Effect of ice formation on selection of habitats and winter distribution of post-young-of-the-year Atlantic salmon parr

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Abstract: We determined how ice affects selection of habitats and distribution of post-young-of-the-year Atlantic salmon (*Salmo salar*) parr during winter. Night snorkeling surveys were completed between November and April to evaluate parr habitat use and movements. Systematic measurements of water depth and velocity were recorded during ice-free and ≤55% iced conditions to quantify habitat availability. Ice formation altered the distribution and reduced the abundance of habitats commonly used by parr; differences between parr habitat use and habitat availability were greatest when ice was present. Edge ice formation resulted in the concentration of flows, and areas of high flow were formed in midchannel; few parr were observed in midchannel after ice had formed. Through the winter, most parr were found lateral to high flows on the ice edge boundary or in the post-ice period lateral to the stream midchannel. The correspondence of parr movements during winter to changes in the physical habitat associated with ice formation indicates that movements and redistributions may be important for survival in streams affected by ice.

Résumé : Nous avons déterminé comment la glace influe sur la sélection des habitats et la distribution des tacons (plus précisément ici des poissons qui ont dépassé le stade de jeune de l'année) du saumon atlantique (*Salmo salar*) durant l'hiver. Nous avons réalisé des relevés nocturnes en plongée libre de novembre à avril pour évaluer l'utilisation de l'habitat par les tacons ainsi que leurs déplacements. Nous avons mesuré systématiquement la profondeur et la vitesse de l'eau dans les milieux libres de glace ou couverts de glace à 55% ou moins pour quantifier la disponibilité de l'habitat. La formation de la glace a altéré la distribution et réduit l'abondance des habitats communément utilisés par les tacons; les disparités entre l'utilisation de l'habitat par les tacons et la disponibilité de l'habitat étaient plus grandes quand la glace était présente. La formation de bordures de glace avait pour effet de concentrer l'écoulement, de sorte que des zones à fort écoulement étaient formées dans la partie centrale du cours d'eau; peu de tacons ont été observés au milieu du chenal après que la glace se soit formée. Durant l'hiver, la plupart des tacons se trouvaient à côté des zones d'écoulement fort à la bordure de la glace ou, dans la période suivant la disparition de la glace, à côté de la zone centrale du chenal. La correspondance des déplacements des tacons durant l'hiver avec les changements dans les caractéristiques physiques de l'habitat associés à la formation de la glace indique que les déplacements et les redistributions des poissons peuvent être importants pour leur survie dans les cours d'eau où se forme de la glace.

[Traduit par la Rédaction]

Introduction

Ice formation is a compelling feature of the winter stream environment that is responsible for the reorganization and redistribution of physical space (Power et al. 1993; Berg 1994; Prowse 1994). Because ice may result in significant changes in physical space, a key concern is how ice formation affects habitat availability for overwintering fish. Habitat availability may be affected directly through physical exclusion of space (Power et al. 1993; Power and Power 1995) or indirectly by causing changes in the physical stream environment, such as flow or water depth, that alter the character of the available habitat (Power et al. 1993). Whether by direct elimination through physical exclusion or alteration in

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character, ice may have a dramatic effect on the suitability of winter habitats and thus overwinter mortality of stream fish (Power et al. 1993).

Low water temperatures that typify the winter period impose physiological constraints on stream fish, influencing habitat selection and activity patterns (Cunjak 1988*b*; Facey and Grossman 1990) that may affect susceptibility to ice-related mortality. Studies of winter habitat selection indicate that habitats are selected to minimize energetic costs (Cunjak and Power 1986*a*, 1986*b*; Heggenes et al. 1993), and thus, depth and velocity refugia or physical structure providing cover becomes a paramount concern (Tschaplinski and Hartman 1983; Cunjak and Power 1986*a*, 1986*b*; Cunjak 1988*a*; Heggenes et al. 1993; Riehle and Griffith 1993; Bonneau et al. 1995). Atlantic salmon (*Salmo salar*) parr in fall–winter have been observed to shelter beneath stones in the streambed during the day (Rimmer et al. 1983; Cunjak 1988*a*) and to seek shelter in a laboratory setting under simulated fall–winter conditions (Fraser et al. 1993, 1995), while emerging from substrate shelters at night to feed (Fraser et al. 1993). Nocturnal activity has been related to foraging (Fraser et al. 1993) and thus may represent a behavioral–energetic relationship (Metcalfe and Thorpe 1992) critical to overwinter survival. The need for low-velocity habitats with cover significantly increases the potential for space limitations during winter if such habitats are in short supply or if ice formation renders them unsuitable. That Atlantic salmon parr remain active at night and engage in winter movements (Cunjak and Randall 1993) indicates that they can react to ice-related changes in the amount and character of the available physical space. Therefore, identifying how habitats are redistributed and how habitat is changed by ice is as important as determining how much space is physically excluded by ice.

Although information on the winter habitat needs of stream fish is increasing, little is known about the interaction among ice formation, habitat suitability, physical space, and the use of physical space by Atlantic salmon parr. Because overwinter mortality is linked to smolt production and because physical space may be related to overwinter mortality, it is important to identify how ice formation affects the distribution and abundance of physical habitat selected by Atlantic salmon parr during winter. Therefore, we asked two questions. (*i*) In addition to reducing the overall area of watered habitat, how does ice formation affect habitats available to salmon; specifically, does ice alter water depths and velocities that parr select? (*ii*) How do parr distributions change during winter in response to complex features of ice formation and resulting effects on water depth and velocity? We addressed the first question by quantifying parr habitat use and then linking it to changes in the abundance and distribution of physical habitat caused by ice. For the second question, we determined patterns in the movements and distribution of parr relative to patterns in the distribution of habitats that parr commonly and rarely selected.

Materials and methods

Study site

This analysis was undertaken in the Rock River, which is a tributary of the West River located in the southern Connecticut River basin, U.S.A. (43°08′N, 73°25′W). We selected a 200-m reach that consisted primarily of riffle habitat dominated by cobble and rubble substrates (Crouse et al. 1981). Seasonally, flow in the Rock River ranges from approximately 0.15 $m^3 \cdot s^{-1}$ in summer to 2.5 $m^3 \cdot s^{-1}$ in spring. Unfed Atlantic salmon fry are stocked annually in May at densities of 30–50·100 m^{-2} and generally produce yearling parr densities of 3–10·100 m^{-2} (McMenemy 1995). Several adult salmon have been observed in the Rock River; however, the majority of parr production is assumed to be from fry stocking.

Habitat availability

Within the 200-m reach, we selected an approximately 55-m section for determining habitat availability by quantifying water depth and velocity and mapping ice cover. Habitat availability was determined under different icing conditions. Significant icing was first observed on the evening of December 12, 1994 (Table 1); habitat availability measurements were completed during the day on December 12 when the study section was in an ice-free condition. Habitat availability was also quantified on two occasions when ice was present: December 15, 1994, and February 1, 1995. Measurements of water depth (nearest 1 cm) and midcolumn water velocity (nearest 1 $cm \cdot s^{-1}$) were recorded at the node of points defined by a 2 × 2 m grid to quantify available habitat in the 55-m section. When surface ice was present, additional measurements were taken at a scale finer than 2 × 2 m to quantify water depths and velocities in the vicinity of the ice edge. The sampling system was based on a stream centerline axis anchored by steel rods roughly bisecting the 55-m section longitudinally and was designed so that specific points (± 0.5 m), defined by the 2 × 2 m scale, could be located on successive sampling occasions. Thus, measurements could be paired between sampling dates. The 2 × 2 m scale was standardized to the December 12 wetted width, resulting in a sample of N = 219 points for each date. Rocks and (or) slush ice at times interfered with the measurement of water depth or velocity; hence, some water depth–velocity pairs were unidentified (UID). The centerline axis also served as the baseline for quantifying ice coverage on December 15 and February 1. On other dates, the percentage of the total surface area of the 55-m section covered by ice was qualitatively estimated (Table 1).

Parr movements, distribution, and habitat use

Only post-young-of-the-year (PYOY) parr or age 1 and age 2 individuals were used in the analysis. All smolts in the Rock River are age 2 or age 3 (Whalen 1998), and thus, most PYOY parr in the fall are expected to smolt the following spring. PYOY parr were discernible from young-of-the-year (YOY) parr, as by winter, PYOY parr are typically ≥25 mm larger than YOY parr.

A contiguous design was adopted to study movements (Armstrong et al. 1994). The 200-m study reach was divided into seven 22- to 30-m contiguous sections; 25 m was the target section length. Based on previous experience, this stream length was expected to contain approximately 10 PYOY parr. Section boundaries were arbitrary, but natural breaks in habitat such as pool–riffle transitions were used to separate contiguous sections where possible.

Before ice formation, parr were collected and marked in each of the seven sections on November 7, 8, and 11, 1994. Up to 10 in each section were collected by snorkeling at night using a small dip net. Parr were selected at random with respect to encounter and success of capture. The position of capture of each fish was marked with a numbered float. Parr were anesthetized with buffered MS 222 (100 $mg \cdot L^{-1}$) and measured for total length (nearest 1 mm). Fish were also weighed (nearest 0.1 g) and a scale sample was collected to determine age. Under anesthetic, a section-specific mark consisting of a unique color of acrylic paint was applied to the pectoral, dorsal, or pelvic fin using a 25-gauge intramuscular syringe. The syringe was implanted in the base of the fin and paint was extruded into the area between the fin rays. Individ-

Table 1. Ice type and estimated percent ice coverage, water temperature, and PYOY Atlantic salmon parr habitat use recorded in portions of the 200-m study reach of the Rock River, including the 55-m section where habitat availability was determined.

Sample date	Ice type (% coverage)	Water temperature (°C)	Parr habitat use N	Water depth (cm), mean ± SE (range)	N	Water velocity ($cm \cdot s^{-1}$), mean ± SE (range)
December 2	IF	1.5	13	38.0±3.1 (23–57)	13	25.2±7.0 (1–65)
December 3	IF	1.5	18	44.7±2.5 (22–64)	18	29.3±5.4 (0–82)
December 12	S (<10), A (90)	0	2	58.0 (36, 80)	2	14 (8, 20)
December 15	S (30), A (<10)	0	3	51.0±3.6 (44–56)	5	55.6±9.2 (29–74)
December 20	S (<10), A (0)	0	4	45.8±6.2 (34–57)	1	3
December 29	S (<25), A (95)	0	0	nd	0	nd
January 3	S (<25), A (33)	0	4	34.0±3.2 (25–40)	4	21.3±9.8 (0–42)
January 5	S (<25), A (95)	0	4	45.0±5.3 (32–58)	4	24.8±10.9 (4–49)
February 1	S (60), A (<5)	0	2	55.5 (50, 61)	2	19.5 (16, 23)
March 2	S (60), A (0)	0	0	nd	0	nd
March 29	IF	4	21	43.7±3.0 (24–75)	22	18.7±4.2 (0–64)
April 2	IF	2	8	55.4±9.1 (18–100)	7	26±11.3 (2–87)

Note: Ice type indicates type of ice present during sampling (IF, ice-free; S, surface ice; A, anchor ice), and percent coverage is the percentage of the river covered by ice on the day of sampling. For parr habitat use, measurements of total water depth and midcolumn water velocity were recorded at the position where parr were encountered. N, number of parr encountered; nd, no data.

uals expressing milt or mature parr received an additional paint mark in the anal fin. All parr also received a visual implant (VI) tag implanted in the postocular adipose tissue (Blankenship and Tipping 1993), enabling identification of individuals. After marking and recovery, each parr was returned to the exact location of initial capture as marked by the numbered float.

A total of 69 parr, 32 mature and 37 immature, were collected and marked. By section, they ranged in mean total length from 130 to 145 mm, except for one YOY parr of 93 mm total length. The physical characteristics of parr in this sample were considered to be representative of the population at large because the mean length and percent mature were similar to samples collected during daytime electrofishing in nearby river reaches (K.G. Whalen and D.L. Parrrish, unpublished data). To evaluate parr movements and habitat use, we divided winter into three periods relative to the presence of ice: (*i*) ice-free from November 12 to December 12, 1994, (*ii*) iced from December 12, 1994, to March 15, 1995, and (*iii*) post-ice from March 15, 1995, to April 7, 1995. To quantify between-section movements, snorkeling surveys of all seven sections were completed twice during the ice-free period on November 15 and 17 and once during the post-ice period on April 7. Complete icing and high flows precluded a survey of all seven sections during the iced period and more than one survey of all seven sections in the post-ice period. To quantify parr habitat use, i.e., water depth and velocity selected by parr, 12 surveys were completed between December 1 and April 2 in portions of the 200-m study reach, which included the 55-m section where habitat availability was quantified. Three surveys were completed in the ice-free period, six when ice was present, and three during the post-ice period (Table 1). In conjunction with sampling for habitat use in the 55-m portion of the study reach where habitat availability was quantified and ice coverage was mapped, the position of parr was recorded using the centerline transect system to quantify changes in spatial distribution over the winter. Observations of marked parr were also recorded during sampling for parr habitat use and spatial distribution that contributed to the database on between-section movements.

Snorkeling procedures

The snorkeling surveys, completed by one diver, were done systematically, i.e., midchannel and lateral habitats were searched as the diver swam in an upstream direction (Cunjak and Power 1986*b*). Effort was made to search under surface ice, but at times, ice conditions precluded safe access to all stream edge habitats. Water temperatures, recorded before each survey with a hand-held thermometer, ranged from 0 to 4°C (Table 1).

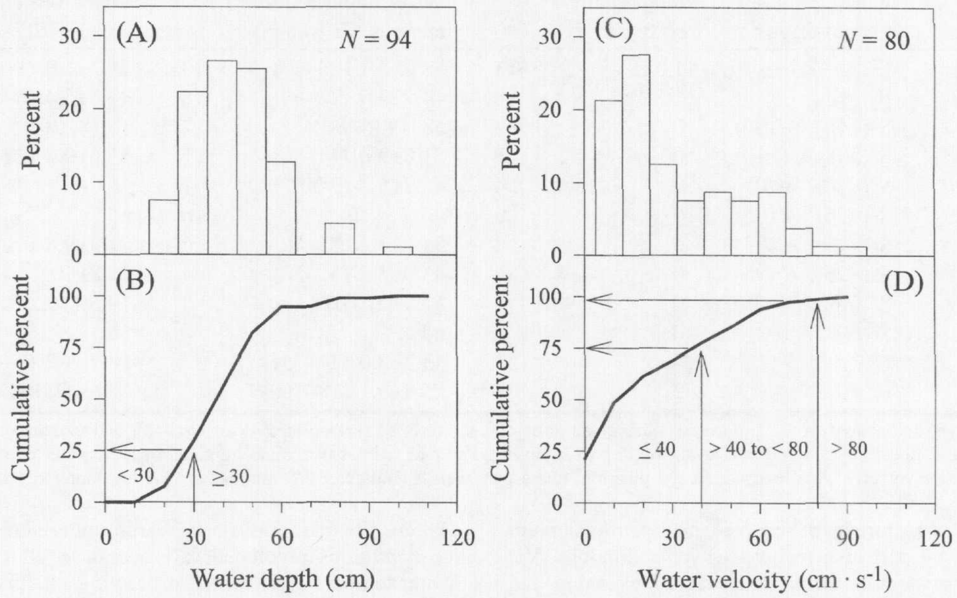
All snorkeling was conducted at night using a hand-held white light, which has been shown to only minimally disturb fish (Heggenes et al. 1993). Only parr observed resting on or above the substrate were enumerated. Surveys began after 19:30 and were completed before 01:00; start times were at least 2 h after sunset. Depending on flow and weather conditions, surveys were generally 1.5 h in duration. Underwater visibility was limited by habitat structure rather than water clarity; however, sampling efforts were at times negated when the water column was heavily laden with frazil ice on especially cold nights (air temperature of –15°C).

Upon encountering parr, the position of each was marked with a numbered float. Only the positions of undisturbed parr were marked; all parr were in contact with the substrate. Total water depth and midcolumn water velocity associated with the position of each parr were recorded, with measurements taken immediately after the completion of the diving survey. Attempts were made to collect all parr encountered using a small dip net. Netted parr were immediately placed into a water-filled metered tube to determine total length and to examine fins for marks or adipose eye tissue for a VI tag (Litvak 1983). After examination, parr were immediately returned to the location of capture by the diver. The length of undisturbed parr observed but not captured was estimated using the method employed by Baltz et al. (1991). Marked parr could be identified by fin markings without capture; however, VI tags could not be read unless parr were collected and examined.

Data analysis

For the analysis of the effect of ice formation on habitat availability, we created a categorical variable, water depth–velocity, for the purpose of evaluating and classifying habitat availability based on parr habitat use. No significant differences were detected among ice-free, iced, and post-ice periods for either mean water depth (ANOVA, p = 0.11) or velocity (Kruskal–Wallis rank test, p = 0.28). Thus, water depth and velocity categories were based on parr habitat use data pooled over the winter period (Figs. 1A and 1C). Water depth was categorized as <30 or ≥30 cm and water velocity as ≤40, >40 to <80, or ≥80 $cm \cdot s^{-1}$. These categories were representative of trends in parr habitat use, as approximately 75%

Fig. 1. Distribution (percentage of total) of observations of PYOY Atlantic salmon parr habitat use recorded during nighttime snorkeling surveys between December 1994 and April 1995 for (A) water depth and (C) water velocity (*N* is the number of observations). Also included are associated cumulative percent graphs for (B) water depth and (D) water velocity used to define joint water depth – velocity habitat categories. Arrows and intervals on water depth and velocity cumulative percent graphs indicate the initial categories used in the creation of the joint water depth – velocity habitat variable.



of the parr encountered over the winter were found at water depths ≥30 cm and approximately 75% of all parr encountered were found at water velocities ≤40 cm·s^{-1} (Figs. 1B and 1D). Observations in the two water depth categories (<30 and ≥30 cm) and three water velocity categories (≤40, >40 to <80, and ≥80 cm·s^{-1}) were cross-tabulated, creating initially six water depth–velocity categories. Because only three observations occurred in the categories of <30 cm and >40 to <80 cm·s^{-1}, <30 cm and ≥80 cm·s^{-1}, and ≥30 cm and ≥80 cm·s^{-1}, these categories were combined and are hereafter identified as "rarely used" habitats. The three remaining water depth–velocity categories considered were <30 cm and ≤40 cm·s^{-1}, ≥30 cm and ≤40 cm·s^{-1}, and ≥30 cm and >40 to <80 cm·s^{-1}. Ice was treated as a separate category where applicable. Water depth–velocity categories for habitat availability were established using the same categorization scheme.

Results

Ice formation

Ice coverage in the study reach was highly variable. Through early February, coverage of surface ice ranged between 10 and 55% and anchor ice up to 95% (Table 1). Associated with the surface ice was a curtain of subsurface frazil ice that in many areas made contact with the stream bottom. Coverage of 100% surface ice observed in mid-February was reduced to 60% by March 2. Coupled with this reduction, the surface ice had become decadent and slumped into the stream channel. By mid-March, ice was no longer a significant factor affecting habitat availability in the study reach.

Ice coverage on December 15 and February 1 was associated with the stream edge and with air-exposed instream rocks (Fig. 2). Between the ice-free condition on December 12 and February 1, the mean ± SE exposed wetted width of the stream segment decreased from 16.7 ± 0.3 m (N = 26) to 8.1 ± 0.5 m (N = 26). A highly significant difference was detected in the distance ice encroached from the northerly and southerly exposed stream banks (paired *t*-test, p = 0.001). The mean ± SE distance ice encroached was 6.5 ± 0.3 m (N = 25) on the northerly exposed bank and 2.2 ± 0.2 m (N = 25) on the southerly exposed bank.

Habitat availability versus use

Proportions of the various habitats differed among sampling dates (Table 2). Habitat availability differed significantly between December 12 and 15 (χ^2 = 19.0, p = 0.001) and between December 12 and February 1 (χ^2 = 13.4, p = 0.004). The proportion of rarely used habitats and ice-occluded habitats increased markedly from about 30% on December 12 to 73% on February 1. Habitat availability between December 15 and February 1 did not differ significantly (χ^2 = 8.0, p = 0.093).

Significant differences were detected between habitat use and availability for all dates (χ^2 > 54.0, p < 0.01) (Table 2). Throughout the winter, parr were distributed over a variety of water depth and velocity habitats, but the majority (62%) were associated with ≥30 cm and ≤40 cm·s^{-1} habitats (Table 2). Based on the distribution of habitats used, we refer to ≥30 cm and ≤40 cm·s^{-1} as "high-use" habitats and to <30 cm and ≤40 cm·s^{-1} and ≥30 cm and >40 to <80 cm·s^{-1} as "medium-use" habitats. The proportion of high- and medium-use habitats decreased from 58 to 26% between December 12 and February 1 (Table 2).

Temporal and spatial distribution of habitats

The alteration of habitats was extensive between the ice-free condition on December 12 and the iced condition on February 1 (Table 3). For each water depth and velocity category, <34% of the observations on December 12 remained within the same category on February 1. The <30 cm and ≤40 cm·s^{-1} category was nearly eliminated between Decem-

Fig. 2. Map (overhead view) of ice formation recorded on (A) December 15, 1994, and (B) February 1, 1995 in the 55-m study section of the Rock River. The dotted line indicates the wetted stream edge recorded on December 12, 1994, during an ice-free condition.

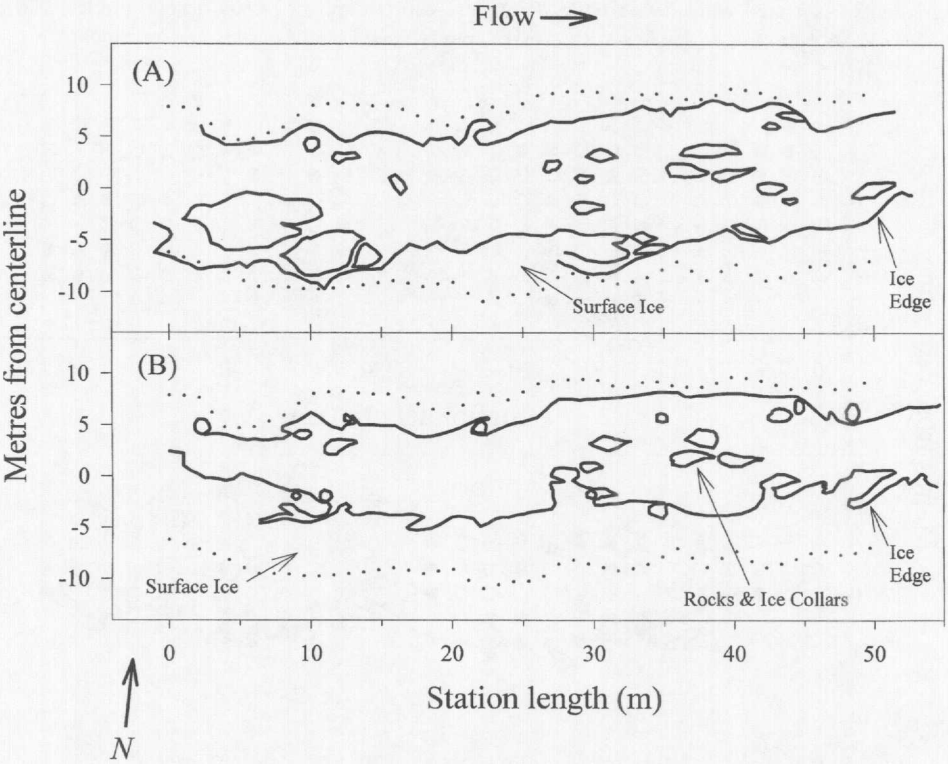


Table 2. Percentage (of row total) of habitat availability measurements on December 12 and 15, 1994, and February 1, 1995, and habitat use by nocturnally active PYOY Atlantic salmon parr between December 2, 1994, and April 3, 1995, by water depth and velocity category.

Sample type and date	Water depth (cm) and velocity ($cm \cdot s^{-1}$) category: <30 cm and ≤40 $cm \cdot s^{-1}$	≥30 cm and ≤40 $cm \cdot s^{-1}$	≥30 cm and >40 to <80 $cm \cdot s^{-1}$	Rarely used	Ice	UID	*N*
Habitat availability							
December 12	16.4 (36)	14.2 (31)	27.4 (60)	29.7 (65)	0.0 (0)	12.3 (27)	219
December 15	0.9 (2)	3.7 (8)	10.0 (22)	20.1 (44)	34.2 (75)	31.1 (68)	219
February 1	1.4 (3)	8.7 (19)	16.4 (36)	17.4 (38)	55.7 (122)	<0.5 (1)	219
Habitat use							
December–April	12.7 (10)	62.0 (49)	21.5 (17)	3.8 (3)	0.0 (0)	0.0 (0)	79

Note: Sample size in parentheses; *N*, total number. "Rarely used" category as described in Materials and methods. UID, sample points where water depth or velocity was not recorded because of interference of rocks or slush ice with measurements.

ber 12 and February 1, as ice was recorded at all but three of the <30 cm and ≤40 $cm \cdot s^{-1}$ habitat points. About one third of rarely used habitats on December 12 increased in suitability, as they were transformed into high- and medium-use habitats on February 1 (Table 3). In total, about 70% of the high- and medium-use habitats on December 12 were recorded as ice or rarely used habitat on February 1.

During the analysis of habitats used, patterns emerged relevant to the distribution of high-use and rarely used habitats. On December 12, the majority of high-use habitat points were found in areas >2 m from the wetted edge of the stream segment, while on February 1 the majority were recorded directly at, or within, 2 m of the ice edge (Fig. 3). Of note were several points of high-use habitat associated with rock and ice complexes in the exposed wetted portion of the stream channel. On December 12, rarely used habitats were interspersed among the remaining habitats (Fig. 3A). Rarely used habitats became concentrated with the formation of surface ice on the stream edge between 0 and 15 m and between 35 and 50 m from the upstream end of the station, where the flow constriction resulting from ice formation was greatest (Fig. 3B).

As described above, the encroachment of ice from the stream edge had the effect of nearly eliminating the <30 cm and ≤40 $cm \cdot s^{-1}$ habitat category, which was primarily laterally distributed on December 12 (Fig. 3A). Other habitat categories used by salmon were laterally redistributed with ice formation rather than physically eliminated (Fig. 3B). High-use habitats found in areas between –8 and 6 m of the stream centerline on December 12 were concentrated into ar-

Fig. 3. Spatial distribution (overhead view) of water depth – velocity habitat points recorded on (A) December 12, 1994, during an ice-free condition and on (B) February 1, 1995, during an iced condition in the 55-m study section of the Rock River. Measurements were recorded at a 2 × 2 m scale and at the same points (± 0.5 m) on each date. Additional measurements were recorded on February 1 to quantify habitat gradients associated with the ice edge. Triangles, <30 cm and ≤40 cm·s^{-1}; solid circles, ≥30 cm and ≤40 cm·s^{-1}; open circles, ≥30 cm and >40 to <80 cm·s^{-1}; squares with crosses, rarely used (see Materials and methods).

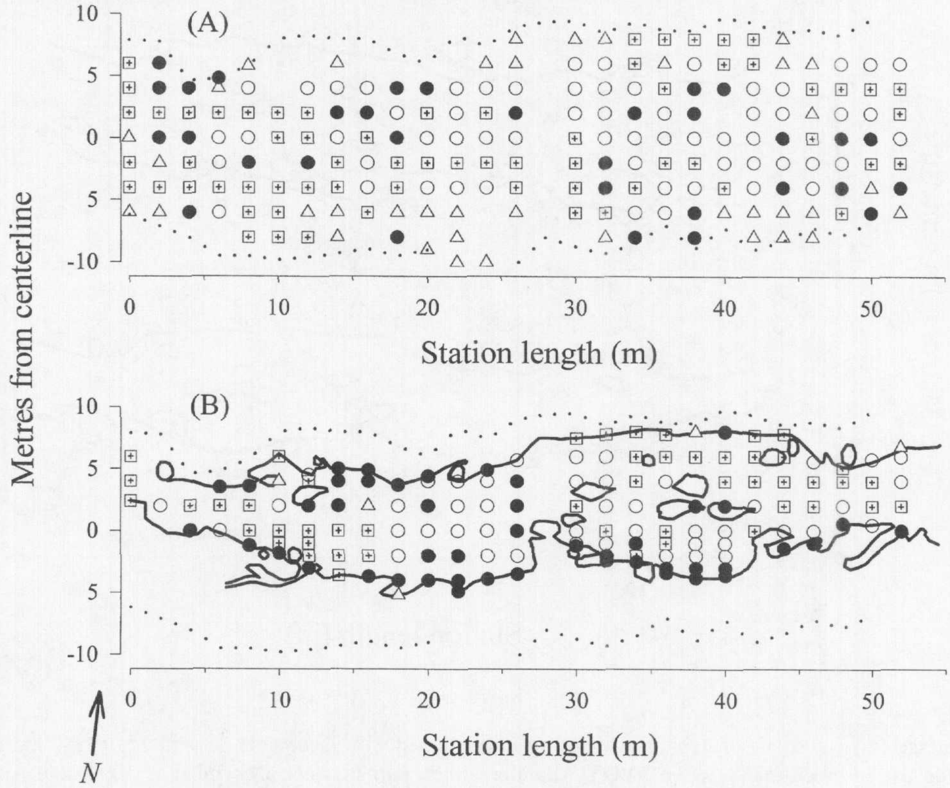


Table 3. Change in habitat in the 55-m section from the ice-free condition on December 12 to the iced condition on February 1.

February 1 water depth (cm) and velocity (cm·s^{-1}) category	December 12 water depth (cm) and velocity (cm·s^{-1}) category: <30 cm and ≤40 cm·s^{-1}	≥30 cm and ≤40 cm·s^{-1}	≥30 cm and >40 to <80 cm·s^{-1}	Rarely used	N
<30 cm and ≤40 cm·s^{-1}	0 (0)	3.2 (1)	0 (0)	1.5 (1)	2
≥30 cm and ≤40 cm·s^{-1}	0 (0)	16.1 (5)	11.9 (7)	9.1 (6)	18
≥30 cm and >40 to <80 cm·s^{-1}	0 (0)	12.9 (4)	33.9 (20)	18.2 (12)	36
Rarely used	8.3 (3)	6.5 (2)	23.7 (14)	27.3 (18)	37
Ice	91.7 (33)	58.1 (18)	30.5 (18)	43.9 (29)	98
N	36	30	59	66	

Note: Percentages are from paired measurements of grid points on each date; thus, cell values represent the proportion of points in each habitat category on December 12, as identified by the column headings, that changed into each habitat category on February 1, as identified by the row headings. Percentages in cells are based on the column total. Sample size in parentheses; *N*, total number.

eas between –4 and 4 m of the stream centerline on February 1. Medium-use and rarely used habitats were affected similarly.

Parr movements and distribution

Between collection and marking in early November 1994 and the completion of the study in April 1995, 59 marked parr were observed both within and downstream of the study reach. Over half (N = 35) of these observations were made during the short period between marking in early November and surveys on November 15 and 17 whereas 41% (N = 24) were made between December 2, 1994, and April 7, 1995. Hereafter, the observation of a marked parr within the section where it was initially marked is defined as "section fidelity." For all observations combined, movement and section fidelity were dependent on parr maturity (χ^2 = 7.6, p = 0.006). For mature parr, 11 of the 30 observed after marking were found outside the section where they were initially marked, while only two of the 29 marked immature parr observed after marking were found outside the section where they were marked. Mature parr accounted for 11 of the 13 observations of movement, which ranged from 20 to

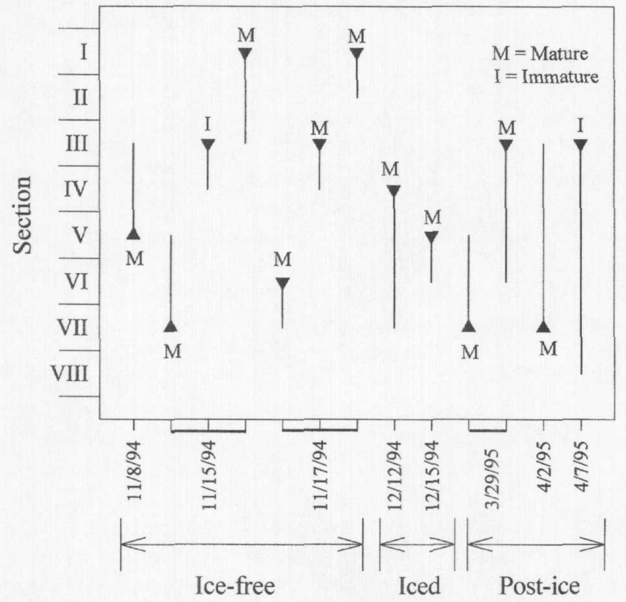


Fig. 4. Between-section movements of mature and immature marked parr by date of observation within periods relative to the presence of ice. Triangles point to the direction of movement and lines indicate the extent of movement.

125 m (Fig. 4). Marked parr moved both upstream (N = 4) and downstream (N = 9) and from every section except section II; movements were not directed to a particular section (Fig. 4).

For the 24 observations of marked parr between December 2, 1994, and April 7, 1995, 18 (eight mature and 10 immature) were made of parr exhibiting section fidelity. The majority (N = 11) of these observations were made on December 2 and 3 before stream icing on December 12. Observations of one or two marked parr remaining within the section of marking were made on December 12, 15, and 20, 1994, and January 3, 1995, dates when ice was a significant habitat variable (Table 1). During the post-ice period on March 29 and April 2, 1995, three marked parr were observed within the section where they were marked in early November.

The spatial distribution of 62 parr was identified in the 55-m section between December 1, 1994, and April 3, 1995: N = 32, ice-free; N = 16, iced; N = 14, post-ice. To assess temporal changes in spatial distribution during winter, observations in the iced and post-ice periods were pooled and considered jointly as "iced/post-ice." In the ice-free period, parr were most concentrated within 5 m of the stream centerline and between 15 and 35 m from the upstream end of the station (Fig. 5A). In the iced/post-ice period, parr were concentrated 3 to 9 m from the stream centerline and between 0 and 15 m from the upstream end of the station and –2 to –9 m from the stream centerline and between 25 and 50 m from the upstream end of the station (Fig. 5C). In the iced/post-ice period, few parr were found near the central vicinity of open water, particularly in areas of high flow, i.e., rarely used habitat, formed by the constriction of flow by edge ice (Figs. 3B and 5C). Eight of the 14 parr observed in the post-ice period were found on the northerly exposed side of the stream (Fig. 5C), positions that had been covered by surface–frazil ice over the winter period (Fig. 2). No movements of specific individuals from midchannel to lateral habitats were identified.

A rock and root-wad complex that existed between 4 and 8 m of the stream centerline and between 0 and 8 m from the upstream end of the station supported high concentrations of parr relative to other areas in the iced/post-ice period (Fig. 5C). Through marks, VI tags, and large size differences, it was determined that individual parr selected positions in the vicinity of the rock and root-wad complex that were within ± 0.25 m of positions selected by parr at other times (Figs. 5A and 5C). One marked parr observed in front of the root wad on January 3 was observed in this same location on March 29, a position initially occupied by an unmarked parr on December 3. The marked parr that occupied the position in front of the root wad on January 3 and March 29 had been marked in section VII, approximately 70 m downstream.

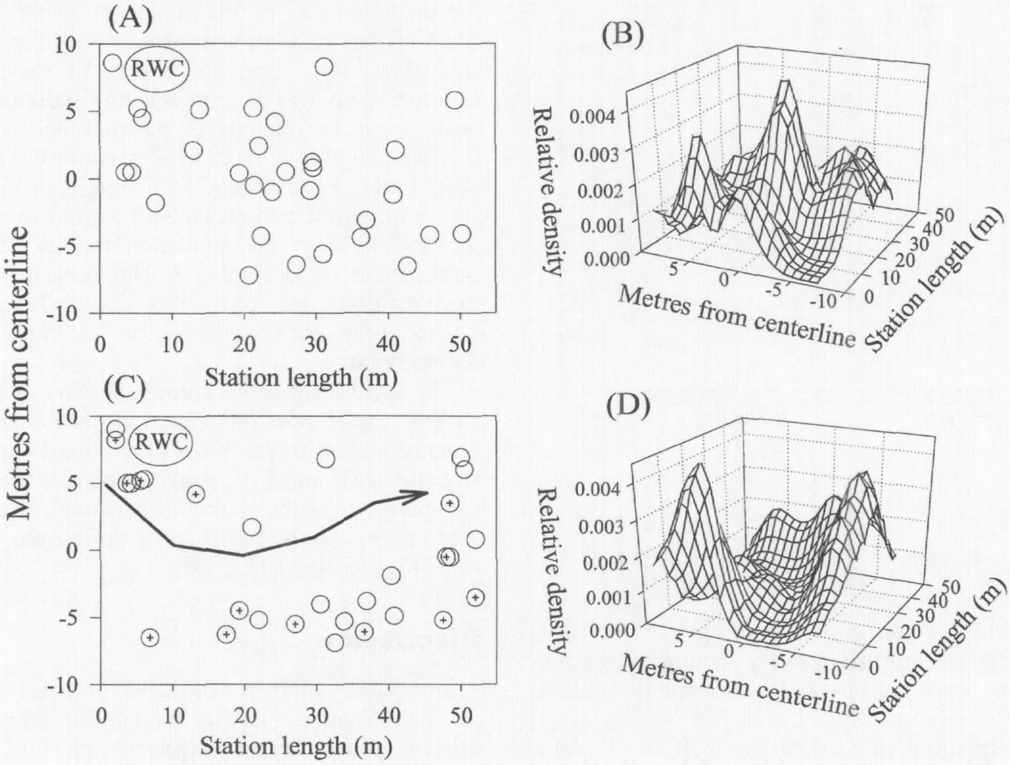
The significant spatial reorganization of parr between the ice-free and iced/post-ice periods is illustrated in a three-dimensional portrayal of the distribution of parr relative density (Figs. 5B and 5D). Peaks in parr distribution in the ice-free period near the station midchannel switched to peaks in areas lateral to the midchannel during the iced/post-ice period (Figs. 5B and 5D).

Discussion

Several key elements of the salmon parr – habitat use versus ice formation – habitat availability interaction were identified that are relevant to the first question of how does ice formation affect habitats available to salmon. Salmon parr exhibited specificity in habitat selection by occupying similar water depth and velocities during winter despite the reduction in the availability of those habitats. For winter habitat use – availability interactions, the selection of only a portion of the available habitat profile is similar to that observed for trout (Cunjak and Power 1986*b*; Chisholm et al. 1987; Heggenes et al. 1993; Brown and Mackay 1995). Although parr habitat use differed significantly from habitat availability when ice was absent, differences between habitat use and availability were most pronounced when ice was present. By nearly threefold, ice reduced the abundance of habitats selected by >90% of salmon parr, and habitats commonly used by salmon parr represented <10% of those recorded when ice was present. The trend for physical space to be reduced with ice formation is consistent with previous studies (Cunjak and Power 1986*a*; Power et al. 1993; Berg 1994). The significance of the finding of parr habitat specificity is that parr are susceptible to reductions in physical space resulting from ice formation. The link established between parr habitat use and ice formation indicates that ice has the potential to affect overwinter survival and thus smolt production.

The lateral growth of ice from the stream margin, which results from the cooling of the stream bank (Prowse 1994), had important implications for available habitat. The edge-focused surface ice created areas of low velocity that enabled suspended frazil ice to accumulate in masses beneath surface ice on the stream edge. These masses may become part of the ice cover facilitating the reduction in physical

Fig. 5. Spatial position (overhead view) of PYOY Atlantic salmon parr in the 55-m study section of the Rock River during the (A) ice-free and (C) iced/post-ice periods, including (B) ice-free and (D) iced/post-ice three-dimensional portrayals of parr relative density. Open circles in Fig. 5C indicate observations of parr in the iced period, with encircled crosses identifying the position of parr in the post-ice period. The general location of the rock and root-wad complex is indicated by RWC. The line and arrow in Fig. 5C indicates the general vicinity of open water on February 1 (see Fig. 3B).



space at the stream margin (Beltaos et al. 1993). As observed in low-velocity, deeper habitats in the Rock River, these masses may eventually solidify, thereby exacerbating the flow diversion caused by surface ice. The accumulation of subsurface frazil ice has been shown to cause significant changes in the distribution of subsurface river flow (Power et al. 1993; Prowse 1994; Power and Power 1995) and result in a reduction in cross-sectional habitat space (Chisholm et al. 1987).

The lateral growth of ice from the stream edge also resulted in the concentration of stream flow and the redistribution of habitats that were often and rarely selected by parr. With ice formation, these habitats became more spatially distinct, yet physically more concentrated. The effects of ice formation, which included reductions in physical space and redistribution of habitat, may cause habitat conditions over the winter to be highly temporally variable. Through the systematic analysis of habitat availability between mid-December and early February, it was determined that the character of the physical habitat at many points changed dramatically with ice formation. The basis of our second question is that as a result of frequent change in the availability and distribution of habitats caused by ice formation, parr may need to physically redistribute themselves to maintain access to suitable habitats.

Over the winter, we observed both between-section movements and a significant spatial redistribution of parr within sections. Although these changes could not be linked to specific icing events, changes in the distribution and character of habitats caused by ice were consistent with changes in the distribution of parr. The spatial redistribution of parr between the ice-free and iced/post-ice periods generally corresponded to the lateral distribution of deepwater (≥ 30 cm) and low-velocity (<40 $cm \cdot s^{-1}$) habitats associated with the surface ice edge whereas the largest reduction occurred near the stream centerline where high flow existed. Where movements related to ice formation have been identified, they have been attributed to changes in habitat suitability, primarily the physical exclusion properties of ice (Chisholm et al. 1987; Cunjak and Randall 1993; Brown and Mackay 1995). The redistribution or loss of suitable habitat has also been identified as a mechanism explaining the distribution and (or) movements of fish in winter (Cunjak 1988*a*; Griffith and Smith 1993, 1995). Our finding that habitats commonly used by salmon parr were significantly altered between ice-free and iced conditions supports the hypothesis that ice is an important force instigating juvenile salmon redistributions in winter (Cunjak and Randall 1993).

As has been observed for trout (Cunjak and Power 1986*b*), ice may also affect parr spatial distribution by providing cover. Even though surface ice had the greatest effect on habitat on the stream edge, once ice forms and persists, ice may create stable habitat conditions relative to open-water areas that are subject to high flows, anchor ice formation, and episodic scouring (Erman et al. 1988; Power et al. 1993). Parr occupied sites within the study reach during the post-ice period that had been covered with surface–frazil ice for much of the winter. Based on observations of stream fish existing beneath ice for extended periods (Power et al. 1993; Power and Power 1995), it is possible that parr lived under the lateral surface–frazil ice during winter and remained there after the ice ceased to persist. Habitat availability below surface ice on the stream edge was not quantified, yet on occasion, space existed between the bottom of the curtain of frazil ice and the stream substrate and parr were observed to escape into this space upon being disturbed. Although the results support the notion that ice reduces available physical space (Chisholm et al. 1987; Cunjak and Randall 1993; Berg 1994), it may be premature to suggest that edge habitats affected by ice were absolutely inaccessible to parr. For future analyses, identifying subice habitat availability and parr distribution, particularly whether parr move into lateral habitats post-ice, will be extremely important to how ice is viewed as a physical habitat feature that results in habitat exclusion.

For salmonids, movements may be directed to habitats where exposure to environmental disturbance during winter is reduced (Tschaplinski and Hartman 1983; Hutchings 1986; Brown and Hartman 1988), and thus, seasonal redistributions may confer an overwinter survival advantage to those individuals that move (Hutchings 1986; Brown and Hartman 1988). Observations of marked parr were insufficient to determine whether movement conferred a survival advantage compared with parr exhibiting section fidelity. Other studies examining fall–winter movements have found similar results in that movements may be exhibited by only a portion of the population (Heggenes et al. 1991; Cunjak and Randall 1993; Brown and Mackay 1995; Griffith and Smith 1995). For Atlantic salmon, our results indicate that parr may exhibit a combination of strategies, first movement and then fidelity, suggesting an integration of strategies for winter survival. The data also suggest that the likelihood of moving between fall and spring may be influenced by parr maturity. Differences in fall–winter activity patterns and habitat needs of mature and immature parr could factor into differences in the propensity for movement, susceptibility to environmental change, and thus winter mortality.

The variable nature of ice formation observed in the Rock River and the dramatic changes in the distribution of winter habitats selected by juvenile salmon that ice caused indicate that there likely is no one-time strategy that parr may select to cope with winter conditions. For parr, the maintenance of activity in winter may depend on the type and extent of ice present. Anchor ice, which was present in the study reach, may form rapidly (Benson 1955), lead to ice dam formation, and dramatically alter flows (Benson 1955; Beltaos et al. 1993; Power et al. 1993), and its release may scour substrates (Power et al. 1993). Although habitat availability was not quantified when anchor ice coverage was extensive, based on observations of parr habitat use, conditions during anchor icing events appeared to be unsuitable for night-active salmon parr. Seasonally, anchor ice may be more prevalent early in winter before surface ice becomes a significant habitat feature (Benson 1955). The early-season formation of anchor ice may thus be coupled with a temperature-based impairment of both the physiological motor (Facey and Grossman 1990) and energetic capacity (Cunjak 1988*b*) of parr. With these multiple stresses, it may be adaptive for parr to cope with anchor ice by taking cover in the substrate as a means of reducing exposure (Cunjak and Power 1986*b*), even if this approach puts them at risk to stranding (Power et al. 1993). Few parr were observed on nights when anchor ice was forming or when the water column was heavily laden with frazil ice. Other forms of ice, such as surface ice, may also form rapidly, but they may be more physically stable and result in more predictable effects on the physical environment (Prowse 1994). A consistent active strategy may expose parr to rapid habitat degradation resulting from anchor ice formation, while a consistent sheltering strategy may expose parr to stranding or scouring and preclude their ability to feed when more stable and persistent forms of ice are present.

During the iced and post-ice periods, the rock and root-wad complex was a key structural element that was extensively used supporting high concentrations of parr relative to other areas. Root wads have been identified as one of the most complex forms of woody debris (Shirvell 1990), a feature shown to be important to coho salmon (*Oncorhnychus kisutch*) during high-flow events in winter (McMahon and Hartman 1989). The rock and root-wad complex and the deepwater ($\geq$ 30 cm) and low-velocity (<40 $cm \cdot s^{-1}$) habitat associated with it may serve as refugia when conditions become limiting and, as we observed, provide shelter for fish moving from other areas (Tschaplinski and Hartman 1983). The concentration of parr near structural elements such as the rock and root-wad complex has important implications for how the effects of ice on winter carrying capacity are considered. For coho salmon, Tschaplinski and Hartman (1983) noted that the loss of woody debris during winter floods resulted in disproportionately large reductions in population size. Ice could have a large effect on population density of juvenile Atlantic salmon if ice occludes habitats where parr are concentrated. Identifying how ice interacts with and affects key structural elements in streams is important for determining the influence of ice on winter carrying capacity for parr.

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