat trout. Baetidae predominated in the diet of bull char, followed by Heptageniidae and Chironomidae. Chironomidae were the most abundant aquatic invertebrates in cutthroat stomach, followed by Baetidae. Aquatic invertebrates other than Chironomidae in the cutthroat diets made up a far smaller proportion than in bull char. Difference in diet composition was not significant between drift versus benthic foragers for bull char when Chironomidae were combined with other aquatic insects ($\chi^2=5.2$, df$=3$, $P>0.05$).

Discussion

The frequency of benthic versus drift foragers was markedly different between bull char and cutthroat trout. About 70% of bull char primarily employed benthic foraging, whereas all cutthroat trout fed almost exclusively from the drift. Differences in the diets of the two species, however, was more distinct than indicated by their foraging mode. Moreover, the discrepancy between their foraging behaviour and the diets suggests that drift foragers of these two salmonids exploited different food items. The most abundant drifting prey were Baetidae, followed by terrestrial invertebrates. Nevertheless, more than a half of the diet of cutthroat trout was composed of terrestrial invertebrates. In contrast, a large proportion of the diet of bull char that were either drift or benthic foragers was made up of baetid nymphs, suggesting that they may have captured these prey from the drift as well as directly from the streambed.

Differences in use of drifting prey between the two species were probably due more to their spatial distribution than to active selection for particular prey items. Furukawa-Tanaka (1992) showed composition of daytime drift was markedly different among vertical layers of the water column; the abundance of terrestrial invertebrates was exceedingly large compared to aquatic invertebrates in a swift surface layer of a Japanese mountain stream pool. In Red Meadow

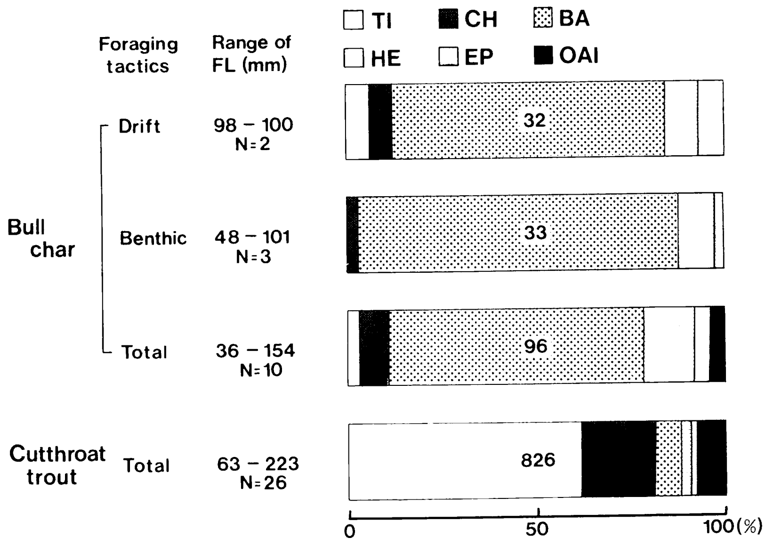

Fig. 2. Percentage by number of invertebrates found in stomachs of bull char and cutthroat trout captured from Red Meadow Creek, Montana on August 8, 1991. Invertebrate taxa were: TI, terrestrial insects; CH, Chironomidae; BA, Baetidae; HE, Heptageniidae; EP, Ephemerellidae; OAI, other aquatic insects. Numbers in bars are total sample size of invertebrates for each group. FL, fork length.

Creek, bull char that were drift foragers held focal points close to the streambed and seldom foraged at the water surface, and those that were benthic foragers rarely swam above the streambed. In contrast, cutthroat trout held focal points in upper layers of the water column, which facilitated their exploitation of surface drift. Therefore, distinct dietary segregation between these two sympatric salmonids appeared to result not only from differences in foraging mode but also in foraging microhabitats.

Although limited in scope, the present study indicates that these two coevolved North American salmonids segregated along several niche dimensions related to microhabitat, including focal point depth and use of overhead cover, as well feeding on different prey. These findings are in accordance with patterns of resource partitioning reported for other pairs of salmonid species coexisting naturally in streams of the Japanese Archipelago: Japanese char, *S. leucomaenis*, vs. Dolly Varden (Ishigaki, 1969, 1987; Nakano, 1991) and masu salmon, *O. masou*, vs. Japanese char (Furukawa-Tanaka, 1988). Thus, such patterns of resource partitioning are likely to be one of the common and important mechanisms allowing coexistence of pairs of stream-resident salmonid species in these two regions.

Talbe 3. Composition by numbers of macrobenthic and drifting invertebrates collected from Red Meadow Creek, Montana during daytime on August 8, 1991. The former is the total of samples collected from two points in a riffle and one in a pool by a Surber net (25×25 cm). The latter is the total from three points in the riffle collected by a drift net (25×25 cm) set for 30 min

	Macrobenthic invertebrates		Drifting invertebrates	
	N	%	N	%
Diptera				
Chironomidae	5	4.0	10	11.1
Simuliidae	1	0.8	9	10.0
Others	4	3.2	0	0.0
Ephemeroptera				
Baetidae	11	8.8	26	28.9
Heptageniidae	46	36.8	9	10.0
Ephemerellidae	2	1.6	5	5.6
Trichoptera				
Ryacophilidae	9	7.2	4	4.4
Others	2	1.6	2	2.2
Plecoptera	38	30.4	2	2.2
Coleoptera	3	2.4	0	0.0
Others	4	3.2	0	0.0
Terrestrial invertebrates	—	—	23	25.6

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アメリカ合衆国モンタナ州の山地渓流におけるブルチャーとカットスロートトラウトの資源利用

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モンタナ州フラットヘッド川水系の山地渓流において，同所的に生息する2種のサケ科魚類ブルチャーとカットスロートトラウトの採餌行動と生息場所の利用様式を潜水観察し，さらに両種の食性を比較した．一般に，渓流性サケ科魚類の採餌行動は，水中の一地点に留まり泳ぎながら流下動物を食べる方法（流下物採餌）と河床近くを広く泳ぎ回りながら底生動物を直接つつくようにして食べる方法（底生採餌）に大きく二分される．両種の採餌行動は大きく異なり，ブルチャーの多くの個体が主に後者の方法を採用したのに対し，観察されたすべてのカットスロートトラウトは前者を採用した．両種間には明瞭な食性の差異が認められ，ブルチャーがコカゲロウ科やヒラタカゲロウ科幼虫等の水生昆虫を多く捕食していたのに対し，カットスロートトラウトは主に陸性の落下昆虫を捕食していた．両種が利用する空間にも明らかな差異が認められ，ブルチャーが淵の底層部分を利用するのに対し，カットスロートトラウトはより表層に近い部分を利用した．また，前者が河畔林の枝や倒木の下などの物陰を利用するのに対し，後者は頭上の開けた場所を利用した．両種の食性と流下及び底生動物の組成を比較した結果，両種

間に見られた食性の差異は採餌行動の差異のみならず採餌空間の違いをも反映しているものと考えられた．このような種間における資源の分割利用が両種の共存を可能にしているものと考えられた．

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