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Changes in Habitat Use and Feeding Chronology of Juvenile Rainbow Trout (*Oncorhynchus mykiss*) in Fall and the Onset of Winter in Silver Creek, Idaho

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We assessed changes in density, distribution, and microhabitat of age-0 rainbow trout (*Oncorhynchus mykiss*) in Silver Creek, a partially spring-fed stream, by periodic snorkeling in August 1987 through January 1988. We examined trout stomach contents and invertebrate drift samples in diel collections in August, September, October, and January to test if the period of feeding shifted from daytime to nighttime, concurrent with a transition to day concealment. In late September, fish aggregated briefly during the day and then began to conceal themselves in macrophyte beds, undercut banks, and submerged sedges and grasses along streambanks as temperature dropped below 8°C in early October. Fish emerged from concealment at night, and numbers of trout visible were greatest 30–60 min after sunset and about 30 min before sunrise. Periods of peak feeding changed from afternoon and evening in August and September, when fish were day active, to mainly at night in October after the initiation of day concealment. Trout did not feed upon abundant chironomids in the daytime drift in October. In January, fish fed at 1–4°C on mayflies, and stomachs were fullest in the early morning. Observations suggest that Silver Creek trout experienced a metabolic deficit that began in September.

Nous avons évalué les changements dans la densité, la répartition et le micro-habitat de la truite arc-en-ciel (*Oncorhynchus mykiss*) d'âge 0 dans le ruisseau Silver, cours d'eau partiellement alimenté par source, en effectuant, entre août 1987 et janvier 1988, des examens périodiques en plongée libre. Nous avons examiné le contenu de l'estomac des truites et des échantillons d'invertébrés présents dans le courant en les prélevant sur un nycthémère en août, septembre, octobre et janvier afin de vérifier si la période d'alimentation passait du jour à la nuit en même temps que les poissons commençaient à se cacher dans la journée. À la fin septembre, les poissons se rassemblaient brièvement pendant la journée puis commençaient à se cacher dans les bancs de macrophytes, à l'abri des sous-berges et parmi les carex et les herbes immergées, le long des rives, quand la température est passée au-dessous de 8°C au début d'octobre. Les poissons sortaient de leur abri la nuit, et le nombre de truites visibles était au maximum 30 à 60 min après le coucher du soleil et environ 30 min avant le lever du soleil. Les périodes où l'alimentation était au maximum, c'est-à-dire l'après-midi et le soir en août et septembre, quand les poissons étaient actifs le jour, se situaient principalement la nuit en octobre après que les poissons avaient commencé à se cacher le jour. Les truites ne se nourrissaient pas des chironomidés qui abondaient dans le courant pendant le jour en octobre. En janvier, elles se nourrissaient d'éphémères à 1–4°C, et les estomacs étaient pleins au maximum tôt le matin. Les observations semblent indiquer que les truites du ruisseau Silver connaissaient un déficit métabolique qui commençait en septembre.

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Winter is a stressful period for stream-dwelling salmonids. Low water temperature slows the rate of digestion and may limit the amount of energy available for metabolism and growth, even if food is available and feeding occurs (Cunjak and Power 1987). A reduction in water temperature reduces the swimming performance of trout (Hartman 1963), which impairs their ability to escape endothermic predators.

At the onset of winter, juvenile salmonids may form aggregations in open water, especially in thermal refuges (Cunjak and Power 1986), or may conceal themselves in woody debris, in interstices of the substrate (Hartman 1965), or under undercut banks (Hillman et al. 1987). Juvenile rainbow trout (*Oncorhynchus mykiss*) that were concealed during the day have been observed to emerge from concealment cover at night (Campbell and Neuner 1985; Contor 1989). Reasons for such a shift in habitat and abandonment of the presumably secure cover of the substrate remain unclear. One hypothesis is that juvenile rainbow trout move out of the substrate at night to feed when they are not vulnerable to day-active predators.

Feeding activity during winter has been described for stream-dwelling juvenile rainbow trout (Maciolek and Needham 1951; Needham and Jones 1956; Cunjak and Power 1987), Atlantic salmon (*Salmo salar*) (Thomas 1962; Smirnov et al. 1976; Riddell and Leggett 1981; Cunjak 1988a; but see Metcalfe and Thorpe 1992), brown trout (*Salmo trutta*) (Maciolek and

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TABLE 1. Densities (fish · m^{-2}) of juvenile rainbow trout estimated by snorkeling 2-m-wide lanes along stream margins and in midchannel portions of Silver Creek, Idaho, in 1987 and 1988.

	Temperature at time of snorkeling	Upper site		Lower site	
		Stream margin	Midchannel	Stream margin	Midchannel
Day					
3 August	17.0	11.9	26.7	7.4	34.7
8 August	16.0	16.7	30.0	18.5	48.0
15 August	15.0	25.0	49.8	12.2	54.0
6–7 September	13.0	5.7	59.0	14.0	61.0
21 September	11.0	2.0	41.0	4.8	38.6
25 September	13.0	5.7	39.4	4.8	48.0
3 October[a]	8.5	0	0	0	0
3 October[b]	13.0	0.4	0	1.4	1.1
16 October	8.0	0.4	0	0.6	0
Night					
17 August	14.0	56.1	20.2	32.4	34.9
26 September	11.0	40.6	20.6	31.5	23.3
17 October	9.5	3.0	1.9	15.8	2.0
13 November	8.0	10.4	2.3	4.5	0.6
20 November	6.0	6.1	0.2	2.0	0.6
20 January	2.0	4.6	0	3.0	0

[a]Morning count conducted at 10:00 MDT.
[b]Afternoon count conducted at 16:30.

within a metre of its original location. Because individual trout were usually visually isolated from one another by macrophytes, a disturbed fish seldom affected others. The snorkeler trained during nights with a full moon when fish could be observed without the aid of a dive light and then when the light was turned on. Awareness of this range of behavior aided the snorkeler in detecting when a fish had been disturbed, so that it could be disregarded. All data for night microhabitat analysis were collected at new moon or when the moon was less than one quarter full.

Microhabitat variables were measured immediately for those focal points marked during the day and the following morning for those marked at night. Variables measured were water depth, focal point elevation (distance above the substrate), focal point water velocity, adjacent velocity (maximum velocity within 30 cm of the focal point), substrate type, type of cover closest to the focal point, and distance to cover. Water velocity was measured with a Marsh–McBirney model 201 velocity meter (accuracy ±2%) with a 3.5-cm-diameter measuring probe. Cover was defined as the nearest structure within 2 m that we felt could provide concealment for juvenile rainbow trout. An "other" cover category was used to include macrophytes other than *Chara* or *Potamogeton* and woody debris. Substrate below the focal point of a fish was categorized as gravel, sand, silt, or clay according to the particle size classification of Platts et al. (1983). Gravel < 10 cm in diameter was the largest inorganic substrate and was too small to provide concealment cover for juvenile rainbow trout.

Based on habitat similarities and failure to detect significant differences (alpha = 0.05, used throughout the paper) in microhabitat values between the two sites, microhabitat data were pooled. Differences in night microhabitat utilization from summer through winter were assessed using a Kruskal–Wallis test. A Wilcoxon rank-sum test was performed on the day microhabitat utilization data because only two sets of observations were made before trout adopted concealment behavior. Changes in the type of cover and substrate used before and after the initiation of daytime concealment were evaluated using a chi-square test.

Feeding Chronology

We assessed the diet of age-0 rainbow trout during 24-h periods in late summer (5–6 August 1987), early fall (19–20 September 1987), early winter (24–25 October 1987), and midwinter (23–24 January 1988). The first three collections encompassed 24 periods beginning at 09:00 and ending at 06:00. Stomach contents were collected from 15 fish at 3-h intervals using gastric lavage. In January, diet was assessed at 09:00, 15:00, and 09:00 because too few fish were available to enable more frequent collection. Nocturnal illumination was provided by a first quarter moon on the August date and conditions intermediate between one quarter and new moon on the other dates.

Age-0 rainbow trout were captured with a backpack electrofisher and anesthetized with tricane methanesulfonate. Gastric lavage was employed, using a number 18 hypodermic needle and a 30-mL syringe to flush the cardiac portion of the stomach. Samples were fixed immediately in 10% formalin. We measured total length of trout to the nearest millimetre and released them after marking with a partial fin clip to preclude their reuse on that sample date.

In the laboratory, invertebrates from trout stomachs were identified under a dissecting microscope to the lowest feasible taxonomic level (usually genus) and weighed to the nearest milligram. Stomach content wet weights were divided by live body weight and multiplied by 100 to yield a relative stomach content wet weight (RWW) for each fish as done by Angradi and Griffith (1989). We used $\log_e(x + 1)$ transformation to normalize the RWW data and single-factor analysis of variance to test for

TABLE 2. Summary statistics for microhabitat variables of juvenile rainbow trout in Silver Creek, Idaho, in 1987 and 1988. Fish were concealed during the day during October–January.

Variable	Month and N	Day Mean	Day SD	Night Mean	Night SD
Total depth (cm)	August,	45	12	45	11
Focal elevation (cm)	N = 87 (day), 8	3	7	4	
Adjacent velocity (cm)	N = 53 (night)	23	7	29	10
Focal velocity (cm)		15	7	13	8
Distance to cover (cm)		28	23	·24	18
Total depth (cm)	September,	51	9	43	12
Focal elevation (cm)	N = 49 (day), 8	3	7	3	
Adjacent velocity (cm)	N = 98 (night)	29	10	25	9
Focal velocity (cm)		14	8	11	7
Distance to cover (cm)		48	30	38	29
Total depth (cm)	October,			37	14
Focal elevation (cm)	N = 48 (night)			37	2
Adjacent velocity (cm)				22	8
Focal velocity (cm)				48	3
Distance to cover (cm)				21	19
Total depth (cm)	November,			35	12
Focal elevation (cm)	N = 44			5	5
Adjacent velocity (cm)				16	9
Focal velocity (cm)				4	2
Distance to cover (cm)				14	10
Total depth (cm)	January,			27	9
Focal elevation (cm)	N = 22			1	1
Adjacent velocity (cm)				16	9
Focal velocity (cm)				3	1
Distance to cover (cm)				13	9

sunset, densities observed at 19:00 (2–5 fish·100 m^{-2}) were similar to those we had noted on 20 November along the margins of the upper and lower sites 2 h after sunset (2.0–6.1 fish·100 m^{-2}) (Table 1).

The pattern for the dawn period in November (Fig. 2) was the reverse of dusk. Before dawn, trout densities rose from 2–3 to 7 fish·100 m^{-2} about 30 min before sunrise. When the light meter indicated the lowest measurable level about 10 min prior to sunrise, all trout had concealed themselves in cover.

Microhabitat Use

Daytime microhabitat used by age-0 rainbow trout in the study sites changed from August to September (Table 2). Fish used significantly deeper water (mean = 51 cm) in September when they were in aggregations than in August (mean = 45 cm). Although focal velocities remained similar from August to September, adjacent water velocity increased significantly from a mean of 23 cm·s^{-1} in August to 28 cm·s^{-1} in September. Fish were found at a significantly greater distance from cover in September (mean = 28 cm) than in August (mean = 48 cm). Daytime focal elevations did not change significantly. In August, 44% of the fish were observed over *Chara*; this changed to 31% in September, with 57% over gravel, a significant change. *Chara* was the closest cover for a greater proportion of fish (92%) in September than in August (68%), also a significant change.

Nighttime microhabitat changed as temperature declined (Table 2). Juvenile rainbow trout progressively moved into shallower water. Mean depth used by fish decreased significantly from 45 cm in August to 27 cm in January. Focal elevation that ranged from a mean of 4–7 cm·s^{-1} in August–November fell to <1 cm·s^{-1} in January, a significant change. Juvenile rainbow trout gradually adopted positions in significantly slower water that were significantly closer to cover. Their mean focal velocity fell from 13cm·s^{-1} in August to 3 cm·s^{-1} in January, and distance to cover decreased from a mean of 24 to 13 cm in January.

Before the shift to day concealment, 54% of the juvenile rainbow trout selected nighttime stations over *Chara*. After the fish began to conceal themselves during the day, they were associated with silt and clay substrates at night significantly more frequently (55%) than with *Chara* (29%). Before adopting daytime concealment behavior, the closest cover at night was *Chara* for 74% of the fish. After the shift to day concealment, trout were observed significantly more frequently near the stream margin and flooded grasses at night (40%) than before, with 53% of the trout closer to *Chara* than to other available cover.

Feeding Chronology

The mean length of age-0 trout used for the diet analysis increased from 68.4 mm (range 49–92 mm) in early August to 85.5 mm (range 58–99 mm) in mid-September, 81.7 mm (range 63–100 mm) in late October, and 91.2 mm (range 68–122 mm) in late January.

During the 5–6 August sample of drift and diet, mean RWW

TABLE 3. Composition of stomach contents of age-0 rainbow trout captured in August, September, and October in Silver Creek, Idaho. For each sample (N = 15 trout), the number of each invertebrate taxon present and its percentage (in parentheses) of that sample are given.

Taxon	Hour of sampling (MDT) 09:00	12:00	15:00	18:00	21:00	24:00	03:00	06:00
5–6 August								
Ephemerella inermis	12 (7)	4 (3)	5 (4)	8 (3)	99 (34)	104 (56)	26 (25)	27 (22)
Baetis sp.	85 (51)	43 (32)	59 (52)	261 (83)	36 (12)	12 (8)	17 (23)	34 (28)
Other Ephemeroptera	36 (21)	48 (36)	18 (16)	6 (3)	74 (26)	20 (12)	13 (28)	17 (14)
Chironomidae	13 (8)	14 (10)	9 (8)	15 (5)	66 (22)	9 (6)	5 (7)	8 (7)
Other Diptera	3 (2)	12 (8)	7 (6)	5 (2)	1 (1)	0	1 (1)	0
Other aquatic invertebrates	18 (11)	14 (11)	14 (12)	18 (7)	13 (5)	11 (7)	12 (16)	35 (29)
Terrestrial invertebrates	1 (1)	0	0	0	0	0	0	0
Total number	168	135	112	314	189	156	74	122
19–20 September								
Ephemerella inermis	0	2 (2)	1 (1)	0	0	0	1 (2)	1 (2)
Baetis sp.	7 (14)	46 (41)	15 (6)	68 (18)	12 (7)	7 (9)	3 (7)	7 (17)
Other Ephemeroptera	3 (6)	3 (3)	9 (4)	5 (2)	9 (4)	6 (9)	2 (4)	0
Chironomidae	4 (8)	35 (31)	213 (76)	237 (62)	74 (46)	6 (8)	13 (20)	7 (17)
Other Diptera	4 (8)	1 (1)	2 (1)	13 (3)	2 (1)	4 (6)	2 (4)	11 (27)
Other aquatic invertebrates	32 (64)	20 (18)	28 (10)	58 (16)	49 (31)	19 (29)	22 (51)	14 (33)
Terrestrial invertebrates	0	5 (4)	10 (4)	4 (1)	15 (9)	28 (39)	0	1 (2)
Total number	50	112	278	385	161	72	43	41
24–25 October								
Ephemerella inermis	0	3 (1)	0	0	0	0	0	0
Baetis sp.	6 (12)	2 (6)	2 (13)	6 (21)	71 (48)	50 (34)	19 (22)	16 (18)
Other Ephemeroptera	6 (12)	2 (5)	1 (7)	0	13 (9)	8 (6)	5 (5)	9 (10)
Chironomidae	7 (14)	1 (3)	1 (7)	3 (11)	4 (2)	5 (3)	9 (10)	3 (3)
Other Diptera	1 (2)	1 (3)	3 (20)	1 (4)	22 (15)	5 (3)	10 (11)	6 (6)
Other aquatic invertebrates	30 (59)	30 (80)	8 (54)	18 (65)	34 (23)	78 (53)	45 (50)	58 (63)
Terrestrial invertebrates	1 (2)	0	0	0	1 (1)	2 (1)	2 (1)	1 (1)
Total number	51	37	15	28	145	148	90	93

stomachs was not correlated with temperature (6.0–10.5°C) or with surface or subsurface invertebrate drift, but was nearly negatively correlated with surface drift density (P = 0.06). Density of chironomids in the surface drift during the day in October was similar to that in September, but much reduced from September densities at night. In October, juvenile rainbow trout in the study area did not exploit the daytime food resource of chironomids that in September had provided up to 75% of the diet. Chironomids comprised 5% of items ingested by fish in October (Fig. 4; Table 3). Trout collected throughout the night had eaten *Baetis* mayflies, and a significant peak in feeding occurred during the night at 03:00 (ANOVA, $P < 0.01$ and Tukey test). Mean densities of chironomids and of invertebrates other than chironomids collected over the diel period were 12.2 (SD = 4.02) and 14.9 (SD = 5.21) organisms, respectively, per cubic metre of water filtered by the drift nets.

In the three samples on 24–25 January, water temperature was 1.1–3.9°C. Mean RWW decreased significantly from 2.1% at 09:00 to 0.5% at 15:00 (ANOVA, $P < 0.05$ and Tukey test) (Fig. 3). A mean of 22.8 food items per stomach was found, and the mayfly nymphs *E. inermis* and *Baetis* sp. together comprised 81–85% of that total (Fig. 4; Table 4). Terrestrial insects and adult Ephemeroptera were absent from the drift samples. Mean density of drift in the three samples was 5.4 (SD = 2.05) chironomids and 20.5 (SD = 7.38) members of other taxa (mostly mayflies drifting at night) per cubic metre of water filtered.

Discussion

Water temperatures in Silver Creek during winter were moderated a few degrees in comparison with most trout streams in the region, but were cold enough to induce behavioral changes in trout. Age-0 rainbow trout in the study sites briefly formed large clusters during the day in late September just prior to the shift in day concealment. Cunjak and Power (1986) found brook trout and brown trout in aggregations in headwaters of the Credit River, Ontario, at temperatures between 0.1 and 5.5°C, although they did not find trout subsequently concealed during the day. Unlike in Silver Creek, surface ice in their study area served as cover. Cunjak and Power (1986) found that trout used deeper water when they formed aggregations. Silver Creek trout similarly used deeper water and were farther from cover in winter when they are hidden in the stream bed (Metcalfe and Thorpe 1992). In their laboratory, salmon showed a loss of appetite even in the presence of excess food. If Silver Creek rainbow trout could be identified as anorexic, it would be during the October period when the abundant chironomids during the day could have benefited the Silver Creek juvenile rainbow trout energetically. Their stomach evacuation rate, based on temperatures during our October sample, might have enabled trout to consume two meals per day. Evidently, the perceived risk of predation (or some other factor) overrode the potential benefit of a second (daytime) meal. By January in Silver Creek, trout activity was more synchronized with the availability of those nocturnally drifting mayflies, and RWW and numbers of organisms in trout stomachs increased. Additional sampling during October–January would be required to more thoroughly assess these observations.

Numbers of Silver Creek trout visible in the water column at night in late November peaked at a light level of 0.001 $W \cdot m^{-2}$ at 30–60 min after sunset, a pattern similar to that observed for age-0 rainbow trout during winter by Contor (1989). The numbers of trout observed just after sunset and before sunrise may be indications of most active feeding activity during twilight, but more observations are needed to evaluate this. We occasionally noted trout feeding during our winter night snorkeling, as did Contor (1989). At summer temperatures, rainbow and brown trout fed at night under laboratory conditions at light levels similar to those during our Silver Creek observations (Jenkins 1969; Robinson and Tash 1979). Hatchery-reared age-0 rainbow trout held in Convict Creek, California, by Jenkins et al. (1970) fed on drifting insects, especially *Baetis* sp., during the night in December at 3–6.5°C. Elliott (1973) made similar observations for brown and rainbow trout at 4.7°C.

Benthic rather than drift feeding by Silver Creek trout would have confounded our results. The occurrence of algae, other plant material, or detritus in stomachs often accompanies epibenthic feeding (Tippets and Moyle 1978). We did not find these materials in the stomachs examined. There was some indication of epibenthic feeding at night in October and January, when the amphipod *Gammarus lacustrus* and larvae of the caddisflies *Hydropsyche* and *Oxyethira*, not collected in the drift, were found in a few stomachs. We saw no evidence of benthic feeding during the day in any of the samples. Cunjak and Power (1987) found evidence of the consumption of benthic organisms in early winter by brown trout, but not by brook trout, in the Credit River.

Early winter has been hypothesized as time of metabolic deficit in trout because of the cost of acclimation to decreasing stream temperatures (Cunjak and Power 1987; Cunjak 1988b). Condition factors of brook trout in the Credit River, Ontario, declined markedly from August to the November–December period (Cunjak and Power 1987), and the energy derived from feeding was insufficient to offset the costs of maintenance metabolism. The most substantial loss in energy content of juvenile Atlantic salmon in a Scottish stream occurred during October–December (Gardiner and Geddes 1980).

Water temperature in Silver Creek was moderated by a few degrees, but there was evidence of a metabolic deficit (Riehle 1990) similar to that for trout at Credit River, Ontario, sites where groundwater maintained mean winter temperatures above 3.5°C (Cunjak 1986). Although we cannot rule out the possibility that other factors may be involved, we speculate that the metabolic deficit faced by Silver Creek trout began in September and October. Mean RWW was 1% or less for the trout we sampled in September and October, lower than that in January, and body condition showed the greatest significant decline in September (Riehle 1990). These observations are consistent with those of Smith (1992), who found that 95% of the winter mortality of age-0 rainbow trout in enclosures in the Henrys Fork of the Snake River occurred within the first 7 wk following initiation of daytime concealment. Further studies are needed to fully understand the behavioral and physiological changes that occur during this critical period of transition for stream-dwelling salmonids.

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TABLE 4. Composition of stomach contents of age-0 rainbow trout collected on 23–24 January 1987 from Silver Creek, Idaho. For each sample, the numbers of each taxon present and its percentage (in parentheses) of the total sample are given.

Taxon	Hour of sampling (MDT)		
	09:00	15:00	09:00
Ephemerella inermis	191 (70)	32 (59)	166 (50)
Baetis sp.	40 (15)	12 (22)	102 (31)
Other Ephemeroptera	10 (4)	3 (6)	11 (3)
Chironomidae	0	2 (4)	24 (7)
Other Diptera	3 (2)	1 (2)	4 (1)
Other aquatic invertebrates	30 (12)	4 (8)	25 (7)
Terrestrial invertebrates	0	0	0
Total number	274	54	332
N (stomachs)	10	9	10

aggregations in September compared with August, when fish stationed individually. Juvenile anadromous salmonids may also aggregate in groups similar to those in Silver Creek immediately before they leave tributary streams at the onset of winter (Hillman et al. 1987). For resident species, we believe that a brief period of aggregation typically may be the initial signal of the major behavioral and physiological changes that occur at the onset of winter.

Data from Silver Creek study sites are in accord with recent observations suggesting that daytime concealment of juvenile rainbow trout may be initiated at temperatures somewhat warmer than previously believed. Hartman (1965) and Chapman and Bjornn (1969) concluded that juvenile steelhead they observed were concealed at temperatures below 4°C. In small streams in Washington, Campbell and Neuner (1985) found that no age-0 rainbow trout remained in the water column below 6.7°C. In our study, juvenile rainbow trout concealed themselves under the stream bank or in aquatic vegetation during the day at 8.5°C in early October. Later in the day, a few fish were found in the water column when temperatures rose to 13°C. Similar results were reported by Hillman et al. (1992) in small Washington streams, where fewer than 20% of the juvenile salmonids present were visible to snorkelers at temperatures below 9°C. Contor (1989) concluded that a threshold temperature for concealment behavior of juvenile rainbow trout in the Henrys Fork of the Snake River, Idaho, was above 7.5°C.

Daytime and nighttime fish densities declined in both Silver Creek sites during the latter part of September prior to the shift to day concealment behavior. This may have been due to downstream movement or mortality, which we did not monitor, or the initiation of concealment behavior by some individuals before the major shift to day concealment at the end of September. The decline in density of fish counted at night was accelerated at the time of the shift to day concealment, suggesting that some fish might have remained in cover throughout the night as well. Griffith and Smith (1993) found that 61–66% of the day-concealed age-0 brown trout and cutthroat trout (*Oncorhynchus clarki*) were observed at night in enclosed sites in the South Fork of the Snake River, Idaho.

Juvenile rainbow trout in the Silver Creek study area moved into stream margins as light levels dropped after sunset during late summer and, to a greater extent, during winter. This also has been noted in some larger streams, where virtually all age-0 trout observed at night (and electrofished from concealment during the day) were within a few metres of the water's edge (Contor 1989; Schrader and Griswold 1992; Griffith and Smith 1993) as well as in small streams in Washington (Campbell and Neuner 1985). Such behavior appears to be a combined response of selecting positions of low velocity and proximity to cover in lower gradient stream reaches.

In Silver Creek, age-0 trout selected slower and shallower water and moved closer to cover and to the stream bottom at night as temperatures decreased. During winter, they associated closely with vertical and undercut banks and submerged sedges and grasses along the bank. Despite a reduction in its volume during our study period, *Chara* provided concealment cover for trout. However, the decline in fish density by an order of magnitude from August through January suggests to us that winter habitat in our study sites was suboptimal. Furthermore, *Chara* volume in Silver Creek typically continues to decline until March (J.S. Griffith, unpublished data). In other Idaho streams less influenced by groundwater, macrophytes (usually *Myriophyllum* sp.) present in early winter typically slough off during November and December and by midwinter do not hold juvenile rainbow trout (Contor 1989; Schrader and Griswold 1992; Smith 1992). Late winter oxygen depletion in side channel pools has killed trout in British Columbia rivers (Bustard 1986) and might be expected in situations where macrophytes are dense and water movement is less than it was in our study sites.

Invertebrate drift in Silver Creek during fall and early winter was low relative to that in summer, as noted in some Canadian streams by Clifford (1978). However, the quality of that drift was high for juvenile trout. The dominant Silver Creek taxa in October and January were immature mayflies and chironomids, which also formed 80–97% of the winter drift sampled in Convict Creek, California, by Reimers (1957). These groups provided the bulk of the diet of age-0 rainbow trout in summer in the Henrys Fork of the Snake River, Idaho (Angradi and Griffith 1989), as well as in Silver Creek in August.

As expected from previous studies, Silver Creek trout fed during early and midwinter. Fewer than 1% of the stomachs we examined in October and January were empty. Four percent of the brown and rainbow trout stomachs examined in Convict Creek, California, by Maciolek and Needham (1952) were empty. Cunjak and Power (1987) noted that 4.4% of the 6–26 cm fork length brook and brown trout they checked in the Credit River, Ontario, during two winters contained no food. Mean stomach fullness exceeded 50% for the Credit River fish, but that parameter and RWW must be evaluated with caution because of their inflation by a reduced digestive rate in winter.

The period during which age-0 trout shifted to day concealment was transitional in their feeding behavior in Silver Creek. Fish exploited an abundant food source, drifting mayflies and chironomids, during the day and at dusk in August and September, before day concealment began. Similar densities of chironomids in the drift during the daytime in October were not available to fish which were concealed at that time. The nearly significant ($P = 0.06$) negative correlation between weight of food in stomachs and surface drift density in October suggests that feeding (primarily on mayflies at night) occurred when drift was low.

The term anorexia (sensu Mrosovsky and Sherry 1980) has been applied to nonsmolting Atlantic salmon parr during the

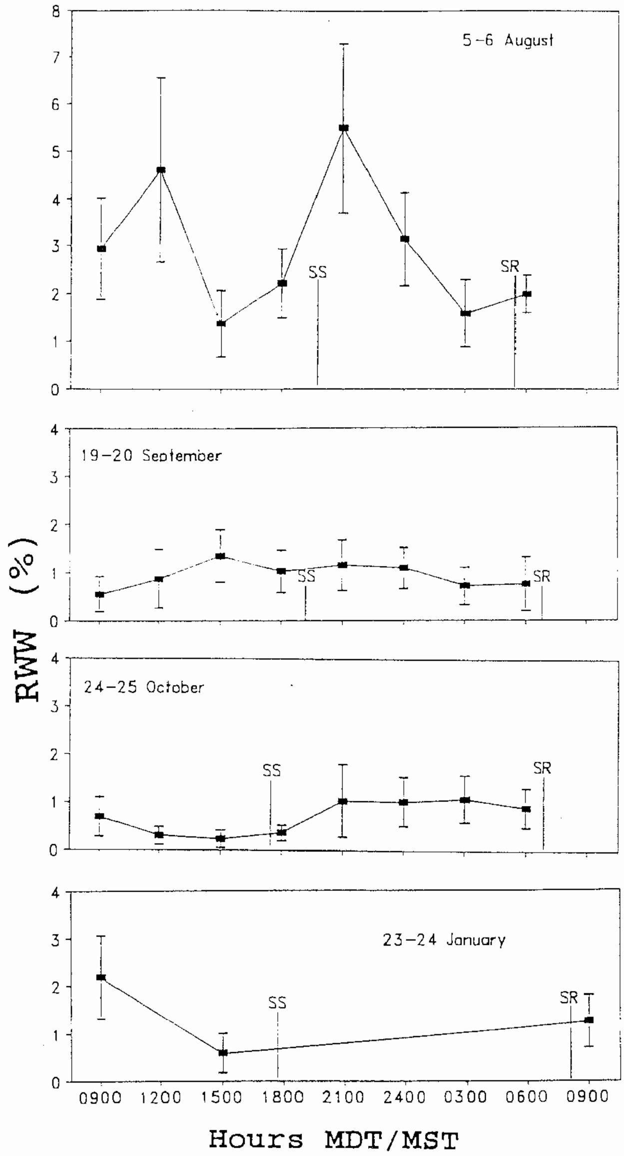

FIG. 3. Diel change in mean relative wet weight of stomach contents (RRW) of age-0 rainbow trout in Silver Creek, August 1987–January 1988. Vertical bars indicate 95% confidence limits. SS, sunset; SR, sunrise.

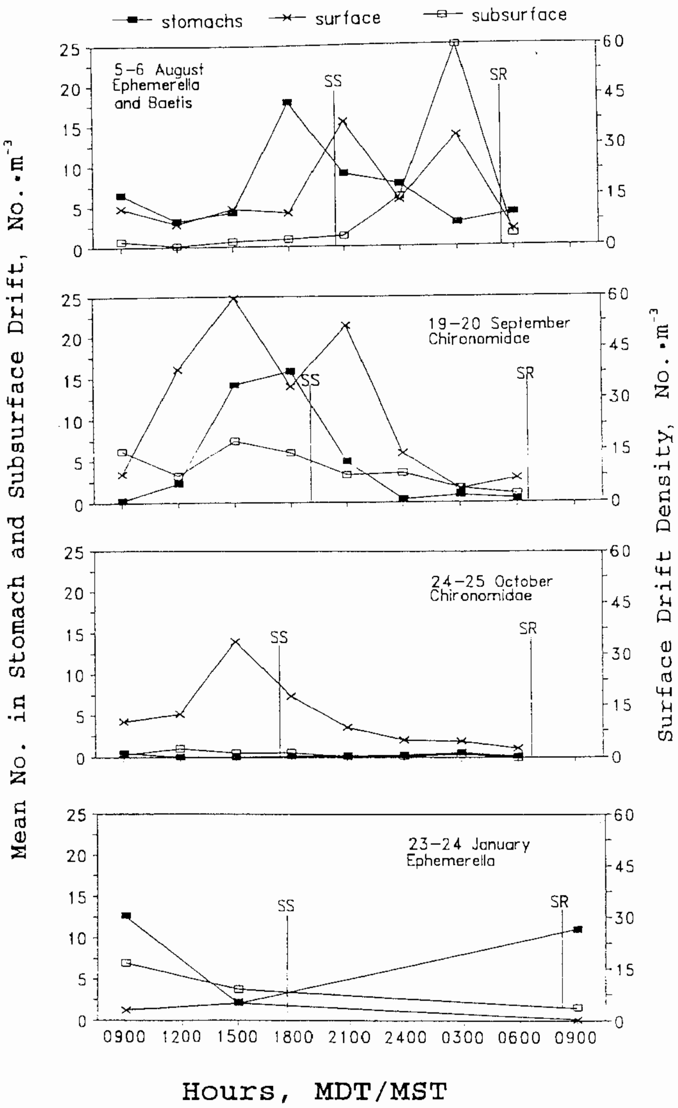

FIG. 4. Diel changes in mean number of prey items eaten by age-0 rainbow trout and surface and subsurface drift of those taxa in Silver Creek, August 1987–January 1988. SS, sunset; SR, sunrise.

was 3.8% for the diel period (Fig. 3) and the mean number of food items per stomach was 11.4. RWW peaked at 5.5% in the 21:00 sample just after sunset and at 4.6% at 12:00 (ANOVA, $P < 0.01$ and Tukey test, $P < 0.05$). Diel change in weight of food in the stomachs was correlated with the density of surface drift ($r^2 = 0.59$, $P < 0.05$), but not with water temperature that ranged from 13.0 to 17.4°C or the density of subsurface drift. Mayflies comprised 78% by number of the food ingested during the diel period. Densities of the relatively large mayfly *Ephemerella inermis* and the smaller *Baetis* sp. increased sharply in the surface drift from 18:00 to 21:00. Mayflies were eaten then, but their frequency in stomachs declined at night (Fig. 4; Table 3). Chironomids were the next most utilized abundant food item after mayflies. They were eaten during the day and at dusk, but seldom at 24:00 or 03:00 despite their continued abundance in the surface drift. Mean density (per cubic metre of water filtered) of invertebrates collected in drift nets (surface and subsurface combined) over the diel period was 35.4 (SD = 13.80) chironomids and 46.9 (SD = 17.35) members of all other taxa combined.

During the 19–20 September sample, mean daily RWW declined to a mean of 1.0% with no significant peaks (Fig. 3), and the mean number of food items per stomach was 9.5. Weight of prey in stomachs was significantly correlated with surface drift ($r^2 = 0.57$, $P < 0.05$) and water temperature that ranged from 9.0 to 12.5°C ($r^2 = 0.65$; $P < 0.05$), but not with subsurface drift. The most numerous prey in the stomachs were larval and pupal Chironomidae, and mayflies comprised only 15% of items ingested (Table 3). During the 15:00 and 18:00 samples, immature Chironomidae comprised 75 and 61% of the stomach contents, respectively. This peak in the number of chironomids in the stomachs in the afternoon followed a corresponding increase in their density in the surface drift (Fig. 4). Mean density of invertebrates collected in drift nets (surface and subsurface combined per cubic metre of water) over the diel period was 30.6 (SD = 12.35) chironomids and 63.9 (SD = 22.37) members of all other taxa combined.

On 24–25 October, mean RWW was 0.8% (Fig. 3), with a mean of 5.1 food items per stomach. Weight of food in the

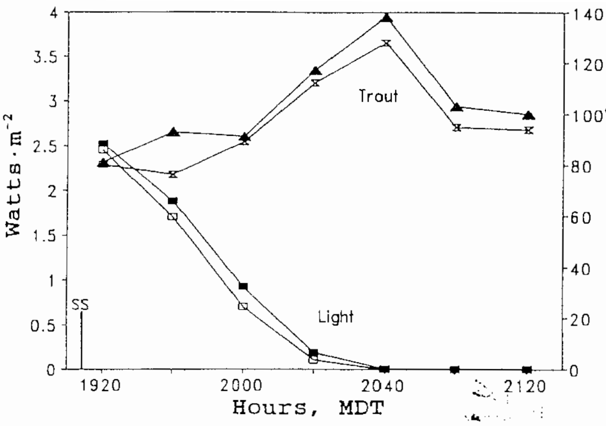

FIG. 1. Changes in density of age-0 rainbow trout visible to snorkelers along the stream margin and light intensity at dusk in Silver Creek, Idaho, on 5 September (open symbols) and 6 September (solid symbols) 1987.

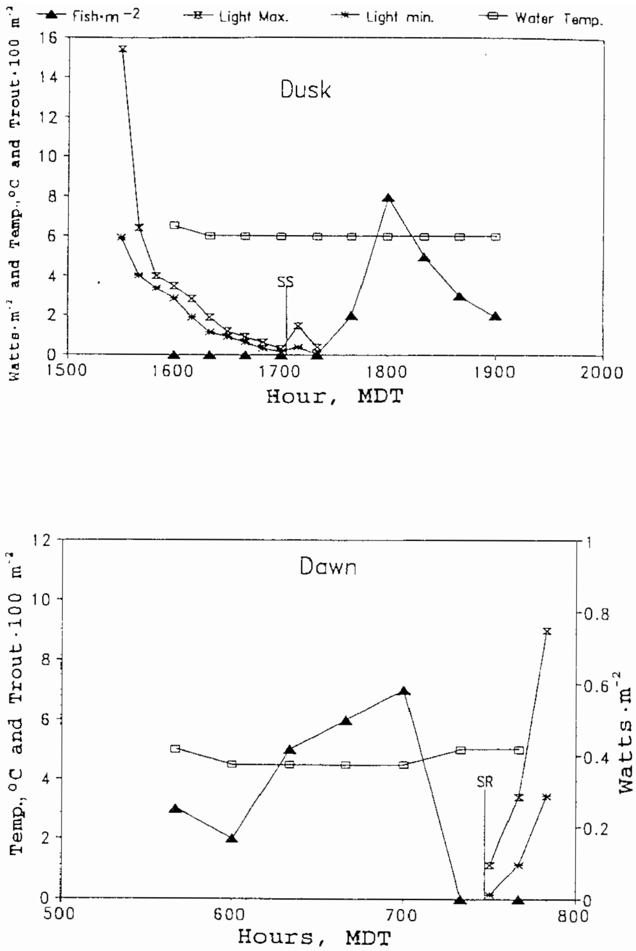

FIG. 2. Changes in density of age-0 rainbow trout visible to snorkelers along the stream margin, maximum and minimum light intensity during each 20-min observation period, and water temperature in Silver Creek at dusk on 20 November and at dawn on 21 November 1987. SS, sunset; SR, sunrise.

diel changes in RWW. Tukey's multiple-comparison test was used to identify the occurrence of peak feeding.

We collected surface and subsurface invertebrate drift at the upstream end of the site from which trout were captured for diet analysis. Six drift nets with 10 × 13 cm openings and 0.24-mm mesh were set for 20 min during each period when trout were collected for diet analysis. Three of the nets were set so that the water surface was at the middle of the net mouth and 5 cm of the net opening was under water, and three nets were set at 0.6 the depth of the water. Following Allan and Russek (1985), flow through each net was estimated from triplicate readings of water velocity within the net mouth at the beginning and end of each collection period. In the laboratory, invertebrates were identified under a dissecting microscope to the lowest feasible taxonomic level, usually genus, and drift was expressed as number of organisms per cubic metre of water filtered. Mean coefficient of variation for each diel sample ranged from 0.31 to 0.39.

Results

Trout Abundance and Distribution

The density of age-0 rainbow trout in daytime peaked in early September and decreased gradually through mid-September in both sites (Table 1). Peak daytime densities were observed on 6–7 September (59.0 and 61.1 fish·100 m^{-2} for upper and lower sites, respectively) in the midchannel snorkel lanes. In August and September, the density of trout remained highest in the midchannel lanes in the day, with densities over 35 fish·100 m^{-2}. However, fish were more abundant along the stream margins than in midchannel at night (chi-square, $P < 0.0001$ for both sites). Overall night densities in August and September were similar to the daytime estimates.

We last observed day-active juvenile trout in the study area on 25 September at 13°C. On that date, all age-0 rainbow trout seen were in aggregations, from a few dozen up to 200 individuals, that included a few age-0 whitefish and age-0 brown trout. Between 25 September and 3 October 1987, water temperature began to drop below 8°C at night and trout began to conceal themselves from the snorkeler during daylight hours. During the morning of 3 October at 8°C, we observed no fish; at 16:30, water had warmed to 13°C and we observed 1.4 fish·100 m^{-2} (Table 1). A few individual trout (<0.6 fish·100 m^{-2}) were visible in open water during the day on 16 October at 8°C.

After fish began to conceal themselves during the day, nighttime densities gradually declined from a peak of 15.8 fish·100 m^{-2} on 17 October to much lower levels in November and January (Table 1). A greater proportion of the population was noted along stream margins than in midchannel (chi-square, $P < 0.05$ for the upper site and $P < 0.01$ for the lower site).

Nocturnal Emergence From Concealment

In September, the number of age-0 rainbow trout observed along the stream margins in the central study site increased as light decreased at dusk (Fig. 1). On 5 September, density was approximately 80 fish·100 m^{-2} when light levels began to decline. When the light meter indicated the lowest measurable level (0.001 W·m^{-2}) 40 min after sunset, density was 127 fish·100 m^{-2} in the two subsequent census periods. On 6 September, we observed the same pattern, with a maximum of 138 fish·100 m^{-2} 30 min after sunset (Fig. 1).

On 20–21 November, a similar change in trout density at dusk occurred, except that no unconcealed fish were evident in full daylight (Fig. 2). Trout left concealment cover and became visible to the snorkeler just as the amount of light became too low to measure with our equipment. After peaking 1 h after

Needham 1951; Reimers 1957; Thomas 1962; Mortensen 1985; Cunjak and Power 1987), and brook trout (*Salvelinus fontinalis*) (Cunjak and Power 1987). However, these researchers did not observe whether feeding occurred at night or during the day.

This study had two main objectives. The first was to assess abundance, distribution and microhabitat use by age-0 rainbow trout in Silver Creek at the onset of winter. We were especially interested in whether fish concealed themselves in the dense beds of perennial aquatic macrophytes that were the main source of cover in the study area. The second objective was to assess the extent of feeding by age-0 rainbow trout and its diel chronology in Silver Creek. We tested if the period of feeding shifted from daytime to nighttime, concurrent with a transition to diurnal concealment behavior in winter.

Study Area

Silver Creek is a spring-influenced tributary of the Little Wood River located on the northern edge of the Snake River Plain in Blaine County, south-central Idaho. The 400-m-long study area, chosen for its abundance of juvenile trout and its accessibility, began approximately 1.5 km downstream from the confluence of Grove and Stalker creeks. The study area was a low-gradient (0.17%), meandering reach that ranged from 25 to 30 m wide. Discharge was relatively constant at about 3 $m^3 \cdot s^{-1}$ during the study period of August 1987 through January 1988, with a slight increase in late summer and early autumn. Specific conductance in August was 365 $\mu S \cdot cm^{-1}$. Water temperature, monitored with a Peabody Ryan recording thermograph in the study area, peaked at 17°C in August. Because of the spring-influenced tributaries, midwinter temperature remained near 4–5°C except for 2 d in early January when daily minima reached 0°C. No anchor ice was observed in the study area, and the only surface ice occurred along stream margins in January.

Although no comprehensive determination of habitat availability was regularly conducted during the study period, we surveyed habitat across 10 transects equally spaced along the study area during the last week of August. Water depth averaged 67 cm (range 61–73 cm). Dense beds of the macrophytes *Chara vularis* and *Potamogeton pectinatus* covered an average of 66% (range 55–74%) of the stream bottom from bank to bank. Substrate under the macrophytes ranged from medium silt to medium sand (0.016–0.5 mm in diameter, based on Platts et al. 1983) and averaged 14 cm deep. Channels (seven at each transect) through the macrophyte beds had fine gravel substrate, 4–8 mm in diameter. No cobble or boulder substrate was present. Undercut or vertical banks extended along >90% of the study area, and there were few margins shallower than about 25 cm. Riparian vegetation consisted of yellow willow (*Salix lutea*), American bulrush (*Scirpus americanus*), sedge (*Carex*) sp., and grasses. By the end of the study period in January, the stream surface area covered by macrophytes had gradually declined by approximately 30%. Water surface elevation, measured on a staff gage in the study area, increased a few centimetres in September, remained nearly constant through November, and dropped in January to a level 12 cm below that in August.

Rainbow trout were the most abundant salmonid in the study area. A few juvenile brown and brook trout were also present, but were not included in the study. Other fish species in the study area in late August, in decreasing order of abundance, were mountain whitefish (*Prosopium williamsoni*), bridgelip sucker (*Catostomus columbianus*), longnose dace (*Rhinichthys cataractae*), and Wood River sculpin (*Cottus leiopomus*). In September and October, most adult trout and nonsalmonids moved out of the study area to deeper water downstream. During winter, a few juvenile mountain whitefish were observed in the study area. Predators that remained in the study area during fall and winter included mink (*Mustela vison*), great blue herons (*Ardea herodias*), common mergansers (*Mergus merganser*), and belted kingfishers (*Ceryle alcyon*).

Methods

We divided the study area into three sites, two each of approximately 100 m at either end and a central site of 200 m. We snorkeled to count fish and assess microhabitat use in each of the distal sites and captured trout by electrofishing for diet analysis in the central site.

Trout Abundance and Distribution

We enumerated juvenile rainbow trout along the stream margin and in midstream by snorkeling along four parallel lanes in each site. The lanes, each 2 m wide and spaced equally from each other, were located along the west stream margin, west midchannel, east midchannel, and east stream margin. A snorkeler crawled slowly upstream and counted fish. At colder temperatures, trout are more easily disturbed (Bustard and Narver 1975). Sudden movements or splashing were avoided to prevent fish from swimming ahead of the snorkeler. At night, we followed the same procedure, using a dive light with a red filter. Daytime snorkeling was conducted between 10:00 and 17:00 Mountain Daylight Time (MDT; MST in November and January), and nighttime snorkeling was initiated 2 h after sunset. Water clarity, which we defined as the distance at which a juvenile trout could be clearly seen by the snorkeler, was 2.5–3.5 m during day and night throughout the study period. Snorkeling was completed at least monthly from August through November 1987 and in January 1988 (Table 1).

To assess the relationship between light intensity and emergence of fish from concealment cover, we monitored trout density at 20-min intervals during dusk and dawn of the September and November sample dates. A snorkeler counted fish along a 2-m-wide, 50-m-long lane along the bank in the central study site. We used a Li-Cor model LI-200SA pyranometer to measure minimum and maximum irradiance during each interval.

Microhabitat Use

Night microhabitat use by juvenile rainbow trout was assessed at five periods from summer through winter (8–9 August, 25–27 September, 16 October, and 13 November 1987 and 20 January 1988). Day habitat use was examined only in August and September; thereafter, most juvenile rainbow trout were concealed during the daytime. We assessed microhabitat use along the four lanes used to estimate fish density at the same time habitat use was assessed. A snorkeler moved upstream and marked fish positions with a flag at the focal point of each fish, taking care to avoid disturbing other trout.

During night dives, we noted the position of each fish before it reacted to the dive light. Once the light beam struck a fish, its typical response was to remain in the same position and then slowly sink to the substrate. As the snorkeler approached more closely, the fish either slowly moved away or swam up in the water column in an erratic manner and then darted into cover