Microhabitat use by juvenile Atlantic salmon (*Salmo salar*) sheltering during the day in summer

Gabe Gries and Francis Juanes

Abstract: Daytime snorkeling surveys were conducted in the Wardsboro Branch, a tributary of the West River, Vermont, U.S.A., in July and August 1996. We documented microhabitat use by 245 juvenile Atlantic salmon (*Salmo salar*) sheltering (i.e., concealed beneath the stream substrate) at water temperatures ranging from 17 to 23°C, well above 10°C, the maximum temperature at which young salmon are thought to shelter during the day. The majority (92%) of sheltering salmon were young-of-the-year salmon (YOY). Of the YOY observed, 45% were sheltering, while 55% were in the water column. In comparison, only 10% of post-young-of-the-year salmon (PYOY; age 1 or older) observed were sheltering, while 90% were in the water column. Sheltering PYOY occupied greater water depths and were found under larger substrate stones than were YOY. Sheltering salmon (YOY and PYOY) were not distributed in proportion to the available microhabitat. Salmon only sheltered beneath unembedded cobble or boulder substrate, and sheltering salmon were found in pool habitats 43% of the time. Daytime sheltering suggests that the current interpretation of juvenile salmon habitat use and behavior during summer is incomplete. The availability of suitable sheltering habitats may be a factor affecting juvenile salmon production.

Résumé : Des plongées durant le jour ont été effectuées dans le bras Wardsboro, tributaire de la rivière West, Vermont, É.-U., en juillet et août 1996. Nous avons étudié l'utilisation de microhabitats chez 245 Saumons de l'Atlantique (*Salmo salar*) juvéniles à couvert (i.e., des saumons à l'abri sous le substrat du cours d'eau), entre 17 et 23°C, bien au-dessus de la température de 10°C à laquelle les jeunes saumons sont réputés s'abriter durant la journée. La majorité (92%) des saumons étudiés étaient des jeunes de l'année (YOY). Parmi tous les jeunes de l'année, 45% se tenaient à couvert alors que 55% se tenaient dans la colonne d'eau. Après cet âge, seulement 10% des poissons (PYOY, 1 an ou plus) s'enfonçaient dans le substrat, alors que 90% nageaient dans la colonne d'eau. Les poissons PYOY à couvert se tenaient à des profondeurs plus grandes et dans du substrat plus grossier que les jeunes de l'année. Les saumons à couvert (YOY et PYOY) n'étaient pas répartis en fonction des microhabitats disponibles. Ils ne se dissimulaient que sous les cailloux et pierres libres dans le substrat, dans les cuvettes des ruisseaux dans 43% des cas. Cette mise à couvert dans des refuges pendant la journée semble indiquer que l'interprétation généralement acceptée du comportement et de l'utilisation de l'habitat pendant l'été chez les saumons juvéniles n'est que partielle. La disponibilité de refuges appropriés influence peut-être la production des saumons juvéniles.

[Traduit par la Rédaction]

Introduction

Juvenile Atlantic salmon (*Salmo salar*) become photonegative when water temperatures drop below 10°C in autumn (Rimmer and Paim 1990), and shelter (i.e., conceal themselves beneath the stream substrate) during the day (Gibson 1978; Rimmer et al. 1983). Daytime sheltering continues during winter (Cunjak 1988; Heggenes and Saltveit 1990), with nocturnal emergence to feed (Fraser et al. 1993). In summer, young salmon are typically photopositive (Gibson and Keenleyside 1966; Rimmer and Paim 1990) and maintain daytime feeding stations on or above the stream substrate (Keenleyside 1962; Gibson 1966; Rimmer et al. 1983). At night in summer, juvenile salmon are often located on or above the stream substrate (Gibson 1966; McKinley 1992; Gries et al. 1997).

Recent research has shown that juvenile Atlantic salmon are more active in the water column at night than during the day in late summer at water temperatures >10°C (LeDrew et al. 1996; Gries et al. 1997). This skewed diel activity pattern suggests that a portion of a given juvenile salmon population may shelter during the day in summer at water temperatures >10°C. However, investigation of summer daytime sheltering by juvenile salmon in the natural environment at water temperatures >10°C has been limited (but see Gardiner 1984), likely because it is thought that sheltering does not occur at these water temperatures (Rimmer et al. 1983; Fraser et al. 1993). Daytime sheltering by juvenile Atlantic salmon during summer (they are referred to hereafter as sheltering salmon) may be a factor affecting production and, if common, would suggest that the current interpretation of salmon habitat use and behavior is incomplete. Our objec-

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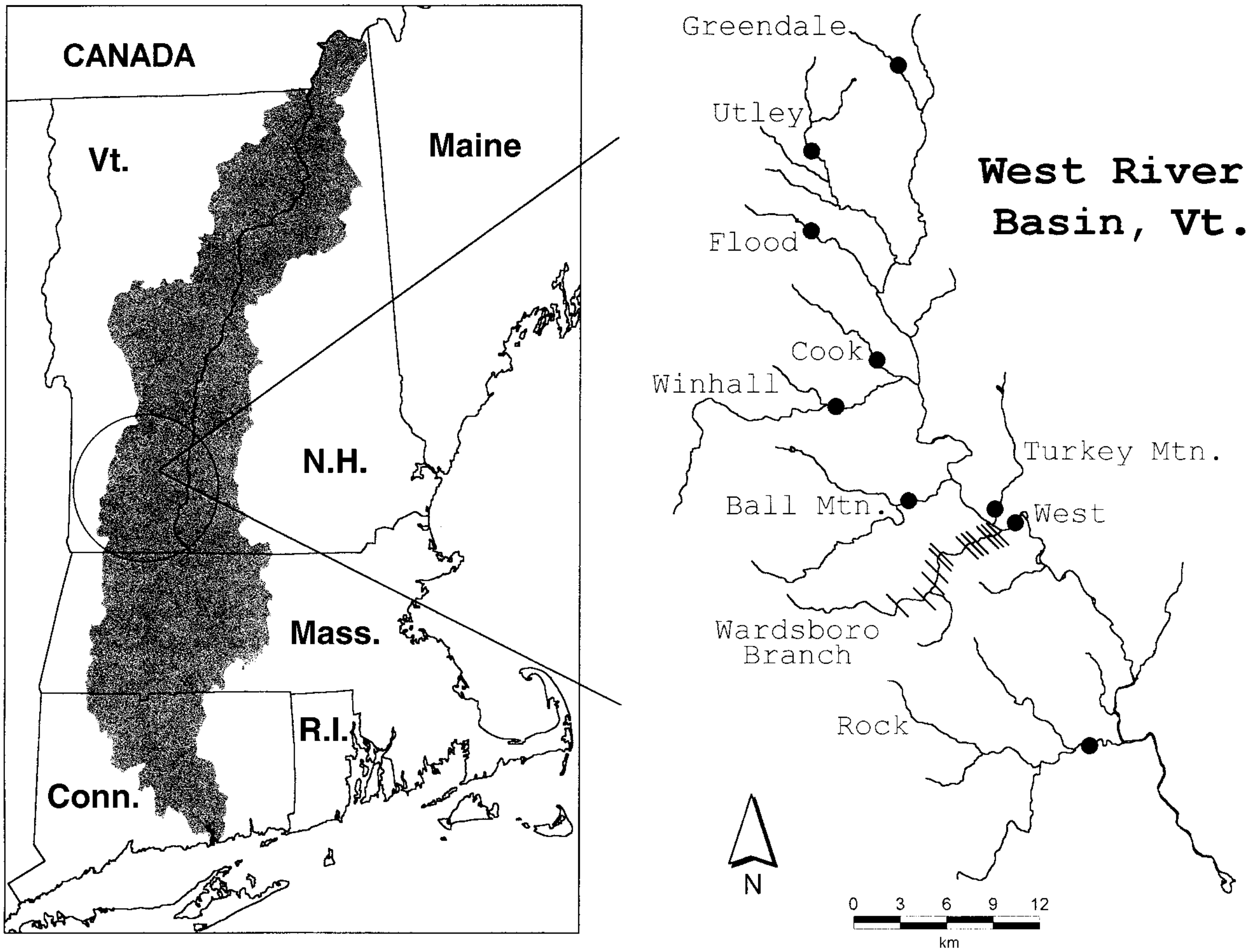
G. Gries[1] and F. Juanes. Department of Forestry and Wildlife Management, Holdsworth Natural Resources Center, University of Massachusetts, Amherst, MA 01003, U.S.A.

[1]Author to whom all correspondence should be sent at the following address: S.O. Conte Anadromous Fish Research Laboratory, One Migratory Way, P.O. Box 796, Turners Falls, MA 01376, U.S.A.

Fig. 1. Location of study sites in the West River Basin, Vermont, U.S.A. Snorkeling sites on the Wardsboro Branch are represented by thick lines (slashes). The solid circles show the approximate locations of brief snorkeling surveys conducted within the Basin (see the text for details). The Connecticut River Basin is shaded.



tives were to evaluate the prevalence of juvenile Atlantic salmon sheltering during the day in summer at water temperatures >10°C and to document microhabitat use by sheltering salmon.

Materials and methods

Study area and species

The Wardsboro Branch is a third-order tributary of the West River, Vermont, U.S.A. (43°08′N, 73°25′W; Fig. 1), which is a tributary of the Connecticut River. The Wardsboro Branch drains an area of approximately 96 km^2, is 19.3 km long, and has a gradient of 2.0%. Average stream width measured in August 1996 was 9.1 m.

Juvenile salmon in the Wardsboro Branch are stocked each April and May as unfed fry (25–30 mm, total length) at a density of 50/100 m^2. Fry are hatched from eggs obtained from sea-run, kelt, and broodstock Connecticut River Atlantic salmon. Most juvenile salmon in the West River Basin migrate as 2-year-old smolts (Whalen 1998). Several adult salmon have been observed in the West River Basin, but natural spawning is minimal. Other fish species occurring in the Wardsboro Branch included longnose dace (*Rhinichthys cataractae*), blacknose dace (*Rhinichthys atratulus*), white sucker (*Catostomus commersoni*), slimy sculpin (*Cottus cognatus*), brown bullhead (*Ameiurus nebulosus*), tesselated darter (*Etheostoma olmstedi*), common shiner (*Notropis cornutus*), and brook trout (*Salvelinus fontinalis*).

Twelve study sites were selected on the Wardsboro Branch (Table 1, Fig. 1). Distance between sites ranged from 0.32 to 2.74 km. We measured available microhabitat at 6 of the 12 study sites (Fig. 2). At these six randomly chosen sites, we placed transects across the stream every 10 m in pool habitats and every 20 m in riffle-run habitats. Water depth and substrate diameter were measured along these transects at 1 m intervals, beginning 0.5 m from the upstream-facing right stream bank.

Snorkeling observations

We performed snorkeling observations at the 12 study sites to evaluate the prevalence of sheltering behavior and document sheltering salmon microhabitat use. We also noted other fish species found sheltering. Study sites were sampled between 10:00 and 16:00 during the study period (23 July to 13 August 1996). Each study site was sampled once and only one site was surveyed per day. Two snorkelers conducted each 2- to 4-h survey. The snorkelers, each assigned to the left or right half of the stream, entered the site at its downstream boundary and slowly moved upstream, recording the number of salmon located on or above the substrate while searching for sheltering salmon by overturning all moveable stones. Stones were overturned in an upstream direction to increase the likelihood that fish would move downstream after being discovered. The locations of the few sheltering salmon that

Table 1. Physical characteristics of study sites on the Wardsboro Branch.

Study site	Area (m^2)	Habitat type[a] (% area) Pool	Riffle-run	Length (m)	Stream width[b] (m) Mean ± SE	Range	N	Gradient (%)	Pool to riffle-run ratio[c]
1	1686	9.5	90.5	153.2	11.24±0.93	4.60–20.56	16	2.5	1:2
2	1930	33.7	66.3	208.7	9.22±0.74	4.28–17.30	21	1.5	4:3
3	2479	18.7	81.3	191.8	13.02±0.86	4.66–19.96	20	2.0	1:2
4	1439	22.5	77.5	168.0	8.45±0.68	4.10–14.51	17	3.0	2:3
5	1333	42.3	57.7	163.8	8.01±0.54	3.20–11.40	18	2.5	5:3
6	2171	25.1	74.9	293.5	7.30±0.45	3.32–14.55	32	1.7	4:5
7	3910	23.6	76.4	375.0	10.45±0.45	5.92–20.70	38	2.2	4:5
8	2628	17.3	82.7	292.5	9.06±0.62	3.59–15.30	30	1.3	2:3
9	2552	33.7	66.3	272.2	9.22±0.53	5.50–15.22	29	2.3	4:4
10	1933	26.6	73.4	246.9	7.89±0.39	4.73–12.40	25	2.2	1:2
11	2059	13.9	86.1	261.5	7.54±0.25	5.80–10.36	26	1.5	1:1
12	2101	21.7	78.3	255.2	8.24±0.60	3.00–15.50	26	1.8	2:2
Total	26221	23.6	76.4						

[a]Pool: water depth >45 cm and surface water velocity <20 cm·s^{-1}; riffle-run: water depth ≤45 cm and surface water velocity ≥20 cm·s^{-1}. Modified after Rimmer et al. (1983).
[b]Measured at 10-m intervals.
[c]Ratio of the number of pools to the number of riffle-runs.

Fig. 2. Frequency distributions of microhabitat variables measured at positions of sheltering young-of-the-year (YOY) and post-young-of-the-year (PYOY; age 1 or older) juvenile Atlantic salmon and at locations used to determine available microhabitat (see the text for details).

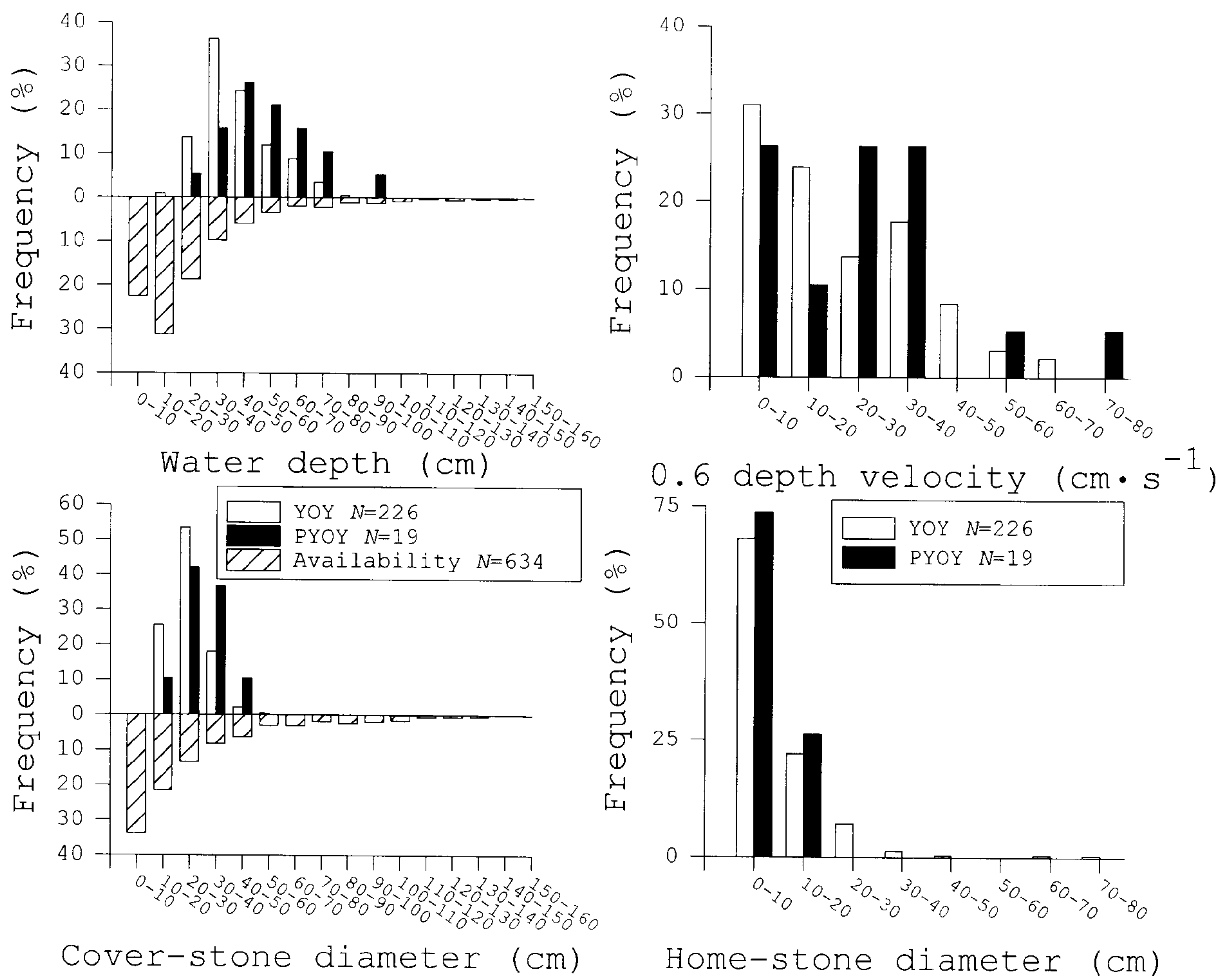


Table 2. Definitions of habitat types and microhabitat variables recorded at locations of sheltering juvenile Atlantic salmon.

Variable	Scale	Definition
Habitat type[a]	Pool or riffle-run	Pool: water depth >45 cm and surface water velocity <20 $cm \cdot s^{-1}$; riffle-run: water depth ≤45 cm and surface water velocity ≥ 20 $cm \cdot s^{-1}$
Water depth	cm	Perpendicular distance from the water surface to the location of the sheltering salmon
0.6 depth water velocity	$cm \cdot s^{-1}$	Water velocity determined at 0.6 water depth, measured downward from the water surface
Home-stone diameter[b]	cm	Longest dimension of the stone directly under the nose of the sheltering salmon
Cover-stone diameter[b]	cm	Longest dimension of the stone beneath which the salmon was sheltering

[a]Modified after Rimmer et al. (1983).
[b]Home and cover stones were classified as sand (<0.2 cm), gravel (0.2–1.6 cm), pebble (1.7–6.4 cm), cobble (6.5–25.6 cm), or boulder (>25.6 cm) after Bain et al. (1985).

moved upstream were noted to insure that these fish were not counted twice. Most salmon observed in the water column moved downstream past the snorkelers as the snorkelers continued their upstream survey. No salmon observed in the water column sought shelter beneath the substrate. Snorkelers communicated with each other so that the entire stream was surveyed and the likelihood of counting fish twice was minimized. Underwater visibility was greater than 5 m, with vision generally more limited by underwater structure than by water clarity. We recorded water temperature with a hand-held thermometer at the end of each survey. Because we could only effectively perform surveys at locations within our physical limits, water depths ≥100 cm and cover stones ≥70 cm in diameter were not sampled. Snorkelers surveyed water depths <15 cm by remaining in deeper water and reaching into shallow areas to overturn stones.

We marked sheltering salmon locations by placing numbered steel washers on the substrate and categorized salmon as young-of-the-year (YOY) or post-young-of-the-year (PYOY; age 1 or older) based on estimated total length. Decision criteria were YOY < 95 mm and PYOY > 105 mm (J.R. McMenemy, Vermont Department of Fish and Wildlife, R.R. #1, Box 33, North Springfield, VT 05150, U.S.A., personal communication). After surveying each site, we recorded habitat type, water depth, 0.6 depth water velocity, home-stone diameter, and cover-stone diameter at each sheltering location (Table 2).

We also conducted brief snorkeling surveys in the West River and eight of its other tributaries (Fig. 1). A snorkeler surveyed a single site on each stream until sheltering salmon were found. We recorded water temperature at the end of each survey using a hand-held thermometer. Microhabitat use was not documented at these sites.

Statistical analyses

We used χ^2 analysis in conjunction with a two-dimensional contingency table to test the null hypothesis that the proportion of salmon sheltering was the same for YOY and PYOY. Sheltering YOY and PYOY salmon microhabitat use was compared using Wilcoxon's rank-sum test. We employed the Kolmogorov–Smirnov test to determine if distributions of water depth and cover-stone diameter used by sheltering salmon were similar to those that were available. Water depths ≥100 cm and cover stones ≥70 cm in diameter were not included in the use versus availability analyses (see above). Statistical analyses were performed using SAS Institute Inc. (1988) and were considered significant at the $P = 0.05$ α level.

Results

We observed 245 juvenile Atlantic salmon sheltering in the Wardsboro Branch at water temperatures ranging from 17 to 23°C (mean ± 1 SE = 20.3 ± 0.5; $N = 12$). YOY salmon were found under the substrate more often than PYOY, accounting for 92% of the total number of sheltering salmon. A significantly greater proportion ($\chi^2 = 70.6$, df = 1, $P < 0.001$) of YOY than PYOY salmon were found sheltering; 45% of the total number of YOY observed ($N = 504$) were sheltering, while only 10% of the total number of PYOY observed ($N = 185$) were sheltering.

Sheltering YOY salmon were located at water depths ranging from 18 to 82 cm (41.8 ± 0.9 cm (mean ± 1 SE); Fig. 2) in areas with 0.6 depth water velocities of 0–67 $cm \cdot s^{-1}$ (20.6 ± 1.1 $cm \cdot s^{-1}$; Fig. 2). The YOY used cobble (62%) and boulder (38%) cover stones ranging in diameter from 10 to 58 cm (24.3 ± 0.5 cm; Fig. 2). All substrates were classified using definitions provided by Bain et al. (1985; Table 2). Sheltering YOY used pebble home stones most frequently (47%), followed by cobble (39%), gravel (8%), and boulder (6%). Home-stone diameters ranged from 0.2 to 70 cm (8.8 ± 0.6 cm; Fig. 2). Sheltering YOY salmon used riffle-run habitats (58%) more frequently than pool habitats (42%).

Sheltering PYOY salmon were located at water depths ranging from 28 to 93 cm (52.5 ± 3.7 cm; Fig. 2) in areas with 0.6 depth water velocities of 0–73 $cm \cdot s^{-1}$ (23.7 ± 4.5 $cm \cdot s^{-1}$; Fig. 2). PYOY used boulder (58%) and cobble (42%) cover stones ranging in diameter from 15 to 44 cm (28.5 ± 1.8 cm; Fig. 2). PYOY used pebble (53%) and cobble (47%) home stones ranging from 2 to 19 cm in diameter (7.4 ± 1.0 cm; Fig. 2). Sheltering PYOY salmon used pool habitats (53%) more frequently than riffle-run habitats (47%).

Sheltering PYOY salmon occupied significantly greater water depths (Wilcoxon's rank-sum test, $Z = 2.90$, $P < 0.01$) and larger cover stones (Wilcoxon's rank-sum test, $Z = 2.41$, $P = 0.016$) than did YOY salmon (Fig. 2). Age-class differences relative to 0.6 depth water velocity (Wilcoxon's rank-sum test, $Z = 0.46$, $P = 0.65$) and home-stone diameter (Wilcoxon's rank-sum test, $Z = 0.30$, $P = 0.76$) were not significant (Fig. 2).

Sheltering YOY and PYOY salmon were not distributed in proportion to available water depths (Kolmogorov–Smirnov (K-S) test, YOY: K-S statistic = 0.59, $P < 0.001$; PYOY: K-S statistic = 0.69, $P < 0.001$; Fig. 2) or cover substrates (K-S test, YOY: K-S statistic = 0.38, $P < 0.001$; PYOY: K-S statistic = 0.51, $P < 0.001$; Fig. 2). Sheltering YOY and PYOY occupied water depths from 0 to 20 cm at lower than expected frequencies. Water depths from 30 to

70 cm were used by YOY at greater than expected frequencies, while PYOY occupied water depths from 40 to 80 cm at greater than expected frequencies. YOY and PYOY used cover stones from 0 to 10 cm in diameter at lower than expected frequencies. Cover stones from 20 to 50 cm in diameter were used by YOY at greater than expected frequencies, while PYOY used cover stones from 20 to 40 cm in diameter at greater than expected frequencies.

Shelter use was solitary except for one instance when we observed two YOY salmon under the same cover stone. Only unembedded cobble or boulder substrates were used as cover stones. Sheltering salmon were frequently patchily distributed, with three or four salmon sometimes sheltering within a 1- to 2-m^2 area. We likely underestimated the number of salmon sheltering, because some fish fled before being identified when we overturned their cover stones. We frequently found salmon sheltering in areas where other salmon were active in the water column. Shelters marked during snorkeling surveys were often occupied again by salmon when we returned to perform microhabitat measurements.

Daytime sheltering in the Wardsboro Branch was a community-wide behavior involving all fish species occurring at study sites except brook trout. Additionally, sheltering by juvenile salmon was not limited to the Wardsboro Branch; we documented sheltering salmon in the West River and eight of its other tributaries at water temperatures ranging from 15 to 22°C (19.3 ± 0.9°C; N = 9).

Discussion

We found juvenile Atlantic salmon sheltering during the day in summer at water temperatures ranging from 17 to 23°C, well above 10°C, the maximum temperature at which young salmon are thought to shelter during the day (Rimmer et al. 1983; Fraser et al. 1993). Daytime sheltering by salmon may, therefore, be restricted to our system, but we suspect that this behavior is widespread geographically and has likely not been investigated because it is thought not to occur at water temperatures >10°C (Rimmer et al. 1983; Fraser et al. 1993). Accordingly, we found only one published field study in which sheltering juvenile Atlantic salmon were searched for during the day at water temperatures >10°C (Gardiner 1984).[2] Gardiner (1984) found that during July and August at water temperatures of 14–15°C, 51% of wild YOY salmon observed by snorkelers in a Scottish stream were sheltering under stones. There is evidence of daytime sheltering at water temperatures >10°C from controlled experiments as well: Gibson (1978) documented sheltering salmon in stream tanks at water temperatures ranging from 10.7 to 20°C, and Fraser et al. (1995) noted juvenile salmon sheltering at water temperatures >10°C in a laboratory setting. Sheltering salmon have also been observed during summer in the southern Connecticut River Basin, Connecticut, U.S.A. (S. Gephard, Connecticut Department of Environmental Protection, P.O. Box 719, Old Lyme, CT 06371, U.S.A., personal communication) and in eastern New Brunswick, Canada (R.A. Cunjak, Department of Biology and Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, NB E3B 6E1, Canada, personal communication), suggesting that sheltering may be widespread. However, detailed surveys of daytime sheltering salmon at different geographical locations are needed to determine the global prevalence of this behavior.

Microhabitat use

We observed sheltering salmon associated with specific microhabitats and were interested in contrasting our results with the results of related research. However, no other summer microhabitat studies of sheltering salmon exist, so we compared our observations with studies of daytime sheltering salmon in autumn (Rimmer et al. 1984) and winter (Cunjak 1988) in eastern Canada.

We found PYOY salmon sheltering under significantly larger cover stones and at significantly greater water depths than YOY. A similar relationship has been reported for cover-stone use by sheltering salmon in autumn (Rimmer et al. 1984) and winter (Cunjak 1988). In contrast, Rimmer et al. (1984) found no difference between the water depths occupied by the two sheltering age-classes in autumn, and Cunjak (1988) discovered YOY salmon sheltering in winter at greater water depths than PYOY.

We observed no significant differences in home-stone diameter or 0.6 depth water velocity between sheltering YOY and PYOY salmon. Cunjak (1988) found sheltering PYOY in winter at lower 0.6 depth water velocities than YOY. Home-stone diameter, as defined in our study, was not quantified for sheltering salmon in autumn (Rimmer et al. 1984) or winter (Cunjak 1988).

Rimmer et al. (1984) and Cunjak (1988) detailed the importance of a substrate of large cover stones for sheltering salmon in autumn and winter, and other studies have shown that an embedded substrate is especially unsuitable for salmonids at low water temperatures (Bustard and Narver 1975*b*; Hillman et al. 1987). Our findings concur with these previous results and show the importance of large, unembedded cover stones for salmon sheltering in summer as well.

We discovered 43% of sheltering juvenile salmon (YOY and PYOY) in pool habitats, although pools accounted for only 24% of the area surveyed, indicating the importance of pools for sheltering. Juvenile salmon occupy pool habitats during summer, but riffle-run habitats are usually selected (Gibson 1966; Elson 1975; Gibson and Dickson 1984; Caron and Talbot 1993). In contrast to our results, Rimmer et al. (1983) discovered only 4% of sheltering juvenile salmon (YOY and PYOY) in pool habitats during autumn, although pools constituted 42% of the available habitat at their study sites. Cunjak (1988) also found the majority of young salmon sheltering during the day in winter in riffle-run habitats, suggesting that habitat requirements for sheltering salmon may change seasonally.

[2] In the only other relevant study found (Rimmer et al. 1983), researchers did not appear to search for daytime sheltering juvenile Atlantic salmon when water temperatures were >10°C: “After the water temperature fell below 10°C, fish were difficult to find in the open stream and searches were then directed at crevices and spaces in the substrate....”

Why do salmon shelter in summer?

Daytime sheltering during summer conditions has previously been observed for juvenile Atlantic salmon (Gibson 1978; Gardiner 1984), YOY brown trout (*Salmo trutta*; Heggenes 1988), young Arctic char (*Salvelinus alpinus*; Adams et al. 1988), and YOY rainbow trout (*Oncorhynchus mykiss*; Culp 1989), but hypotheses to explain why juvenile salmonids shelter during summer are rare (but see Adams et al. 1988). Possible hypotheses include either avoidance of high water temperatures, predators, or competitors, or a low motivation to feed.

Water temperature is known to affect behavior and habitat use by young salmon (Gibson 1978; Rimmer et al. 1983; Fraser et al. 1993; Gries et al. 1997), but it is unlikely that high water temperatures caused the salmon in our study to shelter. Young salmon seek cooler locations when the water temperature rises above 25°C (Gibson 1966; DeCola 1970), and while water in interstitial spaces of the substrate was likely cooler than in the water column (Curry et al. 1991), our surveys were conducted at water temperatures below this critical maximum. Juvenile salmon often cease feeding at water temperatures >22.5°C (Elliott 1991), but the water temperature only exceeded this level on one occasion during our study and salmon in the water column were feeding and holding station at all water temperatures sampled.

Alternatively, salmon may shelter to avoid predators. Predation risk has been suggested as a cause of summer daytime sheltering by Arctic char (Adams et al. 1988) and cyprinids (Fraser 1983; Culp 1989), and is known to affect fish habitat selection (Stein 1979; Dill 1987; Schlosser 1987; Bugert and Bjornn 1991). In some cases, predators influence the use of cover habitats (Cerri and Fraser 1983; Werner et al. 1983*a*, 1983*b*; Power et al. 1985) and reduce feeding activity of juvenile salmonids (Metcalfe et al. 1987; Huntingford et al. 1988; Gotceitas and Godin 1991, 1993). However, various studies suggest larger, older stream salmonids are more wary and use cover to a greater degree than younger, smaller conspecifics (see the review by Grant and Noakes 1987; Mikheev et al. 1994). Because we found a greater proportion of YOY than PYOY salmon sheltering, and 55% of YOY we observed were not sheltering, we believe that factors other than predator avoidance are more likely to have affected the sheltering behavior we observed. Predators did not appear to be abundant at our study sites; only two potential fish predators were observed (both brook trout approximately 30 cm in length) and avian predators were rarely seen.

Intraspecific competition for feeding territories may cause salmon to shelter and may help explain why we found a greater percentage of YOY salmon sheltering than PYOY. During their first season, growing YOY Atlantic salmon shift microhabitats, tending to occupy areas with higher velocity water (Morantz et al. 1987), coarser substrate (Elson 1975; Morantz et al. 1987), and deeper water (Symons and Heland 1978; Kennedy and Strange 1982). This ontogenetic shift in microhabitat use results in a well-documented microhabitat overlap between YOY and PYOY juvenile salmon (Saunders and Gee 1964; Jones 1975; Symons and Heland 1978; Wankowski and Thorpe 1979; Kennedy and Strange 1986; Morantz et al. 1987; Orciari et al. 1994). Because larger stream salmonids are able to dominate smaller conspecifics (Symons 1968; Wankowski and Thorpe 1979; Metcalfe et al. 1992; Johnsson 1993), bigger individuals have an increased ability to compete for food and space (Symons 1974; Wankowski and Thorpe 1979; Grant and Kramer 1990). Consequently, PYOY salmon can influence the habitat choice of YOY salmon (Symons and Heland 1978; Kennedy and Strange 1982; Kennedy 1984). Moreover, habitat selection by juvenile salmon is highly dependent on competition for space and food (Kennedy and Strange 1982; Kennedy and Strange 1986), and redistribution of salmon into suboptimal habitat has been observed at high densities (Elson 1975; Bourgeois et al. 1993). Redistribution of YOY salmon may include movements to locations under stones because visual isolation decreases interactions between juvenile salmon (Kalleberg 1958) and young salmon are less likely to be attacked if they shelter among stones (Kalleberg 1958) or remain stationary and close to the stream substrate (Gibson 1988). YOY salmon may also shelter because an optimum strategy for growth adopted by subordinates may not be to attempt to maximize food intake but to minimize energy expenditure (Metcalfe 1986), with differences in daytime activity between YOY and PYOY possibly acting to reduce intraspecific competition (Magnan and FitzGerald 1984). The effect, if any, of intraspecific competition on sheltering is likely related in part to salmon density. Future research should examine the relationship between salmon density and daytime sheltering.

The higher percentage of YOY than PYOY salmon that we found sheltering may also be related to seasonal patterns of feeding motivation. The feeding motivation of juvenile salmon that will not undergo parr–smolt transformation the following spring (lower modal group; YOY in our study) generally decreases over the growing season, beginning in midsummer, while the feeding motivation of fish that will undergo parr–smolt transformation in the spring (upper modal group; PYOY in our study) increases (Metcalfe et al. 1986, 1988). Metcalfe (1986) hypothesized that differences in feeding motivation exist because lower modal group salmon try to minimize costs instead of maximizing their net energy gain. Lower modal group salmon also consistently hold station at lower water velocities and are more likely than upper modal fish to respond to predators by leaving their feeding station (Huntingford et al. 1988). Thus, if YOY salmon are not motivated to feed, daytime sheltering may allow them to minimize energy loss, avoid predators, and encounter low water velocities. We were unable to assess feeding by sheltering salmon during our surveys, as fish were not observed until they were disturbed by having their cover stones removed.

The significantly greater proportion of YOY than PYOY salmon that we found sheltering (45% of YOY vs. 10% of PYOY) is puzzling because in late summer, PYOY salmon are less active in the water column during the day and more active in the water column at night than are YOY (LeDrew et al. 1996; Gries et al. 1997). Thus, a greater percentage of PYOY salmon may have been sheltering than was documented in our study. This disparity could occur if PYOY sheltering habitat was limited or PYOY were sheltering at water depths too great to sample or under cover stones too large to overturn during our surveys. However, 34% of the available substrate and 28% of the available water depths at our study sites were within the range of microhabitats used by sheltering PYOY salmon. Additionally, at the sites at which we measured available microhabitat, only 11% of stones were of a size that made them difficult to overturn (≥70 cm in diameter) and only 2% of water depths were too deep to sample (≥100 cm). Thus, it appears the difference between the proportions of sheltering YOY and PYOY cannot be fully explained by a lack of available habitat or by an excess of deep water and large, immoveable stones. Interestingly, during daytime snorkeling surveys in summer, Gardiner (1984) discovered 51% of YOY salmon sheltering under stones (the total number observed under and above the substrate was 62), while no PYOY salmon were observed sheltering (the total number observed above the substrate was 2). Different patterns of daily activity among YOY and PYOY salmon should not necessarily be considered abnormal, as mixed temporal patterns have been found for the majority of fish species examined in temperate lakes (Emery 1973; Helfman 1981).

Management implications

The large percentage of salmon we found sheltering suggests that shelter availability may affect juvenile salmon production. Because we also observed that (*i*) sheltering salmon were not distributed in proportion to available microhabitat, (*ii*) shelter use was almost exclusively singular, and (*iii*) shelters were frequently occupied again a short time after disturbance, it is likely that shelter availability may be limited, certain shelter habitats are preferred, or both. Insufficient shelter habitat has been identified as a potentially important factor affecting over-winter population densities of some salmonid species (Bjornn 1971; Bustard and Narver 1975*a*; Rimmer et al. 1983; Cunjak 1988), with movement out of areas without adequate winter shelter habitat (Bjornn 1971). A lack of suitable sheltering habitat (i.e., large, unembedded cover stones) may also be a factor limiting juvenile salmon production during summer, with streams containing smaller cover stones likely being more limiting for PYOY. Information detailing the interstitial requirements and preferences of sheltering salmon (see Gregory and Griffith 1996*a*) may help explain production bottlenecks in some systems.

There may be competition for shelters if availability is limited. Shelter use by juvenile salmon during the day in summer (this study), winter (Cunjak 1988), and fall (Rimmer et al. 1983), and by other juvenile salmonids during the day in winter (Bustard and Narver 1975*a*; Glova 1986; Gregory and Griffith 1996*a*) is almost exclusively singular. Singular occupation of shelters combined with daytime observations of aggressive behavior of YOY Atlantic salmon under cover during summer (Kalleberg 1958) and of other YOY salmonids within winter cover habitat (Glova 1986; McMahon and Hartman 1989; Gregory and Griffith 1996*b*) suggests that intraspecific competition for shelters may exist. A large percentage of the fish community at our study sites sheltered during the day, indicating that interspecific competition for shelters may also occur. Competition for shelters, though, may be reduced by differences in the shelter requirements of fish of different species and sizes (Luckhurst and Luckhurst 1978; Robertson and Sheldon 1979).

Sheltering by salmon may have led to biases in past studies documenting behavior and habitat use by young salmon. Underwater observation is a method commonly used to examine patterns of juvenile salmon habitat use and behavior during the day in summer (Keenleyside 1962; Gibson 1966; Wankowski and Thorpe 1979; Rimmer et al. 1983; DeGraaf and Bain 1986; Morantz et al. 1987; Stradmeyer and Thorpe 1987; Heggenes et al. 1990; Gibson et al. 1993). An assumption of such studies is that the habitat use and behavior of fish determined by means of underwater observations are representative of the entire population. However, underwater surveys often provide lower estimates of juvenile salmon abundance than electrofishing techniques (Gardiner 1984; Cunjak 1988; Heggenes et al. 1990). The discrepancy between these two survey techniques is likely due in part to daytime sheltering; Gardiner (1984) specifically noted that daytime snorkeling counts of juvenile salmon made during summer without searching under stones were lower than counts obtained by electrofishing. Thus, past underwater surveys of salmon habitat use and behavior may have skewed our perception of which habitats are important to salmon in summer and may have biased our interpretation of their behavior as well. Future snorkeling surveys of summer habitat use and behavior should include assessments of sheltering salmon.

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