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Diurnal stream habitat use of juvenile Atlantic salmon, brown trout and rainbow trout in winter

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Abstract The diurnal winter habitat of three species of juvenile salmonids was examined in a tributary of Skaneateles Lake, NY to compare habitat differences among species and to determine if species/age classes were selecting specific habitats. A total of 792 observations were made on the depth, velocity, substrate and cover (amount and type) used by sympatric subyearling Atlantic salmon, subyearling brown trout and subyearling and yearling rainbow trout. Subyearling Atlantic salmon occurred in shallower areas with faster velocities and less cover than the other salmonid groups. Subyearling salmon was also the only group associated with substrate of a size larger than the average size substrate in the study reach during both winters. Subyearling brown trout exhibited a preference for vegetative cover. Compared with available habitat, yearling rainbow trout were the most selective in their habitat use. All salmonid groups were associated with more substrate cover in 2002 under high flow conditions. Differences in the winter habitat use of these salmonid groups have important management implications in terms of both habitat protection and habitat enhancement.

KEYWORDS: diurnal, habitat, juvenile salmonid, stream, winter.

Introduction

Winter habitat of salmonids in high latitude streams is often considered a bottleneck that regulates population size (Harwood, Metcalfe, Griffiths & Armstrong 2002; Maki-Petays, Erkinaro, Niemela, Huusko & Muotka 2004), and in the case of juveniles can impact smolt production (Whalen & Parrish 1999). Solazzi, Nickelson, Johnson & Rodgers (2000) reported that over-winter survival of juvenile salmonids was critical to increased smolt production. It has been widely demonstrated that in response to stressful winter conditions, salmonids in streams exhibit adaptive behaviour to minimise energy expenditures (Heggenes, Krog, Lindaas, Dokk & Bremnes 1993; Elso & Greenberg 2001). Energy conservation strategies of stream salmonids generally begin in late autumn with decreasing water temperatures (Bremset 2000). Responses of juvenile salmonids to the onset of winter conditions in streams include a switch to primarily nocturnal activity patterns (Heggenes *et al*. 1993; Fraser, Heggenes, Mecalfe & Thorpe 1995; Heggenes, Bagliniere & Cunjak 1999, Bremset 2000; Bradford & Higgins 2001), the use of substrate shelters during the day (Valdimarsson & Metcalfe 1998; Heggenes *et al*. 1999; Armstrong & Griffiths 2001; Harwood *et al*. 2002) and reduced movement (Huusko, Greenburg, Stickler, Linnansaari, Nykanen, Vehanen, Koljonen, Louhi & Alfredson 2007).

As juvenile salmonids generally spend daytime periods in substrate shelters during winter, the availability of these specific habitats may influence over-winter survival (Harwood *et al*. 2002). Shelters are often associated with unembedded coarse gravel (Huusko *et al*. 2007), but some salmonids burrow into loose gravel during winter (Meyer & Griffith 1997). Maki-Petays *et al*. (2004), identified these habitats as low-flow refugia for overwintering salmonids. Further complicating the understanding of daytime winter stream habitat use of juvenile salmonids, Valdimarsson & Metcalfe (1998) observed both sheltering (seeking refuge from harsh environmental conditions) and hiding (concealment from specific threats) behaviour of juvenile Atlantic salmon. Regardless of whether or not juvenile salmonids exhibit sheltering or hiding behaviour during daytime in streams in winter, because the fish are sedentary at this time, it is important to identify their diurnal habitat. Many studies of diurnal winter habitat of juvenile salmonids in streams have been in artificial

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streams (Valdimarsson, Metcalfe, Thorpe & Huntingford 1997; Elso & Greenberg 2001; Griffiths & Armstrong 2002; Harwood *et al.* 2002). Studies on winter salmonid habitat in natural streams have been made on either one (Cunjak 1988; Whalen & Parrish 1999; Bradford & Higgins 2001; Maki-Petays *et al.* 2004) or two (Cunjak & Power 1986; Bremset 2000; Enders, Clarke, Pennell, Ollerhead & Scruton 2007) species. The few studies that have examined the winter stream habitat of more than two species in sympatry have described habitat broadly in the context of pools, riffles and runs (Swales, Lauzier & Levings 1986; Bramblet, Bryant, Wright & White 2002).

The diurnal winter habitat use of subyearling Atlantic salmon, *Salmo salar* L., subyearling brown trout, *Salmo trutta* L. and subyearling and yearling rainbow trout, *Oncorhynchus mykiss* 9 Walbaum, was examined in Grout Brook, a second-order tributary of Skaneateles Lake, New York. The objectives of the study were to (1) determine if habitat occupied during winter differed among species/age groups and (2) determine if salmonids were selecting specific habitats by contrasting the habitat used by fish to available habitat within the stream reach.

Methods

Grout Brooks is a high-quality coldwater stream and drains an area of 2455 ha. Throughout much of the stream, an excellent riparian canopy maintains summer water temperatures below 20 °C. Stream discharges during summer is about 0.12 $m^3 s^{-1}$. Diurnal winter habitat use of juvenile salmonids in Grout Brook was examined from 10.00 h to 14.00 h during February 2000 and 2002. Stream discharge in February 2000 was 0.10 $m^3 s^{-1}$ and in February 2002 was 0.27 $m^3 s^{-1}$. Salmonid habitat was examined in a 0.5-km reach that contained juvenile Atlantic salmon and rainbow trout in 2000 and a 0.5-km stream reach that had both of these species as well as juvenile brown trout in 2002. Trout present in the stream represented naturalised wild populations, whereas Atlantic salmon were stocked in the stream the previous June (1999) or July (2001). Rainbow trout in Grout Brook are migratory, departing the stream by the age of two for Skaneateles Lake, then returning as adults to spawn. Juvenile rainbow trout were classified as subyearling (0+) or yearling (1+) based on size. Stream temperatures, recorded with a continuous reading thermograph, can approach 0.0 °C in Grout Brook during winter and average about 3.9 °C. A small amount of anchor ice was present in the stream in 2000. Air temperatures in February 2000 averaged −3.3 °C and 0 °C in February 2002.

Juvenile salmonid habitat was examined using the spot electric fishing technique sampling all potential habitats while sampling upstream (Bovee 1986; Johnson, Dropkins & Shaffer 1992). This technique is considered more efficient than underwater observation to determine the abundance of juvenile salmonids that are sheltering in daytime (Gries & Juanes 1998). A numbered buoy was placed at the site of each fish collection, and the species, number and age class were recorded along with the buoy number. This procedure was repeated until buoys were deployed throughout the 0.5-km stream reach. Later, as each buoy was retrieved, the water depth, water velocity, amount and type of cover, and substrate size were recorded at each spot. Water depth was measured with a wading rod and water velocity was measured at a depth of 0.6 from the surface with a Marsh–McBirney model 201 D digital flow meter. The amount and type of cover present was visually estimated at 5% increments (range 0–100%) as a percentage within a radius of four fish lengths of the location of the buoy (Johnson & Dropkin 1996). Cover was classified as substrate, surface turbulence and vegetative. Most cover observations recorded only a single cover type (65%), the presence of two types of cover was recorded about 30% of the time and all three cover types were judged to be present at about 5% of the sites. Substrate size was estimated using a modified Wentworth particle size scale ranging from detritus (1) to bedrock (8) (Orth, Jones & Maughan 1981). In each stream reach where juvenile salmonid habitat was examined, available habitat was also determined from 25 transects located about 20 m apart. Along each transect, water depth, water velocity, amount and type of cover, and substrate size were measured at stations spaced 0.5 m apart.

The distribution of habitat variables among salmonid groups, and between salmonid groups and available habitat were compared using the Kolmogorov–Smirnov test (Slauson 1988). Differences in the type of cover used were examined using multivariate analysis of variance (MANOVA) with percent cover type as the multivariate response and species/age class as the categorical predictor variable (SAS Institute, Inc 2001). When significant differences were found, a one-way analysis of variance (ANOVA) and Tukey's test were used to determine which categories were different. Principal component analysis (PCA) were used to examine the ordination of habitat variables (ter Braak 1995; ter Braak & Smilaurer 2002). A significance level of $\alpha = 0.05$ was used for all comparisons.

Results

A total of 363 habitat observations of subyearling Atlantic salmon (n = 76), subyearling rainbow trout (n = 207) and yearling rainbow trout (n = 80) were made in February 2000 in Grout Brook. In February 2002, an additional 429 habitat observations were made, including 54 subyearling salmon, 273 subyearling rainbow trout, 54 yearling rainbow trout and 48 subyearling brown trout. Juvenile salmonid densities (no./m^{-2}) ranged from $<$0.01 (subyearling brown trout in 2000) to 0.88 (subyearling rainbow trout in 2002) Table 1. There was no difference ($P > 0.05$) in the size (total length) of the juvenile salmonid age classes between years. In February, during both years, the mean size (total length) was about 88 mm for salmon, 70 mm for subyearling rainbow trout, 111 mm for yearling rainbow trout and 82 mm for brown trout. Available habitat during both years was quantified from 160 observations in each study reach.

As stream discharge was almost 3× higher in 2002, comparisons of salmonid winter habitat between years could not be made. In 2002, the mean depth and water velocity within the study reach were 7.5 cm and 14.9 cm s^{-1} greater, respectively, than in 2000. PCA analysis showed that the habitat used by subyearling rainbow trout was most similar between years and was least similar for subyearling Atlantic salmon (Fig. 1). PCA also revealed that cover and depth governed the habitat use of yearling rainbow trout, whereas substrate and velocity were more important to subyearling salmon. The habitat occupied by yearling rainbow trout diverged the most from available habitat during both years suggesting that yearling trout were the most selective in their habitat use. Axis 1 explained 62.2% of the variation and axis 2, 34.3% using PCA (Fig. 1).

During winter 2000, with the exception of the size of substrate used by yearling rainbow trout, all three groups of salmonids occupied areas that were significantly different from the habitat that was generally available within the stream reach (Table 2, Fig. 2). Salmonids were found in areas that were deeper, faster flowing water, had more cover and larger size substrate than were available on average within the study section. The habitat used by subyearling Atlantic salmon and subyearling rainbow trout did not differ. Mean water velocity used by subyearling Atlantic salmon (32.1 cm s^{-1}) was higher than either group of rainbow trout, but not significantly so. Yearling rainbow trout occupied deeper areas and were associated with more cover than subyearling salmonids.

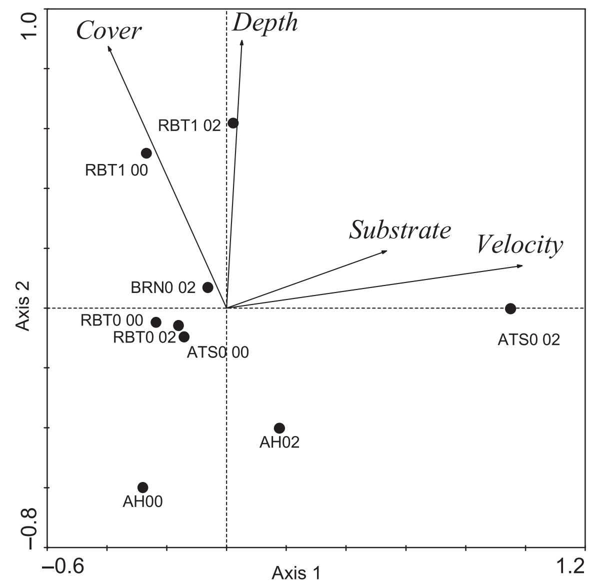

Figure 1. Ordinal representation of habitat data using Principal Components Analysis. ATS0 = subyearling Atlantic salmon, RBT0 = subyearling rainbow trout, RBT1 = yearling rainbow trout, BRT0 = subyearling brown trout, AH = available habitat, 00 = 2000, 02 = 2002.

During winter 2002, with the exception of water velocities occupied by yearling rainbow trout, all four groups of salmonids were found in areas that were significantly different from the habitat that was available within the stream reach (Table 2, Fig. 2). Subyearling Atlantic salmon used the least amount of cover (10.7%), whereas yearling rainbow trout were associated with the most cover (29.0%). Mean water

Table 1. Salmonid densities (no./m^{-2}), mean total length (mm, ±SE) and size range in Grout Brook, February 2000 and 2002

Species/age class	2000			2002		
	Density	Length	Range	Density	Length	Range
Atlantic salmon 0+	0.29	87.7 (1.2)	74–92	0.21	90.1 (0.9)	75–96
Brown trout 0+	<0.1	–	–	0.14	81.7 (0.7)	73–90
Rainbow trout 0+	0.67	68.2 (1.8)	53–78	0.88	72.1 (1.4)	57–81
Rainbow trout 1+	0.42	109.6 (1.1)	90–117	0.28	113.8 (1.3)	95–122

Table 2. Results of Kolmogorov–Smirnov tests comparing intra and interspecific juvenile salmonid habitat use and habitat used by salmonids with available habitat in winter in Grout Brook

Comparison	Depth (cm)	Velocity (cm s^{-1})	Cover (%)	Substrate
2000				
ATS 0+–AH	19.1(1.0)–13.7(0.8)*	32.1(1.8)–24.6(1.6)*	20.2(2.9)–9.6(2.6)*	5.9(0.1)–5.8(0.1)*
RBT 0+–AH	21.8(1.0)–13.7(0.8)*	28.8(2.0)–24.6(1.6)*	20.4(3.0)–9.6(2.6)*	5.9(0.1)–5.8(0.1)*
RBT 1+–AH	31.3(1.6)–13.7(0.8)*	30.3(2.0)–24.6(1.6)*	31.1(4.8)–9.6(2.6)*	5.8(0.1)–5.8(0.1)
ATS 0+–RBT0+	19.1(1.0)–21.8(1.0)	32.1(1.8)–28.8(2.0)	20.2(2.9)–20.4(3.0)	5.9(0.1)–5.8(0.1)
ATS 0+–RBT1+	19.1(1.0)–31.3(1.6)*	32.1(1.8)–30.3(2.0)	20.2(2.9)–31.1(4.8)*	5.9(0.1)–5.8(0.1)
RBT 0+–RBT1+	21.8(1.0)–31.3(1.6)*	28.8(2.0)–30.3(2.0)	20.4(3.0)–31.1(4.8)*	5.9(0.1)–5.8(0.1)
2002				
ATS 0+–AH	24.0(0.8)–21.2(1.3)*	67.5(2.3)–39.5(2.6)*	10.7(1.7)–6.4(2.4)*	6.1(0.1)–5.8(0.1)*
RBT 0+–AH	26.0(1.0)–21.2(1.3)*	30.2(1.9)–39.5(2.6)*	16.2(2.4)–6.4(2.4)*	5.7(1.1)–5.8(0.1)*
RBT 1+–AH	35.2(1.3)–21.2(1.3)*	39.7(2.5)–39.5(2.6)	29.0(4.4)–6.4(2.4)*	6.1(0.1)–5.8(0.1)*
BT 0+–AH	31.8(1.0)–21.2(1.3)*	33.1(1.8)–39.5(2.6)*	15.0(1.2)–6.4(2.4)*	5.6(0.1)–5.8(0.1)*
ATS 0+–RBT0+	24.0(0.8)–26.0(1.0)	67.5(2.3)–30.2(1.9)*	10.7(1.7)–16.2(2.4)*	6.1(0.1)–5.8(0.1)
ATS 0+–RBT1+	24.0(0.8)–35.2(1.3)*	67.5(2.3)–39.7(2.5)*	10.7(1.7)–29.0(4.4)*	6.1(0.1)–6.1(0.1)
ATS 0+–BT0+	24.0(0.8)–31.8(1.0)*	67.5(2.3)–33.1(1.8)*	10.7(1.7)–15.0(1.2)*	6.1(0.1)–5.6(0.1)*
RBT0+–RBT1+	26.0(1.0)–35.2(1.3)*	30.2(1.9)–39.7(2.5)*	16.2(2.4)–29.0(4.4)*	5.8(0.1)–6.1(0.1)*
RBT0+–BT0+	26.0(1.0)–31.8(1.0)*	30.2(1.9)–33.1(1.8)	16.2(2.4)–15.0(1.2)	5.8(0.1)–5.6(0.1)*
RBT1+–BT0+	35.2(1.3)–31.8(1.0)	39.7(2.5)–33.1(1.8)*	29.0(4.4)–15.0(1.2)*	6.1(0.1)–5.6(0.1)*

Values presented are means with standard error in parenthesis. ATS 0 + = subyearling Atlantic salmon, RBT 0 + = subyearling rainbow trout, RBT 1 + = yearling rainbow trout, BT 0 + = subyearling brown trout, AH = available habitat. *Significant difference ($P < 0.05$).

velocity used by subyearling salmon (67.5 cm s^{-1}) was significantly greater than for the three groups of trout. Yearling rainbow trout were found in areas with significantly faster water velocities than subyearling rainbow trout and brown trout. Significant differences occurred in the depth occupied by subyearling Atlantic salmon and yearling rainbow trout, salmon and subyearling brown trout, and between subyearling rainbow trout with both yearling rainbow trout and brown trout (Table 2, Fig. 2).

MANOVA cover type analysis showed no significant differences ($P = 0.34$, Wilks' Lambda = 0.968) in the data for the year 2000; whereas in 2002, differences were significant ($P < 0.0001$, Wilks' Lambda = 0.245). One-way ANOVA of the 2002 data showed the use of all cover types by all salmonid groups were highly significant ($P < 0.001$). In 2002, subyearling brown trout were associated with significantly ($P < 0.05$) more vegetative cover and significantly ($P < 0.05$) less substrate cover than subyearling Atlantic salmon and subyearling and yearling rainbow trout (Fig. 3, Table 3). There were no differences in the amount of substrate cover used by subyearling salmon, subyearling rainbow trout or yearling trout, but there was a significant difference between all three salmonid groups with available cover. All three groups of salmonids used significantly more substrate cover than was available indicating that they were selecting this type of cover. There was also a significant ($P < 0.05$) difference in the amount of substrate cover used by subyearling brown trout compared with available substrate cover. However, in this instance, brown trout used less substrate cover than was available (Fig. 3, Table 3). Under high flow conditions in 2002, all four salmonid groups used significantly ($P < 0.05$) less surface-turbulence cover than was available. Subyearling rainbow trout used significantly ($P < 0.05$) less surface-turbulence cover than subyearling Atlantic salmon and yearling rainbow trout. By contrast, there were no differences between salmon and yearling rainbow trout or between subyearling brown trout and any other salmonid group in the use of surface-turbulence cover (Fig. 3, Table 3). There were no differences ($P > 0.05$) in the amount of vegetative cover type used by subyearling Atlantic salmon and both age class's of rainbow trout.

Discussion

Previous studies on the winter habitat of juvenile salmonids showed a preference for slow-flowing water (Cunjak & Power 1986; Harwood, Metcalfe, Armstrong & Griffiths 2001; Enders *et al.* 2007). This did not occur in Grout Brook in 2000 at stream discharge of 0.10 $m^3 s^{-1}$ and average water velocity of 24.6 cm s^{-1}, as all three salmonid groups occupied faster water velocities than were generally within the study reach. However, under higher stream flows

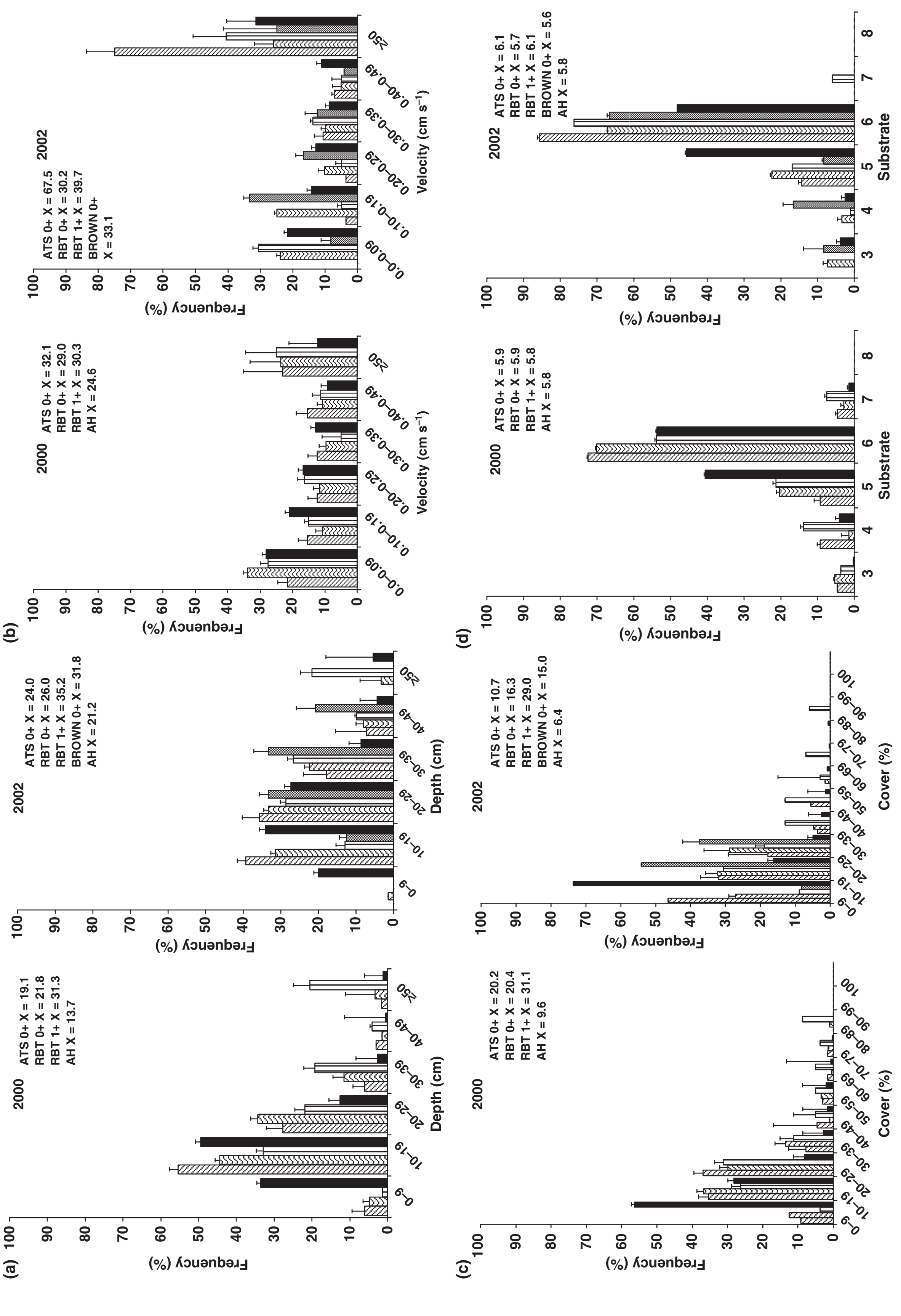

Figure 2. Distribution of subyearling Atlantic salmon (ATS0) (▨), subyearling (RBT0) (▨) and yearling (RBT1) (▥) rainbow trout, subyearling brown trout (BRT0) (▩), and available habitat (AH) (■) during winter in 2000 and 2002 in Grout Brook, NY. (a) = depth, (b) = velocity, (c) = cover, (d) = substrate. Standard error is shown for each distribution.

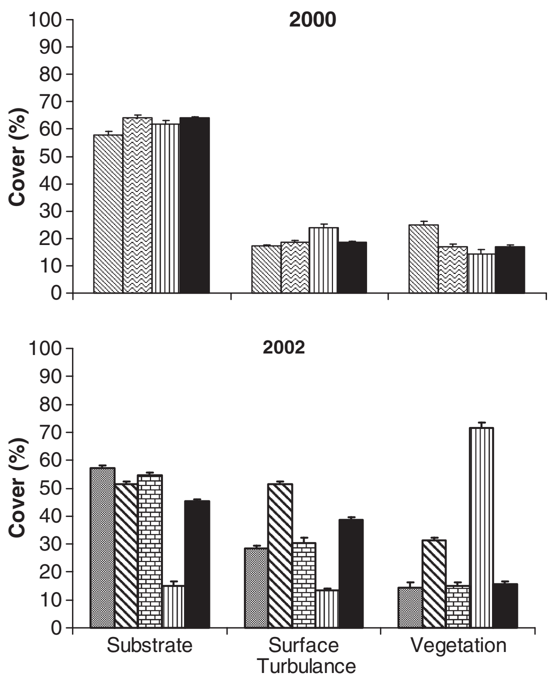

Figure 3. Distribution of the type of cover used by subyearling Atlantic salmon (ATS0) (▧), subyearling (RBT0) (▨) and yearling (RBT1) (▥) rainbow trout and subyearling brown trout (BRT0) (▩), and available cover (AC) (■) during winter in (a) 2000 and (b) 2002 in Grout Brook, NY. Standard error is shown for each distribution.

Table 3. Results of Tukey's HSD all-pairwise comparisons test for 2002 cover data

Source	RBT0	RBT1	ATS0	BRT0	AC
Substrate	72.8^{A}	74.5^{A}	71.5^{A}	8.3^{C}	46.9^{B}
Surface turbulence	8.9^{A}	19.1^{B}	20.9^{B}	8.1^{A}	38.0^{C}
Vegetation	18.3^{B}	6.4^{B}	7.6^{B}	83.6^{A}	15.1^{B}

ATSO = subyearling Atlantic salmon, RBTO = subyearling rainbow trout, RBT1 = yearling rainbow trout, BRTO = subyearling brown trout. AC = available cover, means in a row not followed by a common superscript significantly differ ($P < 0.05$).

in 2002 (discharge $0.27\ m^3\ s^{-1}$, mean velocity $39.5\ m^3\ s^{-1}$), except for subyearling Atlantic salmon, juvenile salmonids were associated with either significantly slower water velocities (subyearling rainbow trout and subyearling brown trout) than were available on average or occupied similar velocities (yearling rainbow trout) compared with those available. During both winters in Grout Brook, subyearling Atlantic salmon occupied faster water velocities than were available, on average, within the study reach. Whalen & Parrish (1999) reported that subyearling Atlantic salmon selected water velocities (12–19 $cm\ s^{-1}$) lower than randomly measured velocities. One possible explanation for this difference is diel variation in habitat use of subyearling salmon, because juvenile Atlantic salmon are considered sedentary and in shelters during the day, field studies of their winter habitat were carried out at night when salmon are thought to be more active and leave their shelters (Whalen & Parrish 1999; Whalen, Parrish & Mather 1999). These diel behavioural patterns could explain the differences between the results from daytime observations and the earlier studies carried out at night. However, Enders *et al.* (2007) found no difference between day and night habitat of juvenile Atlantic salmon in winter. If juvenile salmonids exhibit diel differences in winter habitat use, this could have important implications for habitat management.

Diel differences in the size of substrate used by juvenile salmonids in winter have been reported. Heggenes *et al.* (1993) found that passively sheltering brown trout during the day selected significantly coarser substrate than active fish at night. In Grout Brook, only subyearling Atlantic salmon were associated with larger-size substrate materials than were generally present within the stream reach during both winters. Subyearling brown trout were associated with smaller-size substrate materials compared with all other salmonid groups and available substrate in 2002. During both winters, all salmonid groups occupied areas that were deeper and had more cover than were present on average within the stream reach. Of the four salmonid groups, yearling rainbow trout occupied the deepest areas with the most cover, whereas subyearling Atlantic salmon occurred in the shallowest areas with the least amount of cover.

The large difference in stream discharge between years provided an unexpected opportunity to gain insight into factors governing diurnal winter habitat selection of juvenile salmonids. In 2000, under moderate flow conditions, substrate provided 57% of the recorded cover for subyearling Atlantic salmon, subyearling rainbow trout and yearling rainbow trout. In 2002, under high flow conditions, substrate accounted for 73% of the recorded cover for juvenile salmonids. Conversely, the use of surface-turbulence cover by juvenile salmonids decreased from 24 to 16% between 2000 and 2002 even though available surface-turbulence cover in the stream reach increased from 17 to 38% of the available cover. These results provide additional evidence of the importance of substrate as a key component in diurnal sheltering behavior of juvenile salmonids during winter.

Subyearling Atlantic salmon occupied faster water velocities during the day in both winters, compared with the other salmonid groups and available habitat. These findings conflict with previous observations of habitat use by juvenile Atlantic salmon made at night in winter. As Atlantic salmon was the only salmonid group to be associated with larger substrate materials than were present on average, in the study reach during both years, substrate size (potential shelters) may be more important to salmon than juvenile rainbow trout or brown trout. Subyearling brown trout were mainly associated with vegetative cover.

Habitat based strategies for population enhancement of stream salmonids must consider both seasonal and diel variation in habitat preference. Habitat enhancements based on species preferences determined during a single season can be unproductive (Mason 1976). This study demonstrated distinct differences in the diurnal habitat use of juvenile Atlantic salmon, brown trout and rainbow trout in winter. Of the microhabitat variables examined, cover (both type and amount) differed most among the salmonid groups.

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