

Patterns in apparent survival of Atlantic salmon (*Salmo salar*) parr in relation to variable ice conditions throughout winter

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Abstract: Apparent within-site survival of Atlantic salmon (*Salmo salar*) parr, individually tagged with passive integrated transponders, was not constant throughout the winter period in a 3-year study (2003–2006) in Catamaran Brook, New Brunswick, Canada. Highest decline in apparent survival (19.4%–33.3% of the study population) occurred prior to any ice formation and coincided with early winter acclimatization period (dynamic temperature and discharge regime). Stream discharge and parr maturity were identified to be relevant factors explaining emigration prior to ice formation. Apparent survival was improved during the period affected by subsurface ice and considerably better when surface ice was prevailing, with a decline in population size between 0% and 15.4%. Overall, observed within-site winter mortality was low (4.4%), and the majority of the loss of tagged salmon parr occurred because of emigration. On average, the within-site population of tagged salmon parr declined by 31.7% over the whole winter (November–April). Our data suggest that anthropogenic impacts, like climate change or river regulation, are likely to affect the apparent survival rate and distribution of juvenile Atlantic salmon because of their effects on natural ice regime in streams.

Résumé : La survie apparente dans un même site de tacons du saumon atlantique (*Salmo salar*) porteurs d'un transpondeur passif intégré, ne s'est pas révélée constante au cours de la période hivernale pendant une étude de trois ans (2003–2006) à Catamaran Brook, Nouveau-Brunswick, Canada. Le déclin le plus marqué de la survie apparente (19,4–33,3 % de la population étudiée) se produit avant toute formation de glace et coïncide avec la période d'acclimatation du début de l'hiver (température et régime d'écoulement dynamiques). Nous avons identifié l'écoulement du cours d'eau et la maturité des tacons comme les facteurs pertinents pour expliquer l'émigration avant la formation de la glace. La survie apparente s'améliore durant la période marquée par la formation de glace dans la colonne d'eau et elle est considérablement meilleure quand la glace de surface prédomine; le déclin de la taille de la population varie alors de 0 et 15,4 %. Globalement, la mortalité hivernale observée dans un même site est faible (4,4 %) et la majorité des pertes de tacons de saumons marqués sont dues à l'émigration. En moyenne, la population de tacons de saumons marqués dans un même site a baissé de 31,7 % durant l'ensemble de l'hiver (novembre–avril). Nos données indiquent que les impacts anthropiques, comme le changement climatique ou la régularisation du débit, affectent vraisemblablement le taux de survie apparente et la répartition des jeunes saumons atlantiques par leurs conséquences sur le régime naturel des glaces dans les cours d'eau.

[Traduit par la Rédaction]

Introduction

Winter is recognized to be a critical period for survival of freshwater fishes (Hurst 2007). In fluvial systems, the “winter bottleneck” has typically been associated with energetic imbalance (Finstad et al. 2004a; Næsje et al. 2006), lack of suitable habitat (Gibson and Myers 1988), physical disturbance related to ice dynamics (Maciolek and Needham 1952; Cunjak and Therrien 1998), or interaction of multiple stressors (Lemly 1996). Stream salmonids have often been used as model species to study population dynamics during

winter, and the estimates of winter loss of juvenile salmonids range from 9% to 100% in natural environments (Huusko et al. 2007). There has been, however, a major problem in conducting winter survival studies because the data collection is very difficult in streams with extensive ice cover. Consequently, most estimates of winter survival are from streams where ice conditions do not preclude the entry to study areas during winter months (e.g., Letcher et al. 2002; Finstad et al. 2004a), or the estimates are derived from seminatural settings (Elso and Greenberg 2001; Parrish et al. 2004; Linnansaari et al. 2008). When winter survival is estimated in streams that truly freeze for extended periods, the standard practice has been to resort to a “before–after” approach; that is, the density of fish is estimated in autumn before ice forms and again in spring or early summer when the physical (ice and discharge) conditions re-allow safe and reliable data collection (e.g., Bradford et al. 2001; Lund et al. 2003). Although these studies have been pivotal in providing understanding of population dynamics of juvenile stream salmonids during winter, the relative importance of different periods (e.g., no ice vs. surface ice) of winter for survival has not been adequately assessed in ice-affected riv-

Received 13 November 2009. Accepted 4 August 2010.
Published on the NRC Research Press Web site at cjfas.nrc.ca on 9 October 2010.
J21518

Paper handled by Associate Editor Bror Jonsson.

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Table 1. The dates when mean daily water temperature (T) fell permanently below 10 °C (start of before-ice period), freeze-up started (subsurface ice production), and ice breakup occurred during each of the studied winters with the duration of different periods of winter.

Winter	$T < 10$ °C	Freeze-up	Breakup	Before-ice period (days)	Subsurface ice period (days)	Surface ice period (days)
2003–2004	3 Oct.	3 Dec.	10 Apr.	62	9	121
2004–2005	30 Sept.	9 Nov.	2 Apr.	41	17	128
2005–2006	9 Oct.	6 Dec.	3 Apr.	59	11	119

ers. It is well established, however, that the physical environment varies considerably during the course of winter (e.g., Cunjak et al. 1998; Stickler et al. 2009). Also, fluctuations in juvenile stream salmonid physiology (e.g., energy metabolism) occur in different periods of winter in response to altered environmental conditions with possible bearing on survival (Cunjak 1988; Finstad et al. 2004b; Næsje et al. 2006). Furthermore, the current climate change scenarios predict that drastic changes in ice regime of rivers are likely to occur (Prowse and Beltaos 2002; Prowse et al. 2006). To predict how juvenile stream salmonid populations may be affected by such changes, the effects of different periods of winter on population dynamics must be explicitly understood.

In this study, we followed individually tagged Atlantic salmon (*Salmo salar*) parr during three winters to identify any variation in apparent survival between different periods of winter in an ice-affected stream. Further, we wanted to establish whether precocious maturity, size of salmon parr (length, mass, or condition factor), stream discharge, and (or) water temperature affect the apparent winter survival within the studied sites.

Materials and methods

Definition of periods of winter in relation to ice conditions

In this article, apparent survival was monitored during three winter periods based on distinctive ice conditions of the stream: (i) “Before-ice period” was defined as the time in late autumn when water temperature was <10 °C but no ice had yet formed. The 10 °C threshold was chosen because juvenile Atlantic salmon populations in the studied region exhibit daytime sheltering behaviour when the temperature declines below this value (Rimmer et al. 1983). (ii) “Period of subsurface ice formation” was defined as the time when the channel started to freeze and ice processes were dominated by frazil and anchor ice (sensu Stickler and Alfredsen 2009). (iii) “Period of surface ice formation” was defined as the time when the surface of the stream was mainly, or totally, covered with solid ice and subsurface ice formation was negligible. Events where ice breakup occurred but a subsequent new surface ice cover formed (i.e., midwinter ice breakup) were also included in the surface ice period.

The winter periods were variable in length during each studied year (Table 1). In addition to the three winter periods, apparent survival could be reliably monitored in three study sites in early spring after ice had melted but before the spring (snowmelt) flood and smolt migration precluded reliable fish tracking, so that an overwinter apparent survival estimate could be calculated.

Study area

The research was conducted over three winters (2003–2006) in Catamaran Brook (46°52'45"N, 66°06'00"W), a third-order tributary to the Little Southwest Miramichi River, situated in central New Brunswick, Canada (Fig. 1). The stream discharge was continually monitored in the Middle Reach of Catamaran Brook, and the discharge is approximately 1.9 times higher in Lower Reach than in the Middle Reach (D. Caissie, Fisheries and Oceans Canada, Gulf Fisheries Centre, P.O. Box 5030, Moncton, New Brunswick, Canada, personal communication, 2009). The mean annual discharge at the mouth of the stream is $1.2 \text{ m}^3 \cdot \text{s}^{-1}$. The brook represents a typical temperate Atlantic salmon nursery stream that freezes annually for a period of 3–5 months (Table 1). A fish-counting fence situated 250 m upstream from the mouth of the brook is operated from the beginning of May until mid-November and allows the capture of upstream- and downstream-moving fish (Cunjak et al. 1993). Peak smolt migration typically occurs during the second and third week of May. A detailed description of the physical and biological properties of Catamaran Brook can be found in Cunjak et al. (1990, 1993).

The data for this study were collected from four study sites (Table 2). Sites A and C were located in the Lower Reach and sites D and E in the Middle Reach of Catamaran Brook (Fig. 1). All the study sites were relatively shallow (i.e., not deeper than 1 m during normal flow conditions) but consisted of a variety of mesohabitats from riffles to pools (Table 2). Juvenile salmon densities in the actual study sites were not estimated, but the densities in adjacent locations were obtained during the same week when fish tagging occurred (Table 2). It is also important to note that the lengths of the study sites were variable (Table 2), potentially affecting the validity of the proportionate data of fish emigrating out of the study area. However, detailed data on the movements of the passive integrated transponder (PIT)-tagged fish indicated that the salmon parr generally were either extremely sedentary throughout the winter or travelled beyond a scale where nonstandardized study site size could have introduced bias to the encounter rate of fish (Linnansaari 2009).

Tagging and tracking of salmon parr

Atlantic salmon parr were captured using a backpack electrofishing device (LR-24, Smith-Root Inc., Washington, USA). After capture, the fish were anaesthetized with clove oil (40 ppm, ethanol as carrier), and fork length (L_F , nearest mm), mass (accuracy 0.1 g), and maturity (% precocious males) were determined (Table 3). Incision (~4 mm) was then made ~10–15 mm posterior to the pectoral girdle, and a PIT tag was inserted into the body cavity.

Fig. 1. Location of Catamaran Brook in the Miramichi River basin in New Brunswick, Canada (a, b) and the study site locations (A, C, D, and E) in Catamaran Brook (c). Stream discharge was measured at site D, and a fish-counting fence was situated in the site A. Little Southwest Miramichi River is indicated by L.S.W.

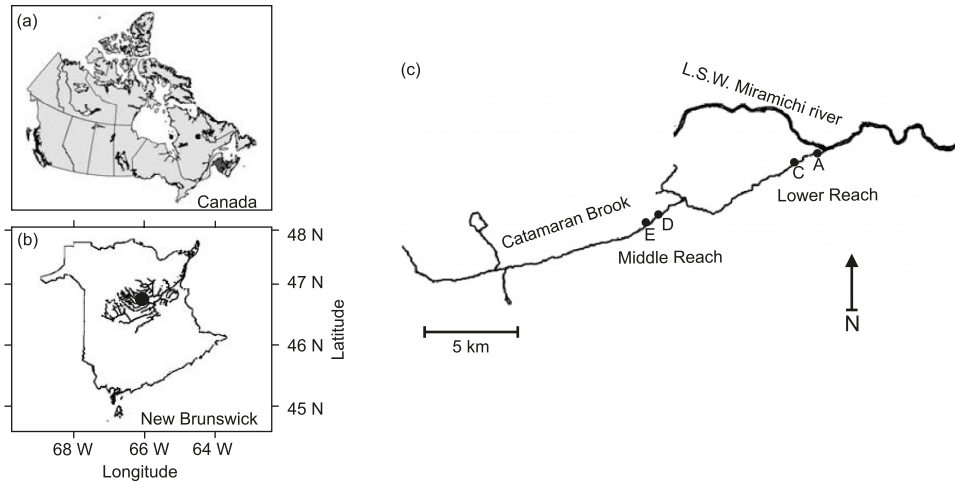


Table 2. Physical properties, juvenile Atlantic salmon density (all age classes), and mesohabitat composition of the four study sites in Catamaran Brook, New Brunswick.

Measure	Study site			
	A	C	D	E
Length (m)	249	103	52	125
Mean width (m)	9.2	10.3	7.5	6.3
Total wetted area (m ²)	2293	1011	383	743
Density (no.·100 m ⁻² ± standard error, SE)	69.4±4.8	54.5±0.8	12.7±0.4	27.1±1.4
Distance from river mouth (km)	0.1	1.0	8.5	8.8
Mesohabitat composition (%)				
Run	6	0	0	0
Glide	12	20	30	21
Pool	7	14	9	7
Flat	15	5	13	12
Riffle	60	61	48	60
Total	100	100	100	100

Note: Mesohabitat classification is based on Borsányi et al. (2004) but modified to be better suited to small streams. All habitats with broken surface pattern (wave height > 4 cm) were termed as “riffle”; the habitats with smooth surface pattern but steep gradient (>4%) were termed as “run”; and the habitats with smooth surface pattern but moderate gradient were termed as “glide” (surface velocity > 0.5 m·s⁻¹), “flat” (surface velocity < 0.5 m·s⁻¹, depth < 0.4 m), or “pool” (surface velocity < 0.5 m·s⁻¹, depth > 0.4 m).

Parr were tagged using 23 mm (0.6 g in air) or 32 mm (0.8 g in air) PIT tags (RI-TRP-WRHP, RI-TRP-WR2B, respectively; Texas Instruments, Texas, USA). The 32 mm tags were used only during the winter of 2005–2006 and only for fish larger than 100 mm L_F ($n = 19$). The incision was closed with a single suture (Monosof black nylon, 6–0 taper, C-1 cutting needle). After tagging, salmon parr were held in large, substrate-filled containers within the study sites and released back to the stream the following morning. The number of fish tagged varied in each study site (Table 3), and the tagging took place from late October to early November (Fig. 2).

Tagged fish were monitored with passive (stationary) and active (portable) antennae using a Texas Instruments Radio Frequency Identification Series 2000 system. The stationary antenna data were used to relate the exact timing of emigration to physical (stream) parameters, whereas the data from active tracking surveys were used to confirm the number of

fish remaining in the study sites and their status (dead or alive).

The stationary antennae were set-up as swim-through gates (7.3–8.6 m in width and 0.5–0.6 m in height), and two antennae were used in sequence to detect the direction of fish movements. The reader system was powered with two 12 V DC deep-cycle marine batteries (in parallel) that were replaced every 3 days. The antennae were tested using a “dummy” tag each time before the batteries were changed to ensure that the antennae had been operational and no data had been lost. The stationary antennae were in use from November to December 2003 at the downstream end of site A and from November 2004 to March 2005 at the downstream and upstream end of site C.

Active tracking with the portable system was carried out mainly using a one-person antenna. Details on construction, accuracy, and efficacy of the antenna have been described previously (Roussel et al. 2000; Linnansaari et al. 2007).

Table 3. Number of Atlantic salmon parr tagged (n) at each study site, with description of mean fork length (L_F), mass, tag-to-fish mass ratio (W_T/W_F), and maturity of the study populations.

	Study site (year)					
	A (2003–2004)	C (2004–2005)	C (2005–2006)	D (2003–2004)	E (2004–2005)	E (2005–2006)
n	57	36	31	28	23	53
L_F (mm)	93±15 (78–140)	97±15 (75–137)	91±16 (79–127)	99±13 (83–130)	115±11 (87–135)	89±11 (73–124)
Mass (g)	9.6±5.7 (5.5–31.2)	10.4±5.5 (5.1–30.1)	8.8±5.4 (5.1–20.5)	12.4±4.1 (6.2–24.9)	16.9±4.7 (6.5–26.2)	8.8±4.0 (5.1–21.6)
W_T/W_F (%)	7.5±2.5 (1.9–10.9)	5.8±2.3 (2.0–11.8)	7.0±2.7 (3.9–11.7)	8.2±2.0 (2.4–9.7)	4.0±1.8 (2.3–9.2)	8.2±2.0 (3.7–11.8)
Maturity (%)	18	22	29	11	9	43

Note: Values are reported as mean \pm standard deviation (SD), with range in parentheses. In addition to tagged fish shown in the table, five PIT-tagged salmon parr from a former study (Kilburn 2004) were located during the first active tracking survey in the site A during winter 2003–2004 and were subsequently used in the study.

The detection distance was measured to be approximately 65 cm for 23 mm tags and 73 cm for 32 mm tags, when the tag's cylindrical axis was held parallel to the plane of the antenna inductor coil loop (maximum read range for vertically oriented tags 89 cm and 96 cm, respectively). Active tracking was carried out multiple times during each period of winter such that the tagged salmon parr were followed under very diverse physical conditions, ranging from ice-free situation to very severe anchor ice events (5.0%–83.9% of the wetted area covered) and eventually to partial (36.8%–92.5% of wetted area) and full surface ice (100%) cover conditions (Table 4, Fig. 2). A two-person antenna (Linnansaari and Cunjak 2007) was used in April 2006 to survey a kilometre of stream both upstream and downstream from the study site E to determine the extent of movements and the fate of salmon parr that had emigrated during winter.

It was assumed that if a PIT-tagged salmon was present in a study site during a tracking survey, it would be detected. This assumption was based on several factors: (i) the chosen study sites were relatively open areas and easy to scan for tags with the portable antenna; (ii) the tracking surveys were carried out during a period of relatively cold water temperature when salmon parr have been shown to tolerate tracking operations without fright bias (Linnansaari et al. 2007; Linnansaari and Cunjak 2007); (iii) the efficacy to recover tags has been shown to be very high for the antenna types used in this study (Linnansaari et al. 2007; Linnansaari and Cunjak 2007); (iv) the tracking was carried out repeatedly (typically 3–13 times) over a 24-h period on each studied date (detailed data on individual trackings are considered elsewhere; Linnansaari 2009); and (v) the structure of the resulting data set indicating that fish that were expected to remain in the study site were either found each time (data analysed based on tracking dates, not individual trackings within each date) or were no longer present (i.e., not found within study site in any later tracking). Thus, the encounter rate was generally considered to be 100%. However, exception to this happened on three dates during surface ice period in site E (2005–2006) when the tracking was carried out only during daylight. It was known from the tracking data during before-ice conditions that the daytime shelter of two PIT-tagged salmon parr was situated under a logjam where the daytime detection was not possi-

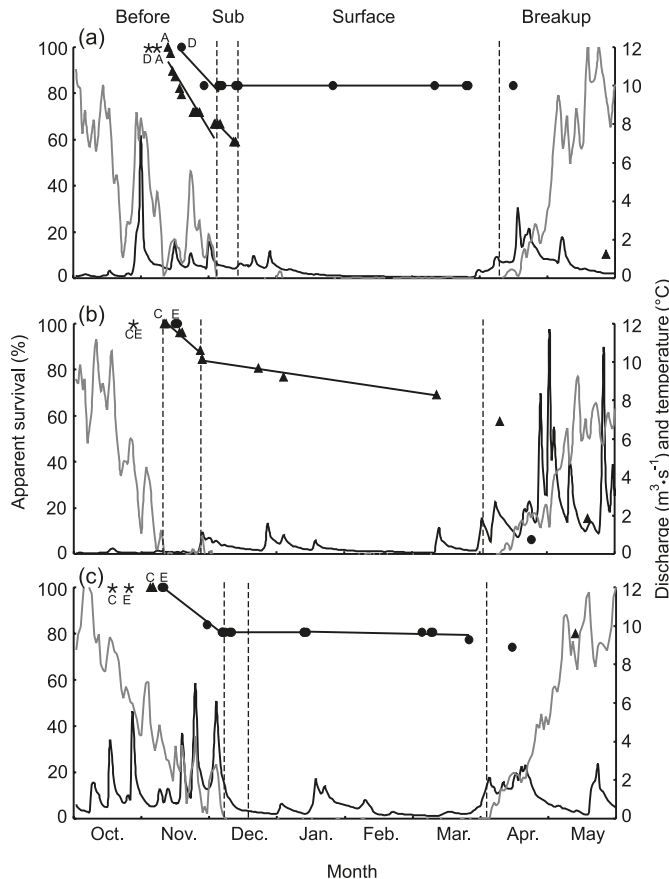
ble if the surface ice was present (owing to insufficient detection distance). These two fish were never detected in daylight if surface ice precluded maneuvering of the antenna, but were always detected adjacent to the logjam if the trackings were also carried out at night, when the fish moved away from the shelter. For these situations (two fish on three dates; $n = 6$), the protocol suggested by Steingrímsson and Grant (2003) was followed. That is, as the two parr were not observed during a particular tracking survey date (daytime data only) but were recovered during both the preceding and the subsequent tracking survey date, the fish were assumed to have remained in the study site. Tag loss was not expected to contribute to fish loss because use of sutures has been shown to effectively eliminate any tag loss (Roussel et al. 2000).

Definitions of ecological measures and statistical analysis

The decline in the number of PIT-tagged salmon parr remaining within the studied sites was reported as apparent survival (sensu Olsen and Vøllestad 2001). The measure represents an underestimate of the true overall survival because the ultimate fate of salmon parr that emigrated from the studied site was unknown (i.e., dead or alive) in most cases. Since the different periods of winter used in this study were variable in duration (Table 1), instantaneous daily loss rates were calculated to facilitate comparisons and to make data more applicable in areas where similar physical conditions occur but the duration of the periods may further vary. Instantaneous daily loss rate (M_i) was calculated for each period as $[\ln(N_{\text{initial}}) - \ln(N_{\text{final}})] \times (D_{\text{final}} - D_{\text{initial}})^{-1}$, where N is the number of parr observed alive, and D is day of year. Again, instantaneous daily loss rate cannot be interpreted as a rate of fish mortality but rather as a daily rate to which tagged fish were no longer found within a study site. Within-site mortality was inferred from a prolonged cessation of movements, and was confirmed in spring during the final tracking survey, by disturbing the substrate to determine if the tagged parr was still alive. In addition, stream banks were searched for tags in spring to document additional mortalities.

The population used for the apparent survival analysis was defined as the number of tagged salmon parr found at each study site during the first active tracking survey, and therefore, tagged salmon parr that were never located within

Fig. 2. Stream discharge (black line), water temperature (gray line), tagging dates (*) in different sites of Catamaran Brook, and apparent survival of Atlantic salmon parr during different periods of the three winters: (a) = 2003–2004, (b) = 2004–2005, (c) = 2005–2006. Triangles and circles represent the data collected from Lower and Middle Reach, respectively, and the letter above the symbol refers to the study site as described in Table 2. Dashed vertical lines represent the different periods of winter (“Before” = before ice; “Sub” = subsurface ice; “Surface” = surface ice; “Breakup” = after ice breakup). Data points within the same period are connected with a simple linear regression line to make the interpretation of the survival pattern more comprehensive. The stream discharge is shown for the site D. Note that no before-ice data is shown in panel B because of early freeze-up.



study sites were omitted from the subsequent analysis of apparent survival (see Results). This was necessary as a precautionary approach because of the pervasive capture method (i.e., electrofishing) and tagging procedure may have artificially increased emigration initially (Nordwall 1999; Brakensiek and Hankin 2007). Handling-related emigration has been shown to mostly occur within 24 h from PIT tagging (Enders et al. 2007). Tagging-related mortality mostly occurs up to 3–5 days after PIT tagging (Sigourney et al. 2005; Bateman and Gresswell 2006), and the majority of displaced fish settle in new areas in less than 3 days (Armstrong et al. 1997). For these reasons, any tagging-induced bias in apparent survival calculations should have been minimized, as the first active tracking of fish followed only after 7–23 days after tagging.

Mean values throughout this article are reported with the corresponding standard error (SE). If multiple group means were compared, logarithmic transformations were used to normalize the data if deemed necessary. The effect of year (Y) was used as a random variable and reach (R) as a fixed factor in analyses. In comparisons examining the parr status (S) as being present or absent, the status was used as a fixed factor in the analyses. Post hoc comparisons were carried out using applicable Tukey-type tests (Zar 1999), and arcsine transformation was applied if post hoc comparisons involved proportions. Data collected from site D were excluded from the statistical analysis for apparent survival because of low sample size ($n = 6$). Continuous data collection from sites E (2004–2005) and C (2005–2006) was not possible, and therefore the apparent survival during each period of winter could not be assessed (i.e., data was limited to autumn–spring survival data). The propensity of emigration for mature versus nonmature parr was examined using odds ratios (Sokal and Rohlf 1995). The odds ratios were tested for homogeneity across the study sites and years using Tarone’s χ^2 test; since the odds ratios were considered homogeneous ($\chi^2 = 2.7$, $df = 5$, $P > 0.05$), the subsequent significance of overall average odds ratio was based on the Mantel–Haenszel estimate ω_{MH} (Sokal and Rohlf 1995). When the exact timing of emigration was known from stationary antennae, its relationship to discharge (Q) and water temperature (T) was examined using logistic regression. The goodness-of-fit of the models was based on the Hosmer–Lemeshow (χ^2_{HL}) test. The relative fit of each of the a priori candidate models was assessed using Akaike’s information criterion (AIC_c) values adjusted for small sample bias (Burnham and Anderson 2002). The relative plausibility of each model was further based on Akaike weights, w_i , so that the most plausible model (i.e., Kullback–Leibler best model; K-L) had the largest weight (Burnham and Anderson 2002). The 95% confidence set of the actual K-L best model was defined as a group of models, arranged by their Akaike weight from largest to smallest, for which the sum of Akaike weights exceeded 0.95. The relative importance of each predictor variable was assessed by summing the w_i values across the models in the confidence set where each variable occurred and was considered significant based on Wald’s measure. The statistical analyses were performed using SPSS 14.0 software (SPSS Inc., Chicago, Illinois).

Results

Apparent survival and observed mortality

Population dynamics before first active tracking survey

The initial decline in the number of tagged salmon parr during the period between tagging and the first active tracking survey was relatively high in all 3 years (Table 5). The decline was similar between the two stream reaches in each year (Fisher exact, $P > 0.05$ for all years). However, interannual differences in the proportionate decline were observed in the Lower Reach, but not in the Middle Reach (Table 5; Lower Reach, $G = 9.37$, $df = 2$, $P < 0.01$; Middle Reach, $G = 3.84$, $df = 2$, $P > 0.05$). A nonquantitative analysis suggested a relationship between high stream discharge fluctuations and the intensity in decline in the number of salmon

Table 4. Number of separate dates during different periods of winter when active tracking surveys were carried out in each study site of Catamaran Brook, New Brunswick, and the total number of active tracking surveys carried out at each site.

Tracking period	No. of tracking dates at each study site (year)					
	A (2003–2004)	C (2004–2005)	C (2005–2006)	D (2003–2004)	E (2004–2005)	E (2005–2006)
Before ice	10	1	2	2	0	3
Subsurface ice	5	4	0	4	2	4
Surface ice	0	0	0	5	0	6
After breakup	1	2	1	1	1	2
Total trackings*	34	16	9	27	10	47

*Tracking of tagged fish occurred multiple times within most dates; these data are considered elsewhere (Linnansaari 2009).

Table 5. The percentage of absent tagged Atlantic salmon parr before first active tracking survey in the two reaches of Catamaran Brook.

	2003–2004	2004–2005	2005–2006
Lower Reach	40.4ab (57)	27.8a (36)	64.5b (31)
Middle Reach	57.1a (28)	30.4a (23)	41.5a (53)

Note: Numbers in parentheses refer to the number of salmon parr initially tagged each year. The values sharing the same letter within each row were not significantly different from each other (Tukey-type post hoc test using arcsine-transformed data; $P > 0.05$).

parr. The lowest decline in both reaches occurred during the winter of 2004–2005, which was a year with **stable** low discharge during the time period from tagging to the first tracking survey (Fig. 2). The highest decline in the number of tagged salmon parr in the Lower Reach was observed in 2005–2006 when a high discharge event occurred between the tagging and first tracking date (Fig. 2), whereas the highest decline in the Middle Reach occurred in 2003–2004 when the tagged salmon parr were released during relatively high stream flows immediately following a high discharge event (Fig. 2).

The decline in the number of tagged salmon parr before the first tracking survey also depended on precocious maturity. The likelihood of mature parr being absent from the study area before the first tracking survey was 2.8 times that of immature parr ($\omega_{MH} = 2.81$, $\chi^2_{MH} = 8.04$, $df = 1$, $P < 0.01$). However, there was no significant difference between absent and resident parr with respect to size (L_F or mass), condition factor (Fulton's K ; Ricker 1975) or W_T/W_F ratio (three-factor $_{(Y,R,S)}$ analysis of variance (ANOVA), all main effects and interaction terms for all four variables $P > 0.05$).

Population dynamics during the monitored period

Apparent survival was lowest during the before-ice period in autumn, and the decline in the number of tagged salmon parr ranged from 16.7% to 33.3% (26.3% for data pooled across sites and years; Table 6, Fig. 2). Apparent survival was better during both subsurface and surface ice periods, the decline in the number of tagged salmon parr ranging from 0% to 15.4% (pooled data across sites and years; 6.9% and 10.0%, respectively; Table 6, Fig. 2). Statistically, the decline in the number of tagged Atlantic salmon parr was significantly higher during before-ice than subsurface ice period (Fisher's exact test with Bonferroni adjusted P ; site A, 2003–2004, $P = 0.020$; site E, 2005–2006, $P = 0.048$), whereas it was similar between subsurface and sur-

face ice periods (site C, 2004–2005, $P = 1.000$; site E, 2005–2006, $P = 0.480$). In total, the tagged salmon parr population declined 16.7%–42.3% over winter (Table 6), but the apparent survival was statistically similar between years ($G = 2.51$, $df = 2$, $P = 0.286$); estimated total decline over winter was 31.7% for the pooled data (i.e., apparent survival of 68.3%) considering the study sites that could be assessed soon after ice breakup.

The mean instantaneous daily loss rate was highest during the before-ice period (Table 6). The fact that the period with surface ice lasted longer than the other winter periods in Catamaran Brook in each study year (Fig. 2) contributed to the low mean instantaneous daily loss rate during surface ice period (Table 6).

The observed within-site mortality during winter was low (pooled data 2003–2006; $n = 8$, 4.4% of the parr observed at least once). On occasion the mortality could be related to predation (i.e., tags recovered from the stream banks, $n = 3$) that occurred before ice cover formed. Of the remaining known mortalities, four took place during surface ice or spring period for unknown reasons, and the timing or the reason for one mortality could not be determined.

Factors affecting apparent survival and observed emigration

The size of the tagged salmon parr in autumn did not affect the probability of remaining within a study site over winter. No statistical differences were observed in L_F , mass, K , or W_T/W_F ratio between the parr that disappeared over winter and those that remained resident within study sites until spring (three-factor $_{(Y,R,S)}$ ANOVA, $P > 0.05$ for all main effects and interaction terms for all four variables). Occasionally, emigration (or involuntary displacement) was influenced by localized "catastrophic events". An example of this was a release and redistribution of a logjam in November 2005 that led to a mesohabitat shift in site E; a section of 20 m² of slow flowing glide habitat was transformed into fast flowing riffle. During the logjam release, all tagged fish ($n = 3$) in the affected area emigrated, whereas no emigration occurred from other parts of the study site regardless of the relatively high discharge during the event.

Stream discharge (Q) proved to be a much more important predictor to estimate the probability of juvenile salmon emigration in Catamaran Brook in winter than stream temperature (T) or their interaction $Q \times T$ (relative variable importance 0.87 for Q , 0.08 for $Q \times T$, and 0.0 for T). All except one of the supported logistic regression models included discharge as a plausible predictor (Table 7). How-

Table 6. Proportional decline of PIT-tagged Atlantic salmon parr population (%) and the instantaneous daily loss rates (in parentheses) in each study site in Catamaran Brook during different periods of winter, with the mean (and standard error, SE) instantaneous daily loss rate (calculated across the study sites) within each period of winter.

	Study site (year)				Mean (SE) loss rate
	A (2003–2004) [n = 39]	D (2003–2004)* [n = 6]	C (2004–2005) [n = 26]	E (2005–2006) [n = 31]	
Before ice	33.3 (0.019)	16.7 (0.011)	NA	19.4 (0.008)	0.014 (0.006)
Subsurface ice	7.7 (0.014)	0.0 (0.000)	15.4 (0.010)	0.0 (0.000)	0.008 (0.004)
Surface ice	NA	0.0 (0.000)	15.4 (0.002)	3.2 (0.000)	0.001 (0.001)
Total winter decline	NA	16.7 (0.001)	42.3 (0.004)	25.8 (0.002)	0.002 (0.001)

Note: Values in brackets (*n*) represent number of tagged parr during first tracking survey; NA, data not available. Resulting total decline of PIT-tagged Atlantic salmon parr population at the end of winter is shown.

*The values from site D are not used to calculate the mean because of the low number of observations.

ever, goodness-of-fit was not very strong for any of the models (P for χ^2_{HL} ranging from 0.06 to 0.36), and there was a large amount of unexplained variability in all models (Nagelkerke pseudo- r^2 ranged from 0.18 to 0.23).

The response of salmon parr to two midwinter moderate discharge events (relative to winter base flow) was analyzed in some detail. The first midwinter flood started 25 December 2004; the second midwinter ice breakup and flood started 15 January 2006; Fig. 2). Based on stationary antenna data, only one tagged salmon parr emigrated from site C during the 2004 event (7 days after the peak flood). No changes in apparent survival were observed during the 2006 event based on active tracking on 19 January 2006 in parts of study site E that could safely be tracked (~35% of the site).

The extent of emigration beyond study site E was assessed in the spring of 2006 with the two-person antenna. Of the tagged salmon parr that were not encountered within study site E after ice breakup, a significantly higher proportion of the immature parr (73%) were found compared with mature parr (9%; Fisher's exact test; $P = 0.008$). Every parr found beyond the study site ($n = 9$) was alive. Furthest fish were found 285 m upstream and 290 m downstream from the study site. Based on the stationary antennae data in the autumn 2003–2004 and winter 2004–2005, it was apparent that longer distance emigration (i.e., >5 km) occurred, as a few parr tagged in the Middle Reach were observed in the Lower Reach emigrating out from Catamaran Brook during autumn ($n = 1$) and midwinter ($n = 2$). All these three parr were of a size that potentially smoltified in spring (L_F : 107–119 mm).

Discussion

The apparent survival of Atlantic salmon parr was not static throughout the winter in Catamaran Brook. Lowest apparent survival was observed in late autumn – early winter before ice formed and coincided with a rapid decline in water temperature and fluctuation in stream discharge. Apparent survival showed more variability during the period dominated by subsurface ice and further improved when surface ice was prevailing. Actual (observed) mortality within

the study sites was low during all three winters. Although winter, as an entity, is sometimes referred to as a critical period for survival for stream salmonids (Cunjak and Therrien 1998; Bradford et al. 2001), the current study emphasized the fact that higher temporal resolution may be necessary to be able to correctly predict possible consequences of anthropogenic impacts in future. For example, if winter is considered as a “bottleneck” for juvenile stream salmonids, the current scenarios on global warming that predict shorter periods with ice and snow in the future for all of Europe and most of North America (Christensen et al. 2007) may be seen as beneficial for salmonid stocks. However, the current study showed that shortening of the ice-affected period of winter would not positively affect apparent survival of juvenile Atlantic salmon. Furthermore, it is possible that the ice-covered period of the year will be replaced with conditions similar to those observed during late autumn – early winter (Prowse and Beltaos 2002), a change that would very likely cause repercussions in terms of declining apparent survival of juvenile Atlantic salmon.

The current study is by no means the first one to report a decline in apparent survival in juvenile stream salmonid populations in late autumn – early winter. Autumnal decline in density of juvenile salmonids seems a widely observed phenomenon (Youngson et al. 1983; Carlson and Letcher 2003; Linnansaari et al. 2009). Also the “winter decline” data in Letcher et al. (2002) shows the steepest decline in the estimated apparent survival of Atlantic salmon during before-ice conditions in autumn in West Brook, Massachusetts, USA. To our knowledge, however, this is the first study where sampling (i.e., tracking) was frequent enough to accurately distinguish and quantify the relative severity of different periods of winter in terms of apparent survival of tagged salmon parr in an ice-covered natural stream. This was also the first to document that the autumnal before-ice period may be the time of the most severe decline in apparent survival.

In Catamaran Brook, many reasons could have contributed to the observed decline in apparent survival in autumn. First, precocious maturity was strongly associated with increased emigration from the study sites coincident with the approaching spawning period. Maturity-related autumn dis-

Table 7. The comparison of logistic regression models for predicting the probability of emigration (P_{emigr}) of salmon parr and the parameter estimates \pm standard error (SE) for each supported model.

Model	AIC _c	w_i	Evidence				
			ratio	Q	T	$Q \times T$	α
$Z_{(Q,\alpha)}$ *	96.9	0.348	1	1.29 \pm 0.34	—	—	-3.02 \pm 0.49
$Z_{(Q,Q \times T,\alpha)}$ *	97.7	0.228	1.5	0.94 \pm 0.46	—	0.15 \pm 0.14	-2.85 \pm 0.50
$Z_{(Q,T,\alpha)}$ *	97.9	0.215	1.6	1.06 \pm 0.40	0.26 \pm 0.25	—	-2.97 \pm 0.49
$Z_{(Q,T,Q \times T,\alpha)}$ *	99.8	0.081	4.3	0.96 \pm 0.48	0.06 \pm 0.61	0.12 \pm 0.34	-2.88 \pm 0.55
$Z_{(Q \times T,\alpha)}$ *	99.8	0.081	4.3	—	—	0.38 \pm 0.11	-2.14 \pm 0.31
$Z_{(T,Q \times T,\alpha)}$	101.6	0.033	10.6	—	—	—	—
$Z_{(T,\alpha)}$	103.3	0.014	24.3	—	—	—	—
$Z_{(\alpha)}$	111.9	0.000	1854.6	—	—	—	—

Note: AIC_c, Akaike's information criterion corrected for small samples; w_i , Akaike weights; Q , stream discharge; T , water temperature; α , estimated constant for each model. Interpretation of w_i is considered as the relative plausibility of candidate models whereas evidence ratio describes the likelihood of the best model being correct over the model in comparison. $P_{\text{emigr}} = 1/[1 + e^{-Z}]$, where $Z = \alpha + \beta_1 X_1 + \dots + \beta_j X_j$, and $X_{1..j}$ are fitted variables, and α and $\beta_{1..j}$ are estimated parameters. Significant variables (Wald's measure, $P < 0.05$) in each model are shown underlined.

*Models within the confidence set.

persal has also been observed in other studies (e.g., Buck and Youngson 1982; Whalen et al. 1999; Linnansaari et al. 2009). Second, the large interannual variability in the estimates of early winter apparent survival suggested that environmental factors might be controlling the survival pattern. In particular, stream discharge seemed to partly explain the phenomenon in Catamaran Brook. In addition to the evidence from the stationary antennae and the logistic regression models where discharge was supported as an important variable, the apparent survival following tagging was highest during the year with the most **stable** stream discharge, whereas largest amount of tagged salmon parr were absent when the release of the fish coincided with high flow events. However, no threshold size for a discharge event triggering emigration could be established. Certainly, the moderate discharge events in midwinter did not cause decline in apparent survival. Therefore, it seemed that the **lowered apparent survival was linked to frequent fluctuation of flow rather than the absolute magnitude of discharge**. Earlier research has shown that early winter period may be energetically demanding for juvenile salmonids, and acclimatization to changing conditions may lead to metabolic deficiencies (Cunjak and Power 1987; Cunjak et al. 1987; Cunjak 1988). The interplay between possible development of metabolic deficiency and lower apparent survival during acclimatization period in early winter warrants further research.

Production of subsurface ice (frazil ice, anchor ice) did not cause drastic decline in apparent survival in Catamaran Brook during any of the three study winters. Although some emigration was observed, the apparent survival was better than during the before-ice period for all studied years. Moreover, no within-site mortality was observed during the subsurface ice period, and it seems that mortality by means of frazil crystals clogging the mouth and gills of fish (Tack 1938; see also Brown et al. 1993) may be a relatively rare phenomenon. Many studies have reported immediate escape responses (Brown and Mackay 1995), large-scale emigration or redistribution (Jakober et al. 1998; Whalen et al. 1999), habitat exclusion (Maciolek and Needham 1952; Stickler et al. 2007), and even mortality (Bradford et al. 2001) for various salmonid populations once subsurface ice conditions occur; hence, such conditions have been considered to be

unsuitable for stream salmonids. By contrast, Roussel et al. (2004), working also in Catamaran Brook, observed high site fidelity during anchor ice events especially in riffle habitats, but the observations were based on a small sample size. In the present study, we followed 83 individuals during multiple, very severe anchor ice events, and our results corroborate those of Roussel et al. (2004). It was evident that the relatively small-sized juvenile salmon that we tracked in the current study were able to find adequate shelter within the interstices of coarse substrate material in Catamaran Brook. Salmon parr are able to bury themselves under 15–20 cm layer of stones (Erkinaro et al. 1994) where the (hyporheic) water temperature is elevated to a level where subsurface ice does not occur (i.e., >1 °C; Caissie and Giberson 2003). Heggenes et al. (1993) suggested that large-sized salmonids (i.e., >25 cm) may not be able to find suitable interstitial cover and therefore adopt different behavioural tactics in winter, including aggregation into pool habitats or emigration. Thus, the contrasting response of salmon parr to subsurface ice between this and some of the former studies (Brown and Mackay 1995; Jakober et al. 1998; Brown 1999) may be a consequence of differences in body size (mean of 8.9–11.5 cm in the current study vs. >25 cm in above mentioned studies) and the consequent ability to find suitable cover during subsurface ice formation. However, the reasons for interannual variability in the proportionate decline in fish numbers during subsurface ice period warrants more research and may be caused by the physical characteristics of anchor ice (Stickler and Alfredsen 2009).

Apparent survival was the highest during the period dominated by surface ice, and the instantaneous loss rate during the period with surface ice was similar to the rate in a regulated ice-covered stream in Norway (0.002 vs. 0.001 in the current study; Linnansaari et al. 2009). Although midwinter is reported to be a period of the year that may limit the production of Atlantic salmon parr because of a low minimum discharge and subsequent limitation in the amount of suitable rearing habitat (Gibson and Myers 1988; Hvidsten 1993), it seemed that the stability of environmental conditions during the ice-covered period of winter overruled possible drawbacks. Loss of wetted area was minimal in the current study, and tagged Atlantic salmon parr were able to

remain very close to their original locations throughout the winter. Moreover, the relatively low density of conspecifics (that might compete for available shelters) further facilitated finding a new location in close proximity of the original location if the original areas became unsuitable (e.g., dewatered). Simulated surface ice cover has been shown to positively affect the energy budget of salmon parr (Finstad et al. 2004b), which indicates that high fidelity can be expected during midwinter, although rarely documented in experiments in situ. Nevertheless, it has to be kept in mind that energy reserves of juvenile salmonids tend to decrease throughout the winter (Cunjak 1988; Næsje et al. 2006), and the effects (e.g., “death toll”) of wintertime carry-on metabolic decline may be realized only after the conditions require higher energetic expenditure, like the period during and immediately after ice breakup. Such speculation is supported by observations from Norway where Finstad et al. (2004a) detected greater mortality of Atlantic salmon juveniles with low energy reserves on two different occasions during a 3-year study; both occasions occurred late winter – spring coincident with temperature–discharge fluctuation.

Overall, the estimate of apparent survival over the whole winter in this study fell within the wide range of survival estimates previously reported for juvenile stream salmonids (Huusko et al. 2007). However, low (actual) within-site mortality throughout the three studied winters and the fact that majority of the emigrant immature parr were re-encountered alive in the two-person antenna survey extended beyond the study site E in the Middle Reach in the spring of 2006 lead us believe that the decreasing number of tagged salmon parr in the studied sites was, at least initially, mainly due to emigration rather than mortality. Regardless of the fact whether the decline of tagged salmon parr was due to actual mortality, it appears that substantial decline in apparent survival of salmon parr must occur also during other seasons than winter in Catamaran Brook, as the annual survival estimates have been previously reported to be only 12.9% for comparable age group (Cunjak and Therrien 1998). Indeed, recent review articles on overwinter survival of stream-dwelling juvenile salmonids do not support the concept that winter should be automatically considered as a specific bottleneck period for survival in temperate areas (Huusko et al. 2007; Carlson et al. 2008).

In conclusion, our data suggest that while a definite decline in apparent survival occurred in winter in Catamaran Brook, the apparent survival of Atlantic salmon parr may not be static throughout the winter in streams where different physical (ice) conditions are experienced. The decline in apparent survival in the current study was most pronounced prior to ice formation but was relatively high and stable especially during the period affected by surface ice. With increasing anthropogenic impacts affecting fluvial biota, it is of crucial importance to continue to study the population dynamics of juvenile salmonids at the subperiod scale during winter in the future.

Acknowledgements

The stream temperature data were provided by Daniel Caissie, Fisheries and Oceans Canada, Moncton, New Brunswick, and the discharge data by Environment Canada's Water Survey of Canada Office in Fredericton, New Brun-

wick. The authors also thank Aaron Fraser for assistance during the fieldwork and for providing the juvenile salmon density estimates. Tor Næsje and two anonymous reviewers provided helpful advice to improve the quality of this article. This paper is a contribution number 106 of the Catamaran Brook Habitat Research Project and is a part of “Effects of winter and ice conditions on the behavior and habitat selection of juvenile Atlantic salmon” research consortium of the Wild Salmon Research Program funded by the Norwegian Research Council (grant 147031/720). Partial funding for the study stemmed from the Canada Research Chairs Program for R.A.C. Jack T.H. Fenety scholarship (Miramichi Salmon Association), John S. Little Fellowship, and Emil Aaltonen Foundation provided additional financial support for T.L.

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