Landscape controls on boulder-rich, winter habitat availability and their effects on Atlantic salmon (*Salmo salar*) parr abundance in two fifth-order mountain streams

M. Coulombe-Pontbriand and Michel Lapointe

Abstract: We test the effect at river reach and segment scales of landscape controls on the distribution of Atlantic salmon (*Salmo salar*) parr densities, as well as associated variations in boulder (diameter ≥ 256 mm) abundance and potential overwintering habitat. This study encompasses data from 45 km of fifth-order mainstem channels along two neighbouring river catchments in the Gaspé region, Québec. At both scales, winter habitat availability was correlated with boulder availability. At the river segment scale (1–5 km), parr densities significantly correlated ($P < 0.05$) with boulder availability along the Bonaventure River, which presented significant intersegment variations in boulder abundances. In contrast, segment-scale boulder and parr abundances were uniformly low along the Petite Cascapédia River. At the reach scale (600 m), positive but less strongly significant boulder – parr abundance correlations were observed in both the Bonaventure and Petite Cascapédia rivers. Spatial variations in boulder abundances in these systems reflected variations in the degree of channel to valley walls coupling and imposed channel formative shear stresses. In similarly boulder-poor segments with comparable fry abundances, parr abundances were significantly greater along the Bonaventure than the Petite Cascapédia River, possibly because of the presence in the former system of nearby boulder-rich refugia segments.

Résumé : Nous avons vérifié à l'échelle de la section et du segment de rivière les effets des facteurs de contrôle du paysage sur la répartition des densités de tacons du saumon de l'Atlantique (*Salmo salar*), de même que les variations associées dans l'abondance des blocs rocheux (diamètre ≥ 256 mm) et dans l'habitat potentiel d'hiver du saumon. Notre étude rassemble des données provenant de 45 km de chenaux principaux de cinquième ordre dans deux bassins versants voisins de Gaspésie, Québec. Aux deux échelles, la disponibilité de l'habitat d'hiver est en corrélation avec la disponibilité des blocs rocheux. À l'échelle du segment de rivière (1–5 km), la densité des tacons est en corrélation significative ($P < 0{,}05$) avec la disponibilité des blocs rocheux le long de la Bonaventure qui présente des variations significatives d'abondance des blocs d'un segment à un autre. En revanche, le long de la Petite Cascapédia, les abondances de blocs et de tacons sont uniformément faibles à l'échelle du segment. À l'échelle de la section (600 m), il existe des corrélations positives, mais moins fortement significatives, entre les abondances des blocs rocheux et de tacons, tant dans la Bonaventure que dans la Petite Cascapédia. Les variations spatiales de l'abondance de blocs rocheux dans ces systèmes sont le reflet des variations du degré de connexion entre le chenal et les murs de la vallée et des contraintes de cisaillement imposées qui sont impliquées dans la formation du chenal. Dans des segments similaires pauvres en blocs rocheux qui possèdent des abondances comparables d'alevins, l'abondance de tacons est significativement supérieure le long de la Bonaventure que le long de la Petite Cascapédia, probablement à cause de la proximité dans la première de segments riches en blocs rocheux qui servent de refuges.

[Traduit par la Rédaction]

Introduction

Because large cobble and boulder substrate is an essential component of rearing, sheltering, and overwintering habitat of Atlantic salmon (*Salmo salar*) parr (ages 1^+ and above, here designated 1^{++}), it has been speculated that in some river systems, long reaches with little substrate coarser than smaller cobbles could be limiting to parr production (Chapman 1966; Cunjak 1996). If this hypothesis is correct, subtle differences in valley and river geomorphology that affect substrate coarseness could account for occasionally striking contrasts in parr abundance between rivers located in the

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same region that otherwise have similar spawning habitat, primary productivity, and overall watershed characteristics (size, hydrology, and geological history). This paper investigates associations at two spatial scales among patterns in 1^{++} parr densities, boulder (particles ≥256 mm) abundances, and availability of winter habitat (defined through a combination of hydraulic and sedimentological criteria) over 45 km of two adjacent fifth-order rivers with similar salmon 0^{+} fry but very contrasted 1^{++} parr abundances. The paper also analyses the nature and spatial scales of the landscape factors that control coarse substrate and par abundance patterns.

The importance of coarse substrate for parr habitat has been confirmed in a number of studies. While feeding during the rearing season, 1^{++} parr generally maintain position behind protruding, larger cobble and boulder size "home stones" at the proximity of fast currents where drifting prey are more abundant (Wankowski and Thorpe 1979; Rimmer et al. 1984; Morantz et al. 1987). Cobbles and boulders also provide cover for sheltering from predation (Valdimarsson and Metcalfe 1998). As water temperature cools down below about 8 °C in autumn and winter, juvenile salmonids switch to a winter, nocturnal behaviour, seeking shelter in large interstices under large substrate during daytime and emerging during nighttime (Cunjak 1988; Heggenes et al. 1993; Contor and Griffith 1995). The effect of a scarcity of coarse substrate on limiting winter habitat and carrying capacity of streams may be particularly strong in regions where winter conditions are severe, such as eastern Canada (Cunjak 1996; Cunjak and Therrien 1998; Cunjak et al. 1998).

Benda et al. (1992) demonstrated the importance of large-scale landscape processes (and their control on the location of boulder-rich and boulder-poor reaches) in structuring salmonid habitat in a river basin. Rice et al. (2001) argued that in mountain valleys, major mesoscale units of stream habitat variation are sedimentary links, defined as lengths of river valley over which substrate size, substrate mobility, and channel geometry change in a predictable way between node points where coarser sediments are reinjected into the river by tributaries or valley side landslides. However, relationships between coarse substrate availability and parr abundance, although well documented at the microscale level (through habitat preferences within a given reach), have not been statistically tested at larger scales across river reaches and river segments. In the study systems, a reach is defined as a river section measuring 600 m, i.e., measuring approximately 10 times the bankfull channel width and including approximately two pool–riffle units (Frissel et al. 1986). Channel segments are defined as the longest river sections (1–5 km or 10–60 times the bankfull channel width) with relatively homogeneous geomorphic character in terms of discharge, substrate calibre, channel slope, and degree of lateral valley confinement.

Two major hypotheses are tested in this paper. The first hypothesis is that along a total length of 45 km of two fifth-order mainstem salmon rivers with similar 0^{+} fry abundances, 1^{++} parr density patterns correlate at the river reach and segment scales with the availability of coarse (boulder) substrate and winter habitat. The second hypothesis is that in these two mountain valley systems, spatial variations in boulder abundance and winter habitat can be predicted from geomorphic variables reflecting the degree of lateral confinement by valley walls (valley to channel width ratio, bankfull shear stresses, and channel shifting rates) and associated lateral supply of coarse substrate.

Materials and methods

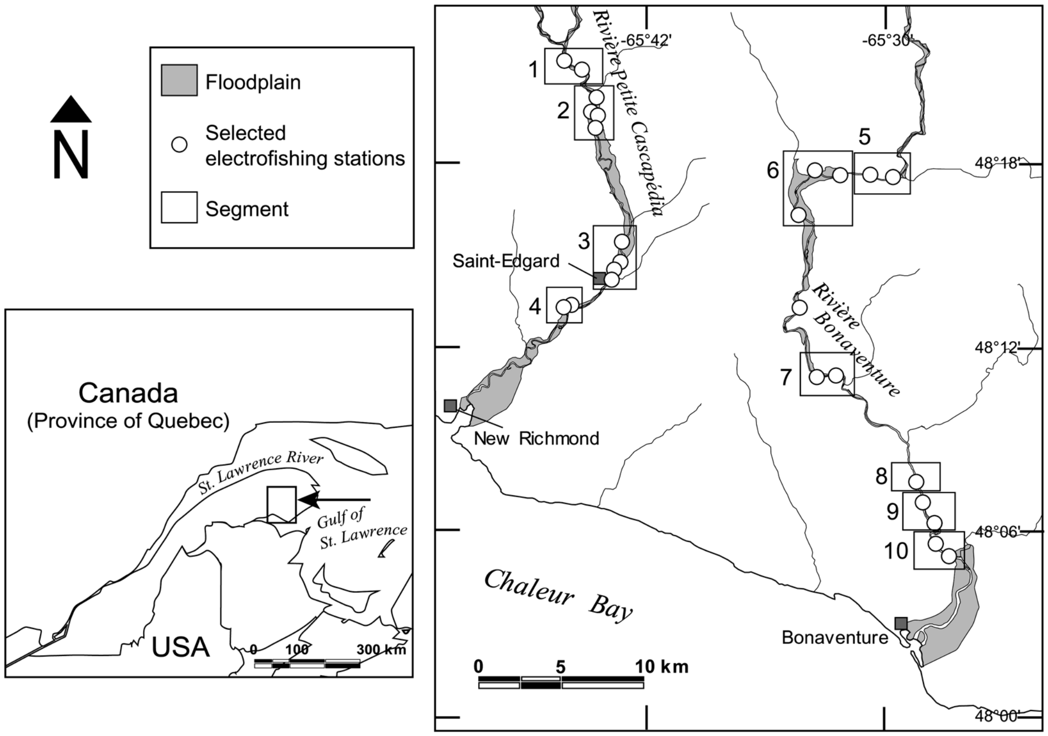
Study sites

The study was performed in the main stems (Fig. 1) of two neighbouring cobble-bed rivers of the Gaspé Peninsula, Province of Quebec, with contrasting abundances of parr and adult Atlantic salmon. The Petite Cascapédia River produces, on average, about three times fewer adult salmon per square kilometre of accessible potential rearing habitat than does the Bonaventure River (Perron 1992*a*, 1992*b*; Dorais 2000), despite intensive stocking of salmon fry and smolts over the 1980–1997 period. Electrofishing inventories performed by the Quebec Wildlife Agency (Société de la faune et des parcs du Québec, FAPAQ) over 10 years show that average observed 1^{++} parr abundance is seven times lower in the Petite Cascapédia than in the Bonaventure River main stem, although, overall, both river main stems have comparable quality of spawning habitat (based on spawning zone grain size analysis and redd surveys; Coulombe-Pontbriand and Lapointe 2004) and similar 0^{+} fry abundance (FAPAQ, 308 chemin Saint-Edgar, New Richmond, QC G0C 2B0, Canada). In particular, redd counts (done over 2 years) were uncorrelated with either fry or parr counts for the following years at either spatial scale. Differences in food production have been discounted as the probable cause of these contrasts in parr abundances; juveniles found in the Petite Cascapédia River are larger at a given age than those found in the Bonaventure River (Dorais 1997). The dominant fish populations in the study rivers are Atlantic salmon, anadromous and resident brook trout (*Salvelinus fontinalis*), and slimy sculpin (*Cottus cognatus*).

The discrepancy in parr (and adult) abundances is puzzling considering the proximity and general similarity of the adjacent watersheds. Both rivers flow in a general north to south direction from the Shickshock Highlands of the Appalachian Mountains into Chaleur Bay, although fault lines locally disrupt their southerly course. The watersheds cross similar bedrock lithological units, which trend east to west. Folded Ordovician to Devonian mudstone, conglomerate, and limestone underlie the rivers' main stems, whereas granitic and ophiolitic rocks dominate in the headwaters near the Shickshocks Highlands. South of the Shickshocks Highlands, the mainstem valleys of these two rivers are incised 200–300 m into the forested plateaus of an old Appalachian erosion surface. Interfluves are relatively flat and the valleys are either flat bottomed with steep walls or V-shaped. Although interfluves are actively being logged in their upper reaches, lower watersheds are predominantly forested. Discontinuous sandy to gravel–boulder terraces of fluvio-glacial origin locally border the floodplains.

The two fifth-order systems are of comparable scale and both show relatively high hydraulic energy levels (70–150 $W \cdot m^{-2}$ of unit flow power at bankfull stage) and high gravel–cobble transport rates. Bankfull channel widths and mean channel gradients in the two study systems are similar: 60 m and 0.20% for the Petite Cascapédia River and 73 m and 0.23% for the Bonaventure River. Although flow-

Fig. 1. Map of study sites along the Petite Cascapédia River and Bonaventure River, Gaspé Peninsula, Province of Quebec, Canada.



ing in a generally wider valley, discharge in the Petite Cascapédia River is about two thirds of that in the Bonaventure River. At the town of St-Edgard, located 9.5 km from its mouth, the Petite Cascapédia River drains a watershed of 1340 km^2 and has a mean flow of 33 $m^3 \cdot s^{-1}$ (1961–1981). By comparison, the Bonaventure River drains a 1910-km^2 watershed and has a mean flow of 52 $m^3 \cdot s^{-1}$ at the gauging station 17 km from its mouth (1965–1983). Both rivers have unregulated snowmelt-dominated hydraulic regimes.

Glacial history

The strongest impacts of the Pleistocene continental glaciations affecting the study rivers until 10 000 years BP were some valley avulsions rerouting river sections and the deposition of a fluvio-glacial esker along the lower Bonaventure River (in segment 8, Fig. 1). In its lower part, the Bonaventure River is incising into bedrock, apparently shaping a young valley after being rerouted from its ancient path at an unknown point in time, possibly during early Pleistocene glaciations.

Filling of the lower valleys with fluvial and deltaic deposits induced by a marine transgression (high relative sea levels) during a period of isostatic land depression shortly after deglaciation is attested by deltas perched 47 m above sea level 7 km upstream of both rivers' estuaries. The clearly visible braided character of fluvio-glacial terraces found locally along valley segments suggests larger sediment supply and greater peak discharges during the paraglacial period (immediately after the glacial period, Church and Ryder 1972) than during present-day conditions. After isostatic uplift and a decline in relative sea level, the study rivers gradually incised into their paraglacial valley fills, mobilizing large quantities of material that was evacuated to the sea or stored in terraces and floodplains or are still being reworked by rivers. In the current conditions, boulder alluvium does not get transported far from local sources and a significant quantity of large boulders found along the bed of the contemporary river systems is inherited from a more energetic paraglacial environment. Contemporaneous sources of coarse material input in the river systems are the local erosion of fluvio-glacial terraces, bedrock valley walls, and the supply from some tributaries

Channel morphology

There is a typical trend, from low-order to high-order streams in mountainous drainage basins, both in the transition of channel morphologies (Montgomery and Buffington 1997) and in the corresponding salmonid habitat structure (Benda et al. 1992). Typically, streams gradually change from alluvium supply-limited, high-energy headwater channels with boulder bed materials (cascade and step–pool types) to transport-limited, low-energy channels with sandy beds (displaying dune–ripple bedforms). In supply-limited channels, the high transport capacity (shear stresses) of typical high flows rapidly evacuates the limited supply of relatively fine alluvium, exposing a lag of boulder-size material that is mobilized only during rare high flow events. On the contrary, plentiful fine alluvium supply exceeds the lower transport capacity (shear stresses) of transport-limited channels, mantling the bed with fine bed material that is mobilized well below bankfull discharge. In between these states, mountain streams transition through moderate-energy cobble–gravel systems with near-bankfull mobilization threshold (plane bed and pool–riffle types).

The nature of sediment supply likewise exhibits a typical downstream transition. Headwater channels are strongly "coupled" with their narrow, confining valleys in a sediment budget sense and directly receive irregular inputs of sediment materials of all sizes from flanking hillsides through landslides, valley wall erosion, and debris flows. In contrast, downstream channels are relatively uncoupled from their valley sides as they migrate relatively freely on extensive floodplains and mainly and steadily receive large amounts of finer, better-sorted material from fluvial transport processes (Montgomery and Buffington 1997). In many fluvial systems such as the fifth-order main stems of the Petite Cascapédia and Bonaventure rivers, this idealized pattern of downstream change in the geomorphic characteristics of the channels (with theoretically monotonic trends in sediment supply, channel shear stress levels, and degree of confinement) is locally perturbed by a variety of mechanisms. Major basin-scale geomorphic events (valley rerouting, glaciation, and stream pirating) and geological controls (faulting and differential bedrock resistance) can impose valley confinement and lateral sediment coupling in channels of any stream order (Montgomery and Buffington 1997). Rice et al. (2001) described frequent, predictable disturbances in the regular downstream fining of bed material and a decrease in channel energy along mountain river systems associated with point-source recruitment zones of coarse sediment at some tributaries and landslide sites.

Although the two study rivers generally flow over their own gravel–cobble alluvium, in a number of places, they are also confined by valley walls or controlled vertically by outcrops of resistant bedrock (Fig. 1). Most of the Petite Cascapédia River valley is relatively wide (typically 0.5–1 km wide), with channel uncoupled from valley walls, whereas much of the Bonaventure River valley is substantially narrower (under 0.5 km) and displays a higher degree of valley side coupling (Table 1). The Petite Cascapédia River exhibits segments with pool–riffle and forced pool–riffle morphologies (Table 1). In addition to these two channel morphologies, the Bonaventure River also displays higher-energy, more supply-limited plane-bed and bedrock-dominated segments (Montgomery and Buffington 1997). Thus, the main stems of the study rivers overall display contrasting valley and channel morphologies. The possible associations between these geomorphic contrasts and the puzzling discrepancy in 1^{++} parr densities between the study rivers despite similar 0^{+} fry abundances are the main focus of this investigation.

Parr abundance record and selection of study sites

Data on relative 0^{+} fry and 1^{++} parr abundance at a network of fixed sites were available from a database collected from 1986 to 1999 by the Quebec Wildlife Agency, FAPAQ, Direction Régionale de la Gaspésie. This database is intended to monitor relative differences in densities rather than absolute abundances and includes the results of electrofishing counts performed in July or August at the same location over 9 years along the Bonaventure River (1986–1993 and 1999) and over 8 years along the Petite Cascapédia River (1986–1988 and 1990–1994). Sampling was performed in 100-m^2 open stations (5 m wide by 20 m long), typically spaced 1 km apart, well away from zones where fry or smolts were stocked. No stocking of 1^{++} parr occurred in the study rivers during electrofishing years. One electrofishing pass of 15-min duration was performed each year at every station. The same operator accomplished electrofishing in any given year. Hand-held fishnets were used. Stations were located on riffles and bar margins or in runs where flow depth was under 50 cm and velocities under 1 $m \cdot s^{-1}$. These conditions where selected to ensure representation of optimal parr habitat in each stream site (M. Dorais, FAPAQ, 124 1re Avenue Ouest, Sainte-Anne-des-Monts, QC G4V 1C5, Canada, personal communication). Despite the interannual variability observed in electrofishing data at any site, such long-term data sets can yield useful insights into systematic spatial patterns in parr abundance by allowing us to compare multiyear average parr density scores within and between study systems. Because parr strongly compete for prime summer feeding habitat, consistently low parr abundances within such habitats indicate that factors other than feeding habitat availability within the adjoining channel stretch restrict parr survival or site fidelity.

In total, 25 of these electrofishing stations were selected for physical habitat analyses, 12 on the Petite Cascapédia River and 13 on the Bonaventure River, as index sites of the 45 km where detailed river surveys were conducted (Fig. 1). Stations were selected to satisfy two criteria: to be representative of the range of observed parr abundances and to allow grouping of a few consecutive stations into river segments that are homogeneous in terms of channel and valley morphology (relative valley width, slope, boulder density, and channel migration rates). At each of these 25 FAPAQ stations, mean annual parr densities were calculated over the years of record. Although the average interannual coefficient of variation in parr densities sampled at any given station was high (84%), across sites, this interannual variation had a common temporal component so that some stations had generally higher parr abundance, whereas others had consistently lower parr abundance. For example, five out of 12 stations on the Petite Cascapédia River and four out of 13 stations on the Bonaventure River consistently displayed lower parr abundances when compared with all electrofishing counts on the same river (two-tailed t tests, $P < 0.05$). In addition, one station displayed significantly higher than average parr counts in the Petite Cascapédia River, whereas two did in the Bonaventure River ($P < 0.10$).

Measurement of boulder density and overwintering habitat

Boulder density and potential overwintering habitat were measured along 600-m-long reaches centred on the FAPAQ stations, usually extending to adjacent riffle zones both downstream and upstream. This chosen reach length was consistent with other studies (Quinn and Peterson 1996; Piegay et al. 2000). Reaches were then grouped into 1- to 5-km-long river segments with relatively uniform morphology, each containing one to five reaches. Since segments were defined to be relatively uniform, the average of within-segment reach-scale values for parr abundance, winter habitat, and boulder density scores was assigned to each river segment. Such detailed surveys cover 45 km of channel length along the two rivers. Although comparably detailed habitat surveys could not be conducted along the whole main stems of both rivers, cursory habitat observations (and FAPAQ juvenile abundance data) were also available for

Table 1. River segment morphology in the Petite-Cascapédia River (P.C.) and Bonaventure River (Bon.).

River	Segment	Channel type	Valley width (km)	Relative valley width	Channel to valley side coupling
P.C.	1	Forced pool–riffle	0.14	4.1	Moderate to high
P.C.	2	Pool–riffle	0.55	15	Low
P.C.	3	Pool–riffle	0.53	12	Low
P.C.	4	Forced pool–riffle	0.29	6.1	Moderate
Bon.	5	Bedrock	0.08	1.5	High
Bon.	6	Pool–riffle	0.58	9.6	Moderate to low
Bon.	7	Forced pool–riffle	0.23	4.1	Moderate to high
Bon.	8	Plane bed–bedrock	0.09	1.6	High
Bon.	9	Plane bed	0.17	2.3	High
Bon.	10	Forced pool–riffle	0.23	3.6	Moderate to high

Note: Channel type is assessed according to the classification scheme proposed by Montgomery and Buffington (1997). Relative valley widths are given as the ratio between valley width and river width.

river sections adjacent to detailed study segments depicted (Fig. 1).

As a quantitative measure of substrate coarseness, the average number of boulders per square metre of channel bed was preferred over the standard bulk-sampling protocol, as described in Church et al. (1987). The method representatively measured reach-scale boulder availability at the bed surface and therefore relates directly to coarse parr habitat quantity. The number of boulders was counted within the boundaries of 1-m^2 bed surface quadrats evenly distributed at 5-m intervals along transects. A particle touching the borders of the quadrat was counted only when more than 50% of its area was included inside the quadrat. The same operator consistently performed boulder counts, thus avoiding differences resulting from operator bias. Within reaches, transects extending between the limits of channel banks were taken every 50 m for a total of 13 transects per 600-m reach. Within the channel parts located between reaches of a given segment, transect spacing was 200 m. Inaccessible deep pools and unusually high-velocity thalweg zones were avoided (5–10% of the cases). The number of boulders counted in each 1-m^2 parcel was first averaged by transect and then by reach and by segment over 45 km of channel length.

Potential overwintering habitat was assumed to depend on the proximity of both suitable nighttime and daytime winter habitats. As water temperature cools down in autumn and winter, juvenile salmonids switch to a winter behaviour, seeking shelter under large-cobble and boulder clusters typically located near the thalweg, the deepest zone of the channel during daytime (Heggenes 1988; Heggenes et al. 1993; Contor and Griffith 1995). Bed surface areas dominated by large cobbles (>128 mm) or boulders with clean (nonembedded) interstices were considered suitable daytime winter habitat. During winter nights, about two thirds of juvenile salmonids migrate to shallow, low-velocity areas along stream banks to feed (Heggenes et al. 1993; Whalen and Parrish 1999). Nighttime winter habitat was defined as channel bed areas with velocities under 20 cm·s^{-1} and depths under 60 cm based on published overwintering microhabitat preferences (Table 2). Potential overwintering habitat was defined as an area of the channel bed meeting nighttime habitat criteria in proximity to cobble–boulder clusters, either within the area itself or within a 5-m-wide zone surrounding that area. Mean water column velocities were estimated at 60% of the depth with a Pygmy current meter. Substrate was visually classified as suitable or unsuitable for winter habitat. Finally, the total estimated area of potential overwintering habitat in a study reach was divided by the total wetted channel area of that reach, measured during low summer flows, to obtain the percent area of available overwintering habitat.

The presence of a thick ice cover made the assessment of potential winter habitat during the winter season impracticable at the scale of the present study. The total channel area meeting the hydraulic criteria for overwintering habitat was surveyed in the field during summer 2000 low flows assuming, as a first approximation, that the patterns of hydraulic conditions observed in a reach during summer low flows were broadly similar to those occurring during low winter flows. Summer 2000 low discharges were only slightly higher than mean winter discharges: respectively 45% and 30% of mean annual discharge or 9.7% and 6.5% of mean peak discharge (Fig. 2). Ice cover, however, could modify the hydraulic conditions. Low-velocity zones situated at the channel margins are prone to freezing into black or frazil ice (Cunjak et al. 1998). Ice cover presents an increased resistance to water flow and a subsequent reduction in velocities. An overall increase in water elevation can therefore be expected. Thus, in winter, low-velocity nighttime habitat under ice cover may in some reaches be more extensive than indicated by our summer surveys, especially in sectors far from frazil sources.

Measurement of bankfull shear stress and channel migration rates

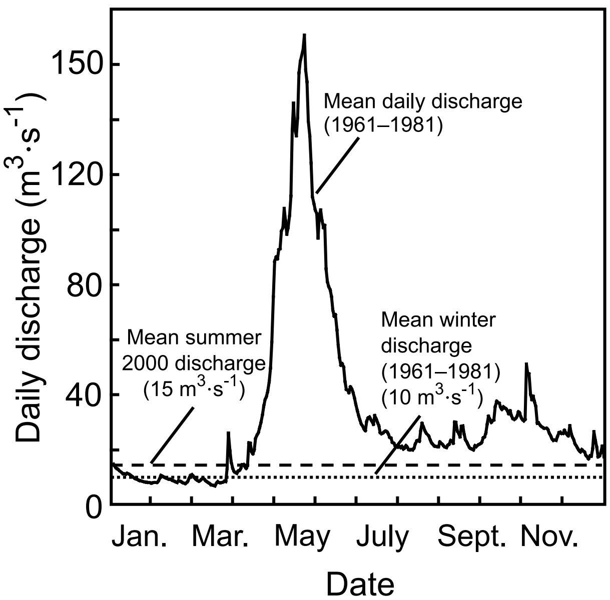
Shear stress represents the average force per unit area applied to bed material and channel forms within a reach by running water and is a common index of energy available for transporting coarse sediment. Shear stresses at or near bankfull discharge are typically associated with a threshold of significant mobilization of bed material and the moulding of the channel perimeter in higher-order plane-bed and pool–riffle channels with cobble–gravel beds (Carling 1988).

Table 2. Review of the microhabitat preferences of Atlantic salmon juveniles during winter.

Reference	Daytime, substrate (cm)	Nighttime Depth (cm)	Nighttime Velocity ($cm \cdot s^{-1}$)
Rimmer et al. 1984	20–40	24–36	<10
Cunjak 1988	16.8–23	40.9–48.9	38.7–45.7
Griffith and Smith 1993	>20	<50	—
Whalen and Parrish 1999	—	15–60	~20

Note: Daytime wintering habitat is defined as cobble–boulder substrate and nighttime habitat as areas of low velocities (<20 $cm \cdot s^{-1}$) and low depths (<60 cm).

Fig. 2. Hydrograph of the Petite Cascapédia River (1961–1981). Mean daily discharges are displayed as a solid line, mean winter discharge (1961–1981) as a dotted line, and mean summer discharge of 2000 (the survey year) as a broken line.



Segment-integrated bankfull shear stress (τ_o) was estimated using Du Boys equation (Lapointe et al. 2000):

$$\tau_o = \rho g D S$$

where ρ is the water density, g is gravitational acceleration, D is channel depth, and S is the channel energy slope. Channel and floodplain topography was surveyed in detailed using a total station and a laser level tied to high-precision control points georeferenced with a differential ground positioning system. Assuming uniform flow conditions, the energy slope of the channel at bankfull stage (S) was approximated by the floodplain slope along the channel margins (Lapointe et al. 2000). Measuring the channel depth (D) for bankfull conditions at riffle crests and averaging by river segment eliminated biases related to difficulties in surveying the deepest pools. This increase in between-segment comparison reliability was, however, gained at the price of a slight but systematic underestimation of the true segment-integrated bankfull shear stresses.

Channel migration was measured at 3-m precision by comparison of multiyear aerial photographs using a Zoom-Transferscope. Bank erosion rates were calculated at the apex of individual channel bends using two series of aerial photographs with a 29-year time span (1963–1992). Photograph scale varied between 1 : 10 000 and 1 : 15 000. Valley bottom width (or floodplain width where high terraces are present) was measured on cross sections from 1 : 20 000 topographical maps aided with stereo-airphoto interpretation.

Results

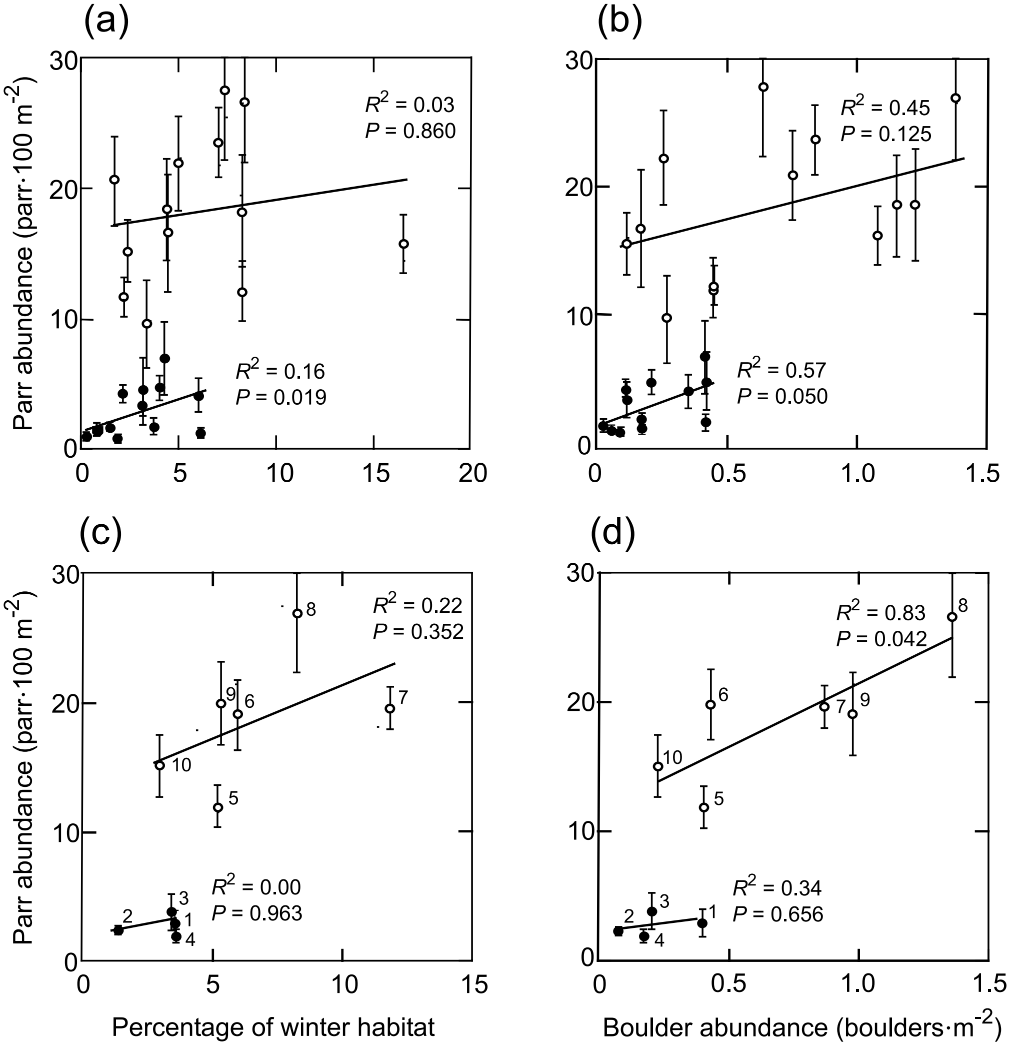
Parr abundance, boulder density, and overwintering habitat

The study reaches of the Petite Cascapédia and Bonaventure rivers present contrasted parr abundance, as well as boulder density and winter habitat scores (Fig. 3). Relative parr abundance scores, in the range 0.6–4.6 parr·100 m^{-2} in the Petite Cascapédia River, are significantly less than the 6.6–26 parr·100 m^{-2} observed in the Bonaventure River (t test, $P < 0.01$). Overall, there are significantly fewer boulders and less winter habitat in the Petite Cascapédia River (0.2 boulder· m^{-2} and 2.8% winter habitat) than in the Bonaventure River (0.7 boulder·m^{-2} and 6.2% winter habitat) (t test, $P < 0.01$).

Pooled data from both rivers (Fig. 3) suggest significant relationships between parr abundance, abundance of boulders, and availability of winter habitat at both scales ($P < 0.01$). However, these pooled associations are mainly driven by the large differences in parr and boulder abundance between the two rivers (Fig. 3, open and solid circles). Relationships between parr abundances and availability of habitat within one population (i.e., inhabiting the main stem of one river) can more easily be interpreted. At the segment scale, parr abundance correlates significantly with boulder abundance in the Bonaventure River ($R^2 = 0.83$, $P = 0.042$) (Fig. 3*d*). Within the Petite Cascapédia River, this relationship is not significant at the segment scale (note that the number of segments in this river, four, is very low). Data trends (Fig. 3) (confirmed by covariance analysis, $P < 0.01$) also reveal a river-specific effect exerted by availability of coarse habitat: even reaches (or segments) with similar low boulder abundances, parr densities are significantly higher on the Bonaventure than on the Petite Cascapédia River (Figs. 3*b* and 3*d*).

Parr abundance does not correlate significantly at the 5% level with the availability of overwintering habitat in either river at either scale, although empirical trends in the relationship are positive (Figs. 3*a* and 3*c*). Winter habitat, as quantified in this study, does not provide a gain in explana-

Fig. 3. Atlantic salmon parr abundance against percentage of wetted channel usable as winter habitat and against boulder abundance at (*a* and *b*) reach and (*c* and *d*) segment scales. Solid circles are data from the Petite Cascapédia River (1986–1993, 1999); open circles are data from the Bonaventure River (1986–1988, 1990–1994). Parr abundances are multiannual averages from electrofishing counts. Vertical bars represent ±1 SE of the mean of multiannual parr abundance.



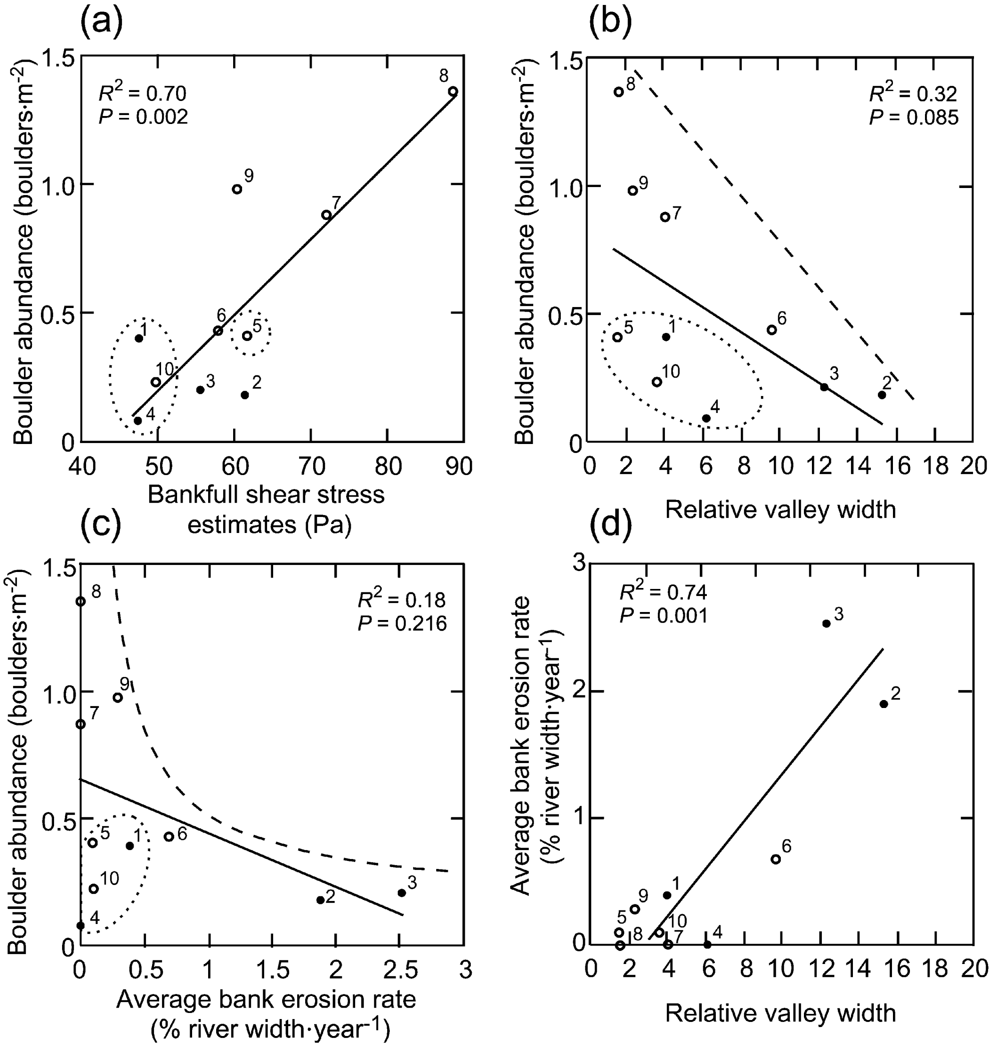
tion of summertime parr abundance patterns over that provided by boulder density. Note that in the study systems, the two predictors are not independent. The availability of overwintering habitat is significantly correlated with boulder abundance at either scale ($R^2 = 0.64$ at the reach scale, $R^2 = 0.78$ at the segment scale). Marginal low-velocity zones are equally widespread along both study systems (*t* test, $P = 0.909$) and the winter habitat scores mostly reflect variations in the availability of coarse substrate for daytime hiding.

Geomorphic controls on the spatial distribution of boulders

The observed patterns of boulder abundances reflect complex, segment-scale differences in the degree of lateral valley confinement and associated variations in coarse substrate supply, channel energy level, and degree of lateral channel instability (Fig. 4). Overall, the Petite Cascapédia River segments display greater valley to river width ratio (i.e., are less laterally confined (Fig. 4*b*)) ($P = 0.058$) and have lower boulder abundance ($P = 0.018$), lower formative shear stress levels ($P = 0.051$), and greater channel shifting rates ($P = 0.096$) than the Bonaventure River segments. Low significance values are due to small number of river segments (10). At the segment scale, boulder abundance is strongly related to channel bankfull shear stress levels across the two systems ($R^2 = 0.70$, $P < 0.01$) (Fig. 4*a*).

Although the relative valley width (Fig. 4*b*) and rates of bank erosion (Fig. 4*c*) do not correlate significantly with boulder abundance at the 5% level, these variables appear to affect the maximum measured boulder abundance, as seen by the shape of the data cluster envelope of the scatterplots (dashed lines in Figs. 4*b* and 4*c*). In effect, in segments within narrow valleys (relative valley width less than 4 (Fig. 4*b*)), a large range of boulder densities are measured depending on the local context, but all laterally unconfined (uncoupled) segments display low boulder density (Fig. 4*b*). Similarly, although the variations in boulder density are considerable in narrow valley segments were the river is laterally confined and thus has low bank erosion rates (Fig. 4*c*), boulder density is very low in segments that are free to me-

Fig. 4. Segment-scale relationships between geomorphic variables of the channel and the valley in the Petite Cascapédia River (solid circles) and Bonaventure River (open circles). Relative valley width is the ratio between the floodplain width and the bankfull channel width. Broken lines represent the trend in maximum boulder abundance (envelope) as a function of (*b*) relative valley width and (*c*) bank erosion rates. River segments confined by valley walls and presenting low boulder abundance are circled with dotted lines in Figs. 1*a*, 1*b*, and 1*c*).



ander in wide valleys and consequently display high lateral instability. When only the segments with the largest boulder densities are considered (segments 2, 3, 6, 9, 7, and 6), maximum boulder abundance decreases strongly with increasing valley bottom width and bank erosion rates ($P < 0.05$). These relationships appear linear for valley bottom width (Fig. 4*b*) and nonlinear for bank erosion rates (Fig. 4*c*).

The majority of coarse sediment sources identified in the Petite Cascapédia and Bonaventure rivers correspond to zones of lateral erosion of the bedrock valley walls and boulder-rich glacio-fluvial terraces emplaced under paraglacial conditions. Overall, such sources of coarse sediment are more frequent along the Bonaventure River than along the Petite Cascapédia River. The most striking source of coarse substrate is observed in segment 8 (with mean boulder density of 1.3 boulders·m^{-2}) where the Bonaventure River is completely hemmed in in a very narrow valley section (valley to channel width ratio of 1.6) while eroding a boulder-rich terrace of subglacial (esker-type) fluvio-glacial origin (Fig. 1). Segment 8 has the highest mean interannual parr density (27 parr·m^{-2}) of either system.

Discussion

Associations between boulder and parr abundance

Along the Bonaventure River, where boulder densities vary greatly between segments, parr abundance values are significantly higher in boulder-rich segments compared with segments with fewer boulders. The same association is not detectable across the four segments of the Petite Cascapédia River, were boulder and parr are quite low everywhere. However, at the reach scale, where variations are stronger and data points more abundant, these relationships also show positive but weakly significant trends in both systems.

The data point to a strong "river-specific effect": i.e., reaches having similar low boulder and winter abundance contained remarkably lower parr abundance in the Petite Cascapédia than in the Bonaventure River. FAPAQ electrofishing data confirm that parr abundances are very low everywhere along the Petite Cascapédia main stem, including the sections between our study segments. This discrepancy suggests that large-scale factors other than boulder or winter habitat abundance at a site might be responsible for the lower parr abundances observed in the main stem of the Petite Cascapédia River (when compared with similarly boulder-poor sections of the Bonaventure River).

The notable dearth of older juveniles in the Petite Cascapédia River cannot be explained by poorer fry production or fry survival conditions. Although midsummer water temperatures are 1–2 °C cooler in the Petite Cascapédia than in the Bonaventure River main stem, the two systems overall have comparable quality of spawning habitat and trophic conditions (Coulombe-Pontbriand and Lapointe 2004). The FAPAQ electrofishing data reveal that mean fry abundances are not statistically different between segments of the two rivers (based on 10 years of surveys at 12 and 13 stations for the respective rivers, $P < 0.05$).

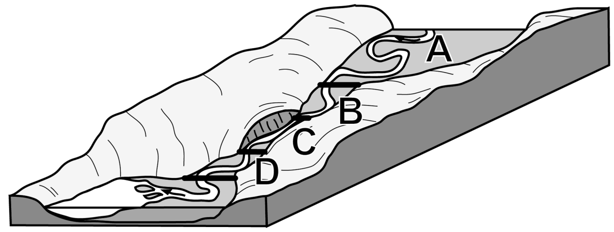
Although we have no direct migration observations to conclusively test this hypothesis, the migration of parr from boulder-poor into available boulder-rich refugia with greater overwintering survival in the Bonaventure River appears to be a likely explanation for the river-specific effect. Cunjak and Randall (1993) reported substantial parr migration during winter and greater site fidelity in stream sections more adequate for overwintering habitat in three streams of eastern Canada. Field surveys along the Bonaventure River show that boulder-poor but parr-rich segments 5, 6, and 10 all lie within a few kilometres downstream of boulder-rich segments or tributaries. In contrast, because of the extreme dearth of coarse substrate along the Petite Cascapédia River, even parr migrating long distances along the main stem of the Petite Cascapédia River would unlikely find substantial quality coarse winter habitat. This appears to impose severe limits on survival of larger parr in this system.

If this interpretation is correct, in rivers with severe winter stress to juveniles, occasional boulder-rich channel units may be necessary to support high parr abundances in boulder-poor valley segments, even when situated kilometres away. This supports the view that the relative arrangement and interconnections, at the valley segment scale, between river main stem and tributary habitats with different physical characteristics need to be considered in future juvenile salmon production models.

Geomorphic controls on the spatial distribution of boulders

Although boulder abundance and segment-integrated shear stresses were strongly correlated, it would be erroneous to conclude that segment-average shear stresses causally explain the distribution of boulder abundance. These variables are mutually interdependent in alluvial rivers: the input in significant quantity of coarse substrates into a reach generally results in steeper slopes and high shear stresses. A reduction in the degree of lateral confinement tends to operate on both variables in the same direction: it diminishes coarse sediment supply from valley sides and allows for lower overall channel energy. We propose a simple landscape model for the main controls on the distribution of boulder-rich parr habitat in confined mountain valley systems with only minor

Fig. 5. Schematic diagram of the river segment types observed in the Petite Cascapédia and Bonaventure rivers: site A, large semialluvial; site B, narrow semialluvial; site C, bedrock dominated; site D, narrow semialluvial with downstream control.



tributary streams, comparable with the study systems (Fig. 5).

In narrow coupled valley sections (site B, Fig. 5), widespread erosion of valley walls and marginal terraces produces numerous contemporary sources of coarse sediment and generally results in coarser bed material. Whether coarse stones observed in the study rivers are derived from contemporary valley-side point sources or are inherited from reworking of paraglacial deposits is difficult to ascertain. According to field observation and theory, boulders originating from limited point sources, such as landslide sites along valley walls and terraces, usually have limited downstream dispersal distances. Through selective transport and abrasion, bed material typically exhibits size fining downstream of its source, if there is no other significant lateral sediment sources (Rice 1999). Moreover, such downstream fining is more pronounced for coarser particles than for finer particles (Seal and Paola 1995) and should be most rapid for boulder-size particles. It is reasonable to assume that mobilization of boulders inherited from high-energy paraglacial ancestral rivers is relatively infrequent under the lower energy conditions of present-day rivers. Boulders present in the channel since paraglacial times presumably rest as lag or static armour deposits that contribute to overall channel coarseness where formative shear stresses are strong enough to prevent burying by finer bed material (i.e., Montgomery and Buffington 1997).

Segments affected by downstream hydraulic controls (such as sea level) that impose low slopes (site D, Fig. 5) tend to maintain lower shear stresses and remain boulder poor, even where laterally confined. Such downstream controls explain the large variations in boulder abundances observed in confined segments. For example, segments 1, 4, 5, and 10 in this study occur in relatively narrow sections of valleys but plot well below the maximum boulder abundance lines (Fig. 4*b*). Segments 1, 4, and 10 are also the three segments with the lowest shear stress conditions (Fig. 4*a*). It is noteworthy that formative shear stresses in these segments are constrained by lower slopes reflecting the downstream control imposed by sea level (segments 4 and 10) and of an outcrop of resistant bedrock across the channel bed (at the end of segment 1). Such transport-limited segments accumulate fine cobble and gravel transported through the upstream reaches. We suspect that in such lower slope segments, fine gravel can rapidly bury any large alluvium produced by the erosion of the valley walls and terraces or inherited from paraglacial material.

Wider, uncoupled valley segments (site A, Fig. 5) present few contemporary sources of coarse substrate. Channels meandering within these wider valleys are less frequently in contact with the valley walls, resulting in fewer lateral sediment sources. In addition, these segments have the freedom to meander, resulting in greater sinuosity, gentler channel gradient, and lower formative shear stresses. Channel conditions tend to rapidly become transport limited, resulting in finer bed material. Finally, in these wide valleys where channel migration rates are high and shear stresses are lower, the probability is high that occasional boulders in transport through these reaches become trapped in pools over time (and eventually buried as a consequence of channel migration).

Bedrock-dominated channels (site C, Fig. 5) seem to obey a different set of rules than do alluvial channels (Thinkler and Wohl 1998). In segment 5, with moderate shear stresses (Figs. 4*a*, 4*b*), the bedrock surface was essentially boulder free. Apparently, any exposed coarse alluvium would rapidly be transported on this smooth bedrock surface and become trapped in deep bedrock pools or deposited in downstream reaches.

Field observations suggest that boulder clusters recently recruited to the channel bed from localized contemporary sources generally display more large interstices than lag boulders inherited from paraglacial material and imbedded in armoured riverbeds. This suggests that the most favourable context ensuring regular distribution of adequate boulder-rich habitat along a stream involves frequent coarse sediment sources along channels with adequate shear stresses to rework these inputs (supply-limited conditions). In the study sites, these conditions were best met in narrow, coupled valleys bordered by coarse terraces of fluvio-glacial origin and in confined valleys where the active erosion of valley walls provides regular sources of interstice-rich boulder clusters.

Management implications

Possible habitat management implications of these findings need to be further tested. Given the preference of 1^{++} parr for habitat containing abundant coarse sediment, it has long been suspected that inserting boulder clusters in boulder-poor reaches may represent a simple and effective solution for increasing salmonid production in rivers (Meyer and Griffith 1997; Cunjak et al. 1998; Valdimarsson and Metcalfe 1998). Although our interpretation of the Bonaventure River data in the Discussion suggests that the separation between boulder-rich sections can be of the order of kilometres in rivers of this size, the optimal spacing of such boulder emplacement needs to be investigated as a function of the physical characteristics of the river.

Furthermore, there is a need to test the long-term cost effectiveness of artificial boulder emplacements as a means of enhancing salmon runs (rather than temporarily redistributing parr among reaches). In mountain valleys, segments that lack coarse particles typically correspond to wide, uncoupled valley segments presenting low lateral constriction and relatively high migration rates. Given the overall high mobility of underlying cobble–gravel substrate, occasional boulder clusters introduced in such an environment may, within a few years, migrate to pools or become buried by point bar accretion as the river shifts, thus becoming inaccessible to parr. To enhance long-term stock levels, the time scale during which artificial boulder emplacement provides useful habitat needs to significantly exceed the generation time scale of the salmon population, unless frequent boulder replacement can be contemplated.

In summary, the present study supports the idea that a lack of boulder-rich habitat may limit Atlantic salmon 1^{++} parr survival in a stream affected by severe winter conditions and highlights the importance of the occasional occurrence of boulder-rich channel units. In the fifth-order study streams, hydraulic and sedimentary conditions ensuring coarse habitat are best met in narrow, coupled valleys segments. These findings also highlight the significance of the link discontinuity concept discussed by Rice et al. (2001): geomorphological discontinuities created by points of coarse material recruitment along the river continuum can create variations in boulder abundance over short distances within channel units that are comparable with variations observable between mountain streams of different orders and can enhance system-level production. Future fish production studies need to account for coupling between fish habitat requirements, channel processes, and valley geomorphology at a relevant scale for watershed management.

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