Nocturnal habitat use of Atlantic salmon parr in winter

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Abstract: We completed 22 night snorkeling surveys between November and March 1995–1997 to quantify Atlantic salmon (*Salmo salar*) parr habitat use relative to habitat availability in the Rock River, Vermont, U.S.A. On average, post-young-of-the-year (PYOY) parr selected greater water depths in winter than young-of-the-year (YOY) parr, whereas YOY and PYOY parr both selected water velocities (≤19 cm/s) that were significantly lower than random measurements (46 cm/s). Maturity of PYOY parr had no significant influence on habitat selection. The majority of YOY and PYOY parr at night were found in contact with the stream bottom resting on silt–sand or gravel substrates in velocity dead-zone habitats created by the stream edge or depositional habitats created by midstream rocks and boulders. The strong selection that nocturnal Atlantic salmon parr exhibit for low water velocity areas in winter indicates the importance of maintaining large instream cover that provides refuges from high flows. The similarity that YOY and PYOY parr exhibited in many elements of habitat selection suggests that both stages may be similarly susceptible to habitat limitations in winter.

Résumé : Nous avons réalisé 22 relevés nocturnes en plongée libre de novembre à mars de 1995 à 1997 pour quantifier l'utilisation par des tacons de saumon atlantique (*Salmo salar*) de leur habitat en rapport avec la disponibilité de l'habitat dans la rivière Rock, au Vermont (É.-U.). En moyenne, les tacons de plus de 1 an se tenaient en hiver dans des eaux plus profondes que les jeunes tacons de l'année, tandis que les deux groupes se tenaient dans des eaux dont la vitesse (≤19 cm/s) était significativement inférieure à celle indiquée par nos mesures aléatoires (46 cm/s). La maturité des tacons de plus de 1 an n'influait pas de façon significative sur le choix de l'habitat. La majorité des jeunes tacons de l'année et des tacons de plus de 1 an reposaient la nuit sur le fond du cours d'eau, sur des substrats de limon et de sable ou de gravier et en eaux stagnantes en bordure du cours d'eau ou dans des zones de dépôt créées par des pierres et des blocs rocheux présents au milieu du cours d'eau. La préférence nocturne marquée des tacons de saumon atlantique pour les zones à faible courant en hiver indique qu'il est important de maintenir dans les cours d'eau un couvert important offrant des abris contre les forts débits. Comme les jeunes tacons de l'année et les tacons de plus de 1 an ont bien des points en commun quant au choix de leur habitat, on peut penser qu'ils pourraient être affectés de façon similaire par les limitations hivernales en matière d'habitat.

[Traduit par la Rédaction]

Introduction

Studies of winter habitat selection of salmonids have identified critical habitats (Cunjak 1988; Griffith and Smith 1993; Heggenes et al. 1993; Brown and MacKay 1995) and mechanisms by which conditions in winter may affect changes in population density (Tschaplinski and Hartman 1983). A number of factors must be integrated in winter habitat selection as environmental conditions change. In winter, environmental conditions may impose significant constraints on fish activity; habitats may experience rapid alteration from ice formation (Power et al. 1993; Whalen et al. 1999), low water temperatures may affect motor capabilities (Rimmer et al. 1985), and extended cold periods may necessitate using stored energy for the fulfillment of metabolic needs (Cunjak and Power 1986*a*). Environmental conditions affecting parr activity and habitat requirements and thus winter survival may vary temporally (Cunjak and Randall 1993; Power et al. 1993) and spatially (Berg 1994; Brown and MacKay 1995). For Atlantic salmon (*Salmo salar*) parr, winter mortality has been estimated to be as high as 60–70% (Cunjak and Randall 1993; Orciari et al. 1994). Because high winter mortality can impact smolt production, understanding the relationship between parr habitat selection and habitat availability, across both temporal and spatial scales, is necessary to evaluate the causes of winter mortality and its effect on smolt recruitment.

Fish age and size may affect activity patterns and in turn winter habitat selection (Cunjak and Power 1986*b*; Heggenes et al. 1993). For Atlantic salmon, young-of-the-year (YOY) and post-young-of-the-year (PYOY) parr may

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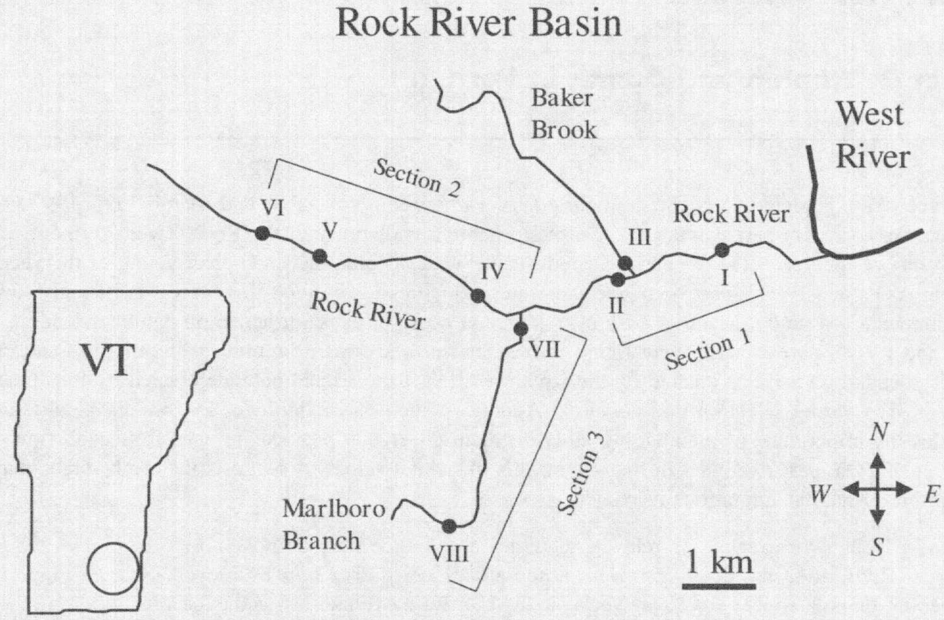
Fig. 1. Rock River Basin, Vermont (inset), and location of eight sites where snorkeling surveys were completed to quantify habitat availability and winter habitat selection of YOY and PYOY Atlantic salmon parr. The circle in the inset indicates the area of enlargement.



select different habitats in summer (Kennedy and Strange 1982) and during the fall–winter transition (Rimmer et al. 1984). It is unknown whether YOY and PYOY parr select different habitats in winter and thus whether they may be similarly susceptible to habitat limitations or potentially compete for preferred areas. For PYOY parr, winter habitat selection may also be influenced by fall maturation, a ubiquitous life history feature in male Atlantic salmon. Mature parr may exhibit greater movements from fall through winter (Whalen et al. 1999), which could influence winter habitat selection.

We determined the relationship between habitat availability and winter habitat selection of YOY and PYOY Atlantic salmon parr in a large southern Vermont tributary of the Connecticut River, U.S.A., that is subject to low winter water temperatures (≤1°C), variable and extensive icing, and periodic winter freshets. We addressed the following questions. (*i*) How does habitat selection of nocturnal Atlantic salmon parr relate to habitat availability in winter? (*ii*) Do YOY and PYOY parr select similar habitats? (*iii*) How does water temperature and ice conditions affect parr activity patterns? Our answers to these questions provide information on habitats potentially important to winter survival of Atlantic salmon parr as well as insight into the prospects for intraspecific competition for winter habitats.

Materials and methods

Study area

Habitat availability and habitat selection of Atlantic salmon parr were studied in the Rock River, a fourth-order tributary of the West River located in the Connecticut River Basin, U.S.A. (42°56′N, 72°39′W; Fig. 1). The Rock River has a basin area of about 155 km^2 and an average gradient of 1.7 m/km. Winter discharge is variable but estimated to range between 0.5 and 2.5 m^3/s. Atlantic salmon parr originate from unfed fry stocked annually in May at densities approximating 50/100 m^2, which typically results in age-1 parr densities of 3–10/100 m^2 (McMenemy 1995). The majority of smolts produced in the Rock River are age 2 (Whalen 1998).

We established eight 100-m sites distributed in upper and lower reaches of three sections of the Rock River Basin (Fig. 1). Sites ranged between 8 and 22 m in mean width and consisted primarily of riffle habitat dominated by cobble and rubble substrates (Crouse et al. 1981).

Parr habitat use

Parr habitat use was determined between November and March in the years 1995–1996 and 1996–1997 by night snorkeling. We divided the November–March winter period as follows: (*i*) November 21 to December 12, early winter; (*ii*) December 13 to February 15, midwinter; (*iii*) February 16 to March 28, late winter. We attempted to equally distribute our sampling effort among winter periods, but ice conditions in midwinter and turbid flows in late winter limited our sampling (Table 1).

Snorkeling procedures were described previously by Whalen et al. (1999). A diver entered the lower end of each site and moved upstream, searching both midchannel and stream margin habitats. Surveys were typically 1.5 h in length and were completed between 18:00 and 01:00. The position of undisturbed Atlantic salmon parr was marked with a numbered float. Parr <95 mm total length were designated as YOY and parr >95 mm total length were designated as PYOY. Previous sampling showed that few YOY parr are >95 mm total length and few PYOY parr are <100 mm total length by winter (K.G. Whalen and D.L. Parrish, unpublished data). Fish length was estimated using the method described by Baltz et al. (1991).

Behavior of parr upon encounter was recorded as resting, swimming, or feeding. We recorded the substrate type that parr were physically resting upon when encountered as silt–sand, gravel, cobble–rubble, boulder, or bedrock (Crouse et al. 1981). Anchor ice was also included as a substrate category. Additionally, we categorized the general habitat character of the position of each parr relative to cover that was defined as features of the physical habitat within about 0.5 m of parr providing protection from the stream

Table 1. Overview of the study design used to evaluate habitat availability versus selection of YOY and PYOY Atlantic salmon parr.

		Winter period			
Section	Site	Early	Middle	Late	*N*
1	I	1	2	1	4
1	II	1	0	0	1
1	III	0	1	0	1
2	IV	1	1	1	3
2	V	1	0	0	1
2	VI	1	1	1	3
3	VII	2	4	1	7
3	VIII	1	0	1	2
	N	8	9	5	22

Note: The cell value is number of snorkeling surveys completed at each site within each winter period. The value in parentheses indicates the number of surveys completed during the day. *N* = number of surveys per site or per winter period. The locations of river sections and sites sre given in Fig. 1.

current. We established three "cover" habitat type categories defined as (*i*) dead zone: parr occupying quiescent habitats formed by the stream edge or large in-stream structure, e.g., boulders, woody debris, (*ii*) depositional: parr occupying the immediate downstream side of substrate, typically laterally compressed against the substrate, and (*iii*) surface ice: parr found beneath surface ice. We also established one "noncover" or "exposed" habitat type category defined as parr exposed to the current with no recognizable physical feature providing cover.

Upon completion of snorkeling, water depth (centimetres) and velocity (centimetres per second at 0.6 × depth) were recorded at the position of each parr as marked by the numbered float. To assess lateral distribution, we recorded distance to the nearest streambank and total stream width at each parr location. Before each snorkeling survey, water temperature was recorded with a hand-held thermometer and the percentage of the total surface area of the site covered by surface and anchor ice was visually estimated.

Habitat availability

To quantify available habitat during the variable ice conditions in early and midwinter, water depth and velocity were recorded at up to 50 randomly selected points within the study site immediately after snorkeling surveys were completed. We termed these measurements random available measurements (RAM). The procedure for RAM was as follows. Beginning at either the upper or lower end of the site, we used a random numbers table to generate *x*,*y*-coordinate pairs to be translated into "paces" by the observer. The *x*-coordinate was paced at a right angle to the river flow and the *y*-coordinate was paced parallel to the river flow. Water depth and water velocity at 0.6 × depth were recorded at the point defined by the randomly selected coordinates. After each measurement, new random coordinates were selected and the procedure was repeated through the entire length of the site. The RAM procedure enabled us to thoroughly, yet efficiently, characterize available water depths and velocities under the constraints of working in high flows and ice-laden rivers at night.

Parr maturity

As part of studies to determine the effect of parr maturity on smolt recruitment (Whalen and Parrish 1999), mature and immature PYOY Atlantic salmon parr were collected by electrofishing in October–November 1995 and 1996 and marked with either an acrylic paint injection to the anal fin (Whalen et al. 1999) or alcian blue dye applied with a panjet (Cunjak and Randall 1993). Additionally, some parr also received a passive integrated transponder (PIT) tag. Marked parr were observed during routine winter diving surveys. The fin paint injections enabled parr maturity to be determined during snorkeling without capturing parr. Other parr, collected using a small dip net, were placed into a water-filled metered tube and inspected for marks (Whalen et al. 1999). The maturity of captured unmarked parr was determined by applying gentle pressure to the vent area and parr freely expressing milt were deemed mature. Some mature parr continued to freely express milt through the end of March, about 5 months after the initial October–November maturation assessment.

Data and statistical analysis

We completed an initial screening analysis to determine the effects of section and winter period on habitat use and availability using analysis of variance (ANOVA). Greater differences in habitat use and availability were found among sections than among winter periods, so we focused on section-specific comparisons of YOY and PYOY parr water depth and velocity selection versus habitat availability (RAM). Additionally, we completed a summary multivariate analysis of habitat selection versus availability including all data collected over the two winters. We plotted water velocity (dependent variable) versus water depth (independent variable) for YOY and PYOY parr habitat selection as well as for RAM for habitat availability and then calculated a bivariate equal-frequency ellipse encompassing $100(1 - \alpha)\%$ of the observations, where $\alpha = 0.25$ (Sokal and Rohlf 1995; SAS Institute 1996). We plotted the equal-frequency ellipses to illustrate the overlap in YOY and PYOY parr habitat selection in relation to habitat availability and the specificity of parr habitat selection for water depth versus water velocity.

We used χ^2 analysis to compare substrate and habitat type use among YOY and PYOY parr. For substrate use, insufficient data were available for bedrock and anchor ice, so these categories were not included in statistical comparisons of substrate use among YOY and PYOY parr. Also, because few parr were found under surface ice, this category was not included in statistical comparisons of habitat type use among YOY and PYOY parr. Regression was used to determine if the number of YOY and PYOY parr observed in the area of the site surveyed was related to date. ANOVA was also used to determine if significant differences existed in average water temperature and ice coverage among winter periods.

We applied a $\ln(x + 1)$ transformation to YOY and PYOY parr water velocity selection data to correct for positive skewness and improve normality; nontransformed values are reported in the graphs and text. The Tukey–Kramer studentized multiple range test was used when a significant difference ($\alpha = 0.05$) among means was identified by ANOVA. Statistical significance for all analyses was considered at $\alpha = 0.05$.

Results

All snorkeling surveys were completed at water temperatures between 0 and 3°C. Mean water temperature tended to be colder in midwinter (0.4 ± 0.2°C) than in early (1.4 ± 0.3°C) and late winter (1.2 ± 0.3°C), but differences were not significant (ANOVA, $p > 0.05$). Average percent ice coverage was five- to 10-fold greater in midwinter (36 ± 11%) than in early (3 ± 2%) and late winter (7 ± 6%) (ANOVA, $p < 0.05$).

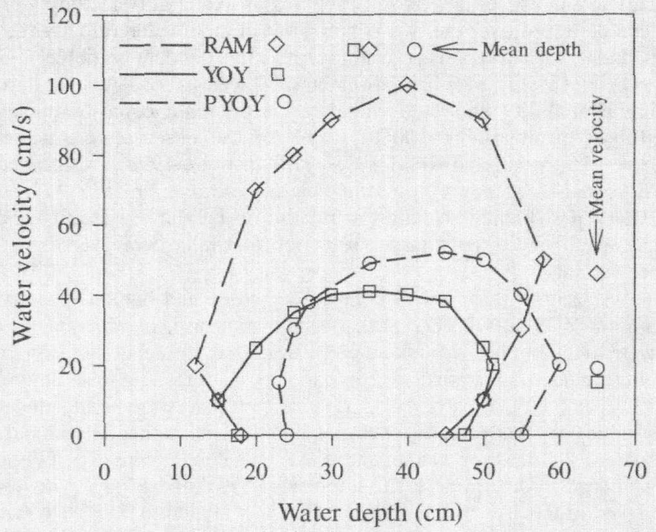
Over the 2 years, we completed 22 night snorkeling surveys, eight in early winter, nine in midwinter, and five in late winter (Table 1). Observations of nocturnal habitat use for parr were roughly equally distributed between YOY (N = 128) and PYOY (N = 127).

Table 2. Mean (±SE) water depth and water velocity selected by YOY and PYOY Atlantic salmon parr versus RAM for habitat availability by section (see Fig. 1).

	Water depth (cm)				Water velocity (cm/s)			
Section	YOY	PYOY	RAM	$p < 0.05$	YOY	PYOY	RAM	$p < 0.05$
1	34±2 (30) *a*	45±3 (23) *b*	40±1 (132) *ab*	***	12±3 (29) *a*	17±4 (21) *a*	57±3 (133) *b*	***
2	33±2 (31)	39±2 (33)	35±1 (224)	ns	12±3 (31) *a*	21±4 (33) *a*	44±2 (224) *b*	***
3	33±2 (41) *b*	41±1 (61) *a*	33±1 (254) *b*	***	19±3 (40) *a*	18±3 (61) *a*	44±2 (254) *b*	***

Note: Sample size is given in parentheses. The overall mean given in the last row is the weighted average. Results of within-site ANOVA: ***$p < 0.05$; ns, $p > 0.05$. Means not sharing a common letter are significantly different (Tukey–Kramer studentized range test).

Fig. 2. Bivariate plot of water depth versus water velocity for YOY (N = 99) and PYOY (N = 115) Atlantic salmon parr habitat selection and RAM (N = 610) recorded for habitat availability. Shown are representative points and lines defining the equal-frequency ellipses calculated to encompass 75% of the observations for each case. Overall univariate means for water depth and velocity are also plotted.



Habitat selection versus availability

Within each section, greater contrast between habitat selection of YOY and PYOY parr versus habitat availability existed for water velocity than for water depth (Table 2). PYOY parr tended to select deeper water than YOY parr as well as RAM, whereas both YOY and PYOY parr selected water velocities that were at least twofold lower than RAM (Table 2).

The bivariate summary of water depth versus water velocity illustrates the large degree of overlap in habitat selection of YOY and PYOY parr (Fig. 2). YOY and PYOY parr selected only a portion of available water velocities, whereas their water depth selection encompassed nearly the entire range of available water depths (Fig. 2). On the water depth axis, the PYOY parr ellipse extended beyond the RAM ellipse, indicating that some PYOY parr preferred water depths greater than those commonly available (Fig. 2).

Parr behavior and substrate and habitat type use

Behavior of YOY and PYOY parr upon encounter was very similar, as 97% of the 101 YOY and 96% of the 111 PYOY parr observed were resting in contact with the substrate. For both stages combined, only five parr were swimming upon encounter and only two were feeding. YOY and PYOY parr also used similar substrates (χ^2 = 5.0, $p >$ 0.05), with the majority found on silt–sand and gravel (Table 3). For both YOY and PYOY parr, the number of observations in each substrate category tended to increase with decreasing substrate size. YOY and PYOY parr were occasionally observed resting on anchor ice.

YOY and PYOY parr differed in habitat type use (χ^2 = 8.0, $p < 0.05$; Table 4). Most YOY parr were found in deadzone and depositional habitats, whereas observations of PYOY parr were nearly equally distributed among habitat types (Table 4). Generally, PYOY parr showed a greater tendency to be found in exposed habitats than YOY parr, a trend that had a temporal component. The proportion of observations of PYOY parr using exposed habitats decreased from 40% in early winter to 12% in late winter.

Parr were found close to the stream edge. The average stream width was 11 m at each YOY parr location and 12 m for PYOY parr. On average (±SE), distance from the stream edge was 2.2 ± 0.2 m for YOY parr and 2.6 ± 0.1 m for PYOY parr.

Seasonal activity patterns

We tested for the effect of year in a two-way ANOVA, including winter period for both the number of YOY and PYOY parr observed, to determine if pooling over years was possible. Year effects were not significant for PYOY parr (ANOVA, $p > 0.05$) but were significant for YOY parr (ANOVA, $p < 0.05$). Thus, to evaluate temporal trends in abundance for YOY parr, we used residuals of parr observations.

No relationship between residuals of the number of parr observed and date was found for YOY parr (regression, $p >$ 0.05). A significant relationship was found between number of PYOY parr observed and date (regression, $p < 0.05$, r^2 = 0.46; Fig. 3*a*). The number of PYOY parr observed was variable in all winter periods, decreasing from early winter to consistently low numbers through midwinter. The number of PYOY parr increased between midwinter and late winter but remained lower than numbers of parr observed in early winter. We plotted water temperature and percent ice coverage for each sample date to evaluate the influence of environmental factors on the number of PYOY parr observed, but no pattern between PYOY parr abundance and water temperature or percent ice coverage was evident (Fig. 3).

Parr maturity

Over the 2 years, we identified the state of maturity of 65 of the 127 PYOY parr observed: 29 mature and 36 immature. Mature and immature parr exhibited similarity in habi-

Table 3. Number of YOY and PYOY Atlantic salmon parr using different substrates during night snorkeling surveys between November and March, 1995–1996 and 1996–1997.

	Silt–sand	Gravel	Cobble–rubble	Boulder	Bedrock	Anchor ice	Total
YOY	47 (46)	30 (29)	11 (11)	12 (12)	1 (1)	2 (2)	103
PYOY	38 (33)	46 (40)	16 (14)	10 (9)	2 (2)	2 (2)	114
Total	85 (39)	76 (35)	27 (12)	22 (10)	3 (1)	4 (2)	217

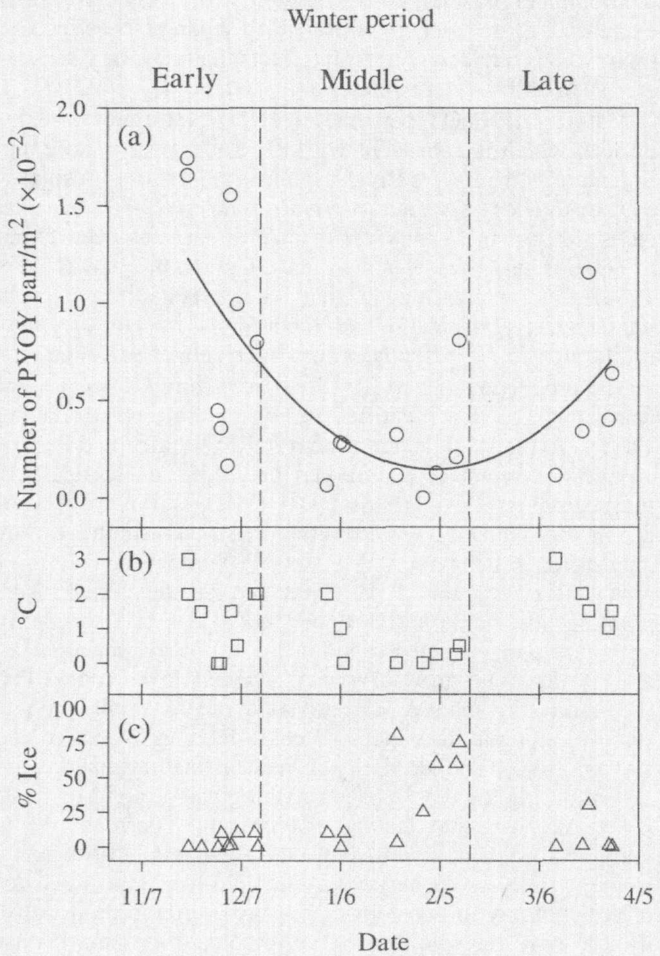
Note: Parenthetical values are percentages of the row total, except those in the bottom row, which are percentages of the column total.

Table 4. Number of YOY and PYOY Atlantic salmon parr using different habitat types during night snorkeling surveys between November and March, 1995–1996 and 1996–1997.

	Habitat type				
	Exposed	Dead zone	Depositional	Under surface ice	Total
YOY	18 (18)	36 (35)	47 (46)	1 (1)	102
PYOY	35 (32)	39 (36)	33 (31)	1 (1)	108
Total	53 (25)	75 (36)	80 (38)	2 (1)	210

Note: Parenthetical values are percentages of the row total, except those in the bottom row, which are percentages of the column total.

Fig. 3. Relationship of date to (*a*) number of PYOY Atlantic salmon parr observed, (*b*) water temperature, and (*c*) percent ice coverage recorded during 22 night snorkeling surveys. Broken vertical lines are the boundaries of the early-, mid-, and late-winter periods. The line in Fig. 3*a* is the fitted second-order polynomial ($p < 0.05$, $r^2 = 0.46$).



tat selection, as they selected similar water depths (ANOVA, $p > 0.05$) and velocities (ANOVA, $p > 0.05$). There was no evidence for differences among winter periods in the proportion of PYOY parr that were mature ($\chi^2 = 1.2$, $p > 0.05$), indicating no evidence for seasonal differences in activity pattern based on life history.

Discussion

Nocturnal YOY and PYOY Atlantic salmon parr exhibited specificity in habitat selection, with greater contrast between selection versus availability for water velocity than for water depth. The relationship between habitat selection and availability may provide clues to mechanisms by which changes in habitat could affect parr survival. The bivariate analysis of water depth versus water velocity showed that most YOY and PYOY parr exploited the full range, and beyond, of commonly available water depths, yet only a narrow range of available water velocities. The specificity that parr exhibit in selecting low water velocity habitats suggests that if these habitats are lacking or reduced during winter, parr survival may be reduced. The effect of changes in habitat availability on parr survival will ultimately depend on the amount of physical space parr require to feed and shelter. Measurements of how much habitat parr use are needed to determine how significant changes in habitat availability may be to winter survival when conditions become limiting.

PYOY parr occupied deeper waters and showed a tendency to use more exposed habitats than YOY parr, but generally, both PYOY and YOY parr exhibited similar preferences for low water velocity areas and most other elements of habitat selection. In differing sizes of nonanadromous brook (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*), larger, older trout selected deeper water and at times higher water velocities than younger trout (Cunjak and Power 1986*a*, 1986*b*; Heggenes et al. 1993; Mäki-Petäys et al. 1997). As with nocturnal Atlantic salmon parr in winter, trout exhibited relatively stronger selection for water velocity than for water depth (Cunjak and Power 1986*a*; Mäki-Petäys et al. 1997). The similarity in YOY and

PYOY parr habitat selection may be a response to a common environmental limiting factor such as low water temperature that may place limitations on activity independent of parr age (Graham et al. 1996).

The similarity in YOY and PYOY parr winter habitat selection has several consequences, e.g., (*i*) YOY and PYOY parr may be similarly susceptible to habitat limitations in winter and (*ii*) habitat limitations could result in competition for suitable areas. Several factors may ameliorate these effects, particularly the potential for interstage competition. Winter is a period of exceptional stochasticity in habitat conditions for juvenile Atlantic salmon (Cunjak and Randall 1993; Whalen et al. 1999). Continued disturbance of the physical habitat would limit the establishment of equilibrium conditions and the potential for competitive interactions (e.g., Hemphill and Cooper 1983). Typically, parr that we observed were distributed in patches, indicating the likelihood of competitive interactions was not strong. Trout that are territorial at other times of the year alter their behavior in winter and become tolerant of conspecifics, often aggregating in pools (Cunjak and Power 1986*b*). We observed no aggressive interactions among parr; rather, conspecifics were tolerant of others as close as 10–20 cm. A lack of aggressive interaction was also observed by Heggenes et al. (1993) and interpreted as an indication of a reduced focus on food acquisition in winter and, in turn, maintenance of territorial boundaries.

Our observations of parr habitat use are consistent with an overwinter strategy of minimization of net energy loss and basic maintenance rather than net energy gain and excessive activity (Heggenes et al. 1993). As reported for juvenile brown trout in the wild in winter (Heggenes et al. 1993) and for juvenile Atlantic salmon under winter-simulated conditions in the laboratory (Fraser et al. 1993), parr exhibited quiescent behavior, being often motionless upon encounter while resting in contact with the stream bottom. As observed for juvenile brown trout at night in winter (Heggenes et al. 1993), salmon parr were predominantly observed over fine-grained substrates, such as silt–sand and gravel, in dead-zone and depositional areas or habitats offering some recognizable cover from river flow. Where parr were found in higher flow areas, they often laterally compressed their body and fins against the downstream surface of the substrate. This behavioral regulation of position appeared to help minimize displacement by turbulent near-bottom flows. All features of Atlantic salmon parr winter habitat use that we identified, including behaviors presumably to resist displacement and minimize energetic demands, signify the importance of low water velocity refugia and thus the need to maintain large instream structure that provides cover from high flows and ice.

Parr were closely associated with the stream edge despite the presence of more ice in edge areas than in the mid-channel. Flows under edge ice are minimal and when ice is not present, the stream edge provides refugia from high flows (Whalen et al. 1999). In contrast, the midchannel may be more often free of ice but subject to substrate scouring and higher flows (Erman et al. 1988; Whalen et al. 1999). We observed few salmon parr appearing to directly use surface ice as cover, which is in contrast with observations for trout where surface ice is a significant source of winter cover (Cunjak and Power 1986*b*). In our system, surface ice is labile relative to rocks and other forms of instream structure that provide more permanent flow refugia. The rarity of parr use of surface ice for cover may have been a consequence of the impermanence of ice rather than an indication of avoidance by parr.

The observation of fish sheltering in the substrate during the day in winter coupled with the observation of fish above the substrate at night has been interpreted as an adaptive response to capricious winter habitat conditions (Heggenes et al. 1993) as well as a predator avoidance mechanism (Valdimarsson and Metcalfe 1998). Atlantic salmon parr in the Rock River system are active at night at water temperatures ranging between 14 and 23°C in late summer (Gries et al. 1997). We have observed night-active salmon parr in all seasons and identified some similarities in habitat use and behavior at night in summer as observed here under winter conditions (K.G. Whalen and D.L. Parrish, unpublished data; see Metcalfe et al. 1997). Our findings are consistent with a laboratory analysis where there were differences in daytime sheltering of juvenile salmon but consistent nocturnal activity at water temperatures ranging from 2 to 18°C (Fraser et al. 1995). These results suggest that nocturnal activity in winter is a continuation of behavior exhibited at other times of the year rather than an adaptive response specifically for winter conditions. Because the adaptive or evolutionary significance of nocturnal activity will depend on the complete seasonal context within which this behavior is expressed, more research is needed to separate the effects of night versus day behavior from effects that may vary seasonally such as between summer and winter.

Maturity of PYOY parr had no significant effect on habitat use, which is consistent with the finding for mature and immature parr in West River tributaries to exhibit no significant difference in winter survival (Whalen 1998). In some cases, fall to spring survival of mature parr has been found to be substantially lower than that of immature parr (Myers 1984). Our results suggest that where such differences in winter survival of mature and immature parr occur, they may not be driven by differences in winter habitat selection.

The proportion of parr identified as mature (45%) at night was similar to that identified during daytime electrofishing surveys in the Rock River system (49%; Whalen and Parrish 1999). Mature and immature parr may differ energetically at the beginning of winter (Simpson 1992), and as a result of life history pathway, e.g., smolting versus nonsmolting, they may differ in behavior and exhibit dissimilar frequencies of nighttime emergence. A paradigm that has developed incorporating this theme is that upper modal fish (i.e., primarily immature parr expected to smolt the following spring) continue to feed and grow in winter, whereas lower modal fish (i.e., primarily mature parr expected not to smolt) enter a state of anorexia in winter and cease feeding (Metcalfe and Thorpe 1992). The similarity in percent mature that we observed during the day by electrofishing and at night by snorkeling suggests that mature and immature parr emerge at night at a frequency consistent with their relative frequency in the system. From our work, we can provide no evidence of a dichotomy in behavior or seasonal differences in activity for parr on smolting versus nonsmolting life history trajectories that have been observed under controlled conditions (Metcalfe and Thorpe 1992; Valdimarsson et al. 1997). Further analysis from different regions on winter activity patterns of mature and immature parr is warranted because of the significance of parr maturation to smolt recruitment (Myers 1984; Whalen and Parrish 1999).

The decline in the number of PYOY parr observed between early and midwinter could not be fully attributed to mortality because of the rebound in late winter to higher relative abundance. Heggenes et al. (1993) found a similar result for wild brown trout: late-winter (March) numbers of trout observed were higher than numbers observed during midwinter (January–February). Declines in relative densities were observed to accompany decreases in water temperature between fall and the onset of winter for juvenile rainbow trout (*Oncorhynchus mykiss*) (Riehle and Griffith 1993). Although the relative abundance pattern for PYOY parr was not related to water temperature or ice condition recorded on the sample date, average water temperatures in midwinter were significantly lower than those in early and late winter. In many instances, 7–10°C has been quoted as a threshold temperature that elicits behavioral responses, e.g., daytime sheltering, in juvenile salmon (Rimmer et al. 1983; Fraser et al. 1993). Small changes in water temperature that occur near the freezing point of freshwater, well below 7–10°C, could also cause behavioral changes and affect frequency of night emergence (Griffith and Smith 1993).

We hypothesize that differences in PYOY parr relative abundance over the winter may reflect behavioral changes related to the trade-off between the ability and need to meet a metabolic deficiency and the profitability and costs of activity. Unlike species of marine fish that have evolved to survive in chronically near-freezing and super-cooled conditions (DeVries 1988), Atlantic salmon have no known specialized mechanism for metabolically coping with near-freezing and super-cooled water. For subarctic brook trout, a compensatory physiological response occurs at 0°C where trout lower their metabolic demand, enabling them to survive for long periods without feeding (Cunjak and Power 1986*b*). Thus, less frequent activity may be necessitated at low water temperatures in midwinter because of lower metabolic demand, which is advantageous because low temperatures restrict swimming ability (Rimmer et al. 1985; Graham et al. 1996). Even though feeding may not be sufficient to offset the metabolic deficit occurring in winter (Cunjak and Power 1987), winter survival may be enhanced by acquiring some food rather than starving. We observed few instances of feeding by parr, but our sampling was not geared toward behavioral observations. Diet analysis on wild individuals has shown that Atlantic salmon parr continue to feed during winter, even in ice-covered streams at water temperatures near 0°C (Cunjak 1988). Although activity of salmon parr may be more infrequent in midwinter, the maintenance of foraging activity at water temperatures near 0°C may be an opportunistic behavior to offset an accumulated metabolic deficit.

In summary, Atlantic salmon parr exhibited specificity in nocturnal habitat selection. Differences in habitat quality among sites, specifically those habitats often selected by parr, could contribute to spatial variability in winter survival. YOY and PYOY parr were similar in most elements of behavior and habitat use, suggesting that both stages may be similarly susceptible to habitat limitations in winter. Generally, our observations of parr behavior and habitat use are consistent with a wintering strategy focusing on minimizing energetic loss rather than maximizing energetic gain. Habitat features such as large instream structure create low water velocity refugia that parr exploit to minimize exposure to high flows. Activity patterns of parr changed over the winter, and generally, fewer parr were observed in midwinter when water temperatures were at their minimum. The maintenance of activity at water temperatures near 0°C may reflect a trade-off between the need to feed to offset a metabolic deficit and the profitability and costs of activity. Further work to determine how the energetic condition of parr affects habitat use and survival would greatly contribute to the understanding of the effects of winter on recruitment success.

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