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Does life-history variability in salmonids affect habitat use by juveniles? A comparison among streams open and closed to anadromy

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Summary

1. Migratory and resident forms of salmonids coexist in many river systems. Although such coexistence is widespread, little is known about its ecological basis and no studies have compared the habitat use of premigratory juveniles and residents.
2. We employed a comparative approach to explore the differential habitat use of juvenile anadromous and resident brook trout. This required the investigation of habitat use in streams closed to anadromy, containing only resident brook trout *Salvelinus fontinalis* ('resident-only' streams) and streams open to anadromy, containing coexisting Atlantic salmon *Salmo salar* and anadromous and resident brook trout ('migrant-resident' streams).
3. We demonstrate that fast habitats (riffles) are occupied more frequently in streams with migratory brook trout relative to riffle habitats of streams with only resident brook trout. In contrast, occupation of slow current velocities (pools) was observed in both migrant-resident and resident-only streams as both stream types contain resident brook trout. The net effect is a wider distribution of occupied habitats (pool and riffles) in migrant-resident streams relative to resident-only streams, resulting in few, if any, unused habitats.
4. These results are consistent with previously reported bioenergetic, morphological and stable isotope differences observed between anadromous and resident brook trout.
5. Our findings suggest that a link exists between juvenile habitat use, metabolic costs and life-history strategies.

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Introduction

Interspecific comparisons investigating habitat use between salmonid species are common (Gibson 1966, 1973; Fausch & White 1981; Fausch 1993; Heggenes, Saltveit & Lingaas 1996).

For example, coho salmon *Oncorhynchus clarki*, steelhead trout *Oncorhynchus mykiss* and cutthroat trout *Oncorhynchus clarki* can be observed to live sympatrically in natural streams, occupying deep, low velocity pools, shallow high velocity riffles, and intermediate habitats, respectively (Bisson, Sullivan & Nielsen 1988). Another well studied example is that of anadromous Atlantic salmon *Salmo salar* coexisting with anadromous and resident brook trout *Salvelinus fontinalis*, who both compete for similar resources and habitats leading to territorial and agonistic behaviours, with salmon gaining better feeding opportunities in fast waters (Gibson 1973). These types of observations have contributed to the current understanding of salmonid habitat use, outlining the importance of competition (Fausch & White 1981; Elliott 1990), density-dependent effects (Armstrong & Griffiths 2001; Young 2004) and individual suitability (McLaughlin & Grant 1994; Peake, McKinley & Scruton 1997) for occupying (or selecting) specific habitats in driving the patterns observed in nature.

It has been suggested that salmonids tend to position themselves in current velocities at which net energy benefits are maximized, balancing the trade-off between

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swimming costs and the delivery of drifting prey (Fausch 1984; Hughes & Dill 1990; Hill & Grossman 1993). Although swimming in fast currents is more costly than swimming in slow currents (Beamish 1980), there is the potential for better food returns in faster currents because the delivery of drifting prey is higher (Grant & Noakes 1987; Hughes & Dill 1990). This indicates that fish regularly occupying high-cost habitats (fast currents) experience reduced growth efficiencies (the ratio of growth to consumption) in comparison with fish occupying low-cost habitats (slow currents or pools), but with higher food acquisition. Indeed, it has been demonstrated in the field that anadromous Atlantic salmon (occupying fast currents) attain higher consumption rates than coexisting resident brook (occupying slow currents), but lower growth efficiencies (Tucker & Rasmussen 1999).

In situations where competition pressure is high, driven largely by limited resources, subordinate individuals may be displaced from their preferred habitat to less favourable ones by more dominant individuals (Connell 1983), often leading to a poorer growth return relative to that experienced prior to the displacement (Rosenfeld & Boss 2001; Young 2001). Individuals may adopt a dispersal/migratory strategy in order to escape this type of competition pressure. Competition pressure may also be minimized if sympatric species are inherently better adapted for dominating specific microhabitats, limiting their interactions and consequently lowering their energetic requirements (through aggression) of defending a particular territory (Elliot 1990; Cutts, Adams & Campbell 2001).

Certain adaptations in body form can facilitate swimming in different velocity regimes. For example, possessing a more streamlined body form will minimize the effects of drag, reducing the costs of swimming (Pettersson & Brönmark 1999). In addition, the ability to swim in different currents will also be governed by individual variations in metabolic scope. Laboratory studies have demonstrated that wild Atlantic salmon attain a higher sustained, higher prolonged and a higher maximum swimming speed than brook trout (Peake *et al*. 1997; McDonald, McFarlane & Milligan 1998) supporting field observations that Atlantic salmon employ faster currents than brook trout (Gibson 1966, 1973; Griffith 1972; Heggenes *et al*. 1996). Because different species of salmonids vary in their metabolic capacity for swimming in currents, it is very likely that such differences may also be found within a species exhibiting different life-history strategies. Indeed, variations in metabolic costs have been linked to differences in life-history strategies within species. For example, it has been shown that Atlantic salmon with higher standard metabolic rates (SMR) and higher levels of aggressiveness migrate sooner than those with lower SMR (Metcalfe & Thorpe 1992; Metcalfe, Taylor & Thorpe 1995; Cutts, Metcalfe & Taylor 1998, 1999). Similarly, sea-run forms (migrants) of brown trout are more aggressive than their resident counterparts, suggesting a genetic basis to the differential behaviours (Lahti *et al*. 2001). Such differences in metabolic costs (and habitat use) within a population may lead to the adoption of anadromy or residency as life-history strategies.

Intraspecific forms of migratory and resident fish coexist in many river systems. Well known examples include resident rainbow trout *Oncorhynchus mykiss* and anadromous steelhead found in Pacific drainages (Scott & Crossman 1973), and in Europe, resident brown trout and sea trout *Salmo trutta* commonly coexist (Jonsson 1985; Bohlin, Dellefors & Faremo 1996). Most charrs (*Salvelinus*) also exhibit this pattern throughout their range (Power 1980). Despite the prevalence and the economic importance of this coexistence, little is actually known about its ecological basis and no studies have compared the intraspecific habitat use of premigratory juveniles and residents. We would expect coexistence between life-history variants to be strongly enhanced if premigratory juveniles of anadromous forms occupied different microhabitats than residents in the spawning and nursery stream systems.

It has recently been demonstrated that juvenile anadromous brook trout (migrants), in the year(s) prior to migration, exhibit higher consumption rates than coexisting resident brook trout (residents), but lower growth efficiencies, indicating differences in metabolic rates between the two forms (Morinville & Rasmussen 2003). Given the link between habitat use and metabolic costs in salmonids, it is likely that migrants are attaining higher consumption rates and their observed elevated costs by occupying faster current velocities than residents.

Although previously reported stable isotope analyses and energy budgets suggest juvenile anadromous brook trout to occupy different habitats than resident brook trout (Morinville & Rasmussen 2003), direct habitat use observations have not been feasible. Until recently, no method was available to distinguish between migratory and resident brook trout in the field (Morinville 2005), because no obvious differences exist between the two forms. The genus *Salvelinus* exhibits the least pronounced anadromy of salmonids with migrations limited to a hundred kilometres from river mouths (Power 1980), and no smoltification occurs in juvenile migrants (McCormick, Naiman & Montgomery 1985). As a consequence, migrants could only be differentiated from juvenile residents if they were captured during their outmigration in a trap or at sea (Morinville & Rasmussen 2003; Thériault & Dodson 2003) thus limiting the ability to directly investigate their habitat use patterns in streams.

Owing to these limitations, we employed a comparative approach to explore the intraspecific habitat use of juvenile migrant and resident brook trout to better understand the link between habitat use, metabolic costs and life-history strategies. This required the investigation of habitat use of brook trout in streams closed to migrant fish, containing only resident brook trout ('resident-only' streams) and streams open to migrant fish, containing coexisting juvenile migrant brook trout, Atlantic salmon and resident brook trout ('migrant-resident' streams).

Given our previous work, we hypothesized that fast habitats (riffles) would be occupied more frequently in streams with migratory brook trout than streams with only resident brook trout. In contrast, occupation of slow current velocities (pool habitats) in both migrant-resident and resident-only streams was expected as both stream types contain resident juvenile brook trout. The net effect should be a wider distribution of occupied habitats (pool and riffles) in migrant-resident streams relative to resident-only streams. Because Atlantic salmon have high consumption rates, low growth efficiencies and higher metabolic rates (Tucker & Rasmussen 1999), migrant-resident streams were expected to have juvenile Atlantic salmon occupying riffle habitats at a higher proportion than slow habitats.

Study area and methods

This study was conducted in the Ste. Marguerite River watershed (48°27′ N, 69°95′ W) in the Saguenay region of Quebec, Canada (Morinville & Rasmussen 2003). The Ste. Marguerite River is home to the largest anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Anadromous brook trout outmigrate from the system as early as age 1+ (Thériault & Dodson 2003).

HABITAT USE

Two comparative approaches were taken to investigate the habitat use of brook trout in migrant-resident and resident-only streams: (1) comparing fish occupancy (density) in a migrant-resident and resident-only stream using dichotomous surrogates of current velocity (pool and riffle habitats), and (2) describing fish habitat use relative to current velocities available in the habitat across multiple migrant-resident and resident-only streams. All sampled streams are headwater streams and flow directly into the Ste. Marguerite River. All sampling was conducted following the spring (mid-May to mid-June) outmigration period. Apart from young-of-the-year brook trout (YOY), brook trout remaining in streams following this period are mostly 1+ and 2+, with 3+ and older making up about 10% (resident-only stream) to 25% (migrant-resident stream) of the population, and at densities of no more than 2 per 100 m^2 and 1 per 100 m^2, respectively (Lenormand 2003). Accordingly, the majority of trout remaining in streams are juveniles.

Pool and riffle use of fish in anadromous-resident and resident-only streams

The pool and riffle occupancy of fish from a migrant-resident stream (Édouard) was compared with that of a resident-only stream (Épinette) during the summer of 2003. Édouard contains no barriers to migrant fish in the lower 1 km, and juvenile Atlantic salmon, migrant brook trout and resident brook trout coexist. Longnose dace *Rhinichthys cataractae* are also found in the lowest sections but at low densities (< 2/100 m^2). Following the spring outmigration, the population of brook trout remaining in the stream comprises an unknown proportion of 'true' residents and future migrants. YOY also consist of both future migrants and residents. In contrast, Épinette contains a 'pure' resident brook trout population, as fish movement from the Ste. Marguerite River into Épinette has not been possible for the last 40 years due to the presence of a poorly constructed culvert at its mouth. Substrates in both Édouard and Épinette range from sand in the lower 100 m, to fine gravel and pebbles, to gravel and finally to coarse cobble and small boulders in the reaches above an upstream impassable waterfall. Stream gradient ranges from 1·7% in the lower reaches to 8% in the reaches prior to the impassable waterfall in Édouard. In Épinette, stream gradient ranges from 1·7% in the lower reaches to 7% in the upper reaches. Very few deep pools except at higher gradients are found in the streams. In the summer, habitats mostly consist of shallow riffles and pools, and smooth, laminar flow areas. These two streams were selected for comparison as they are the two most accessible and physically similar streams in the Ste. Marguerite watershed, with the main difference being the presence or absence of anadromous fish. Summer water temperatures were also very similar and did not differ during sampling (both were at 18 °C).

Habitat sections were selected and identified 1 day prior to the day of fishing. Streams were ascended beginning at the mouth and pool or riffle sections that were about 20 m^2 in area were selected for sampling. Riffles and pools were chosen so as to be as similar as possible between the two streams and the 20-m^2 criterion minimized the habitat size effect on our sampling efficiency. All habitat-specific sections had similar depths and substrates thus minimizing any intrahabitat differences between streams. Habitat sections were considered pools if current velocities were below 14 cm s^{-1} and had depths between 30 and 45 cm, while riffle sections had current velocities above 22 cm s^{-1} and had depths of less than 20 cm. Habitat sections were not contiguous; that is, there was a minimum distance of 10 m between any selected pool and riffle.

All fish (brook trout and Atlantic salmon) were captured, using a backpack electrofisher (Smith-Root, Inc. model 12A), the day following the selection of habitat sections. Field crews consisted of one fisher and two netters. The fisher and netters were the same for both stream samplings. Fishing occurred from downstream to upstream until all selected habitat sections had been crossed. Electrofishing was limited to one pass through each habitat section. All fish collected from each sampled section were identified and enumerated. Fish were then released back into the sampled section. Both streams were fished on sunny days starting mid-morning and ending no later than early afternoon.

The mean number of fish found in each section (number of fish per 20 m^2 section) was calculated for each habitat type and for each stream. The density of fish (YOY brook trout, brook trout and Atlantic salmon) found in pool and

Table 1. Length, basin area, reach length, mean wetted width (± 1 SD), mean depth (± 1 SD) and mean pool depth (± 1 SD) of reaches in migrant-resident and resident-only streams sampled in 2002

Stream type	Stream	Basin area (km^2)	Reach length (m)	Mean wetted width (m)	Mean depth (cm)	Mean pool depth (cm)
Migrant-resident	Édouard	*c.* 9	1075	2·9 ± 1·1	20·4 ± 10·6	35·6 ± 8·3
	Morin	*c.* 18	200	5·3 ± 1·6	23·2 ± 10·1	34·7 ± 6·7
	Allaire below	*c.* 28	190	5·8 ± 2·2	26·9 ± 11·3	39·1 ± 7·9
	Portage below	na	160	2·9 ± 1·3	22·1 ± 14·4	29·2 ± 10·4
Resident-only	Épinette	*c.* 11	200	3·5 ± 1·7	17·7 ± 11·2	31·1 ± 7·6
	Allaire above	*c.* 28	170	5·4 ± 1·7	26·7 ± 9·9	29·5 ± 3·2
	Portage above	na	75	3·1 ± 1·3	23·5 ± 13·9	32·9 ± 14·8

na, not available.

riffle habitats were then compared within, and between streams using two-way ANOVA, or standard *t*-tests using SYSTAT (Version 10·2).

General stream habitat use of fish across migrant-resident and resident-only streams

The stream habitat use of fish relative to that available in the habitat was investigated in reaches from four streams open (migrant-resident) and three streams closed to anadromy (resident-only) over a 2-month period during the summer of 2002 (Table 1). Four migrant-resident streams (Édouard, Morin, and the lower sections of Portage and Allaire that are below a waterfall) were selected and contained Atlantic salmon as well as brook trout migrants and residents. Longnose dace were also found in both Portage and Morin stream. Morin substrate ranges from coarse cobble and small boulders in the upper reaches, to gravel, to fine gravel and pebbles and finally to sand in the lower 250 m. Habitats range from riffles, very few pools, to smooth, shallow, laminar flow areas. Stream gradient is lower in the lower reaches at 1·7%, ranging up to 6·8% in the upper reaches. Stream gradient in Portage ranges from about 2% in the first 100 m up to 6% in the reach closest to the first impassable waterfall. The gradient decreases to 2% in the reaches above the impassable waterfall. The lower reaches consist of sandy substrates, followed by fine gravel and pebbles, to coarse cobble and boulders in the upper reaches. In contrast, Allaire runs over a bed of large boulders of 0·5–1 m in diameter, especially in the upper reaches, mixed with large cobble, rubble and coarse gravel. Habitats are typically rapids and riffles, interspersed with pools, and vertical drops can often exceed 0·5 m at summer water levels. Allaire is steep even in its lower reaches (3%) and increasing to about 7% in the reaches below the first impassable waterfall.

Sections from three resident-only streams were selected including Épinette and sections located upstream of an impassable waterfall on both Portage and Allaire streams. Stream sections above the waterfall on both Portage and Allaire were similar to other streams, with gradients ranging between 2% and 4% and exhibit similar substrate sizes.

Sampled reaches ranged between 80 m and 1 km long, with the majority being approximately 200 m in length (Table 1). Approximately 1 km of Édouard stream was fished in order to provide an example of an entire stream open to migrant and resident fish. Fish (brook trout and Atlantic salmon) were captured following the same procedure as that outlined above. The same fisher and netters fished both upstream and downstream reaches of a stream containing a barrier (e.g. sections of Allaire below and above the waterfall). All streams were sampled starting early morning and ending no later than mid-afternoon.

Current velocities were measured in the mid to upper water column (at a depth approximately 0·8 from the stream bed) in each stream section, using a Pygmy-Gurley current meter (Model D625, Model 1100 digital flow indicator). Current velocities were taken at the beginning and end of each section (every 5 m) at three locations transecting stream flow. The mean of the beginning and end velocities of each section was taken as the section's mean velocity. Each fish captured in each section was then attributed the respective velocity for that section. This method provided a general description of the habitats surrounding the fish, instead of a description of its precise location at the moment of capture. This approach was considered more suitable because it is impossible to estimate location from electrofishing since fish can be pulled in from relatively far away.

Current velocities in Édouard and Épinette streams were re-sampled during the summer of 2003 over a 2-day period in order to verify that the beginning and end velocity measurements of each section adequately described the mean section velocity. Reaches of 100 m on both streams were marked every 5 m. Velocities were taken at the beginning and end of sections as described above, and at four random positions by creating an imaginary grid over each section and selecting positions generated from a random number table. The mean of the random position velocities was then calculated and compared with the beginning and end of section mean velocities using paired *t*-tests.

A proportional frequency distribution curve was generated for the habitat use of each fish species for each stream and compared with the available habitats

in the stream. Kolmogorov–Smirnov (K-S) tests were used to compare the frequency distribution of habitat velocities to the velocities of Atlantic salmon and brook trout. All statistical analyses were conducted using SYSTAT (Version 10·2).

Results

HABITAT USE

Pool and riffle use of fish in migrant-resident and resident-only streams

The objective of choosing similar habitat-specific sections resulted in a final selection of 18 pools and riffles in the migrant-resident stream (Édouard), and 17 pools and riffles in the resident-only stream (Épinette). In total, 59 young-of-the-year (YOY) brook trout, 85 juvenile brook trout and 34 juvenile Atlantic salmon were captured in the migrant-resident stream. In the resident-only stream, 23 YOY and 95 juvenile brook trout were captured.

1. *Juvenile brook trout and Atlantic salmon*. The mean number of juvenile brook trout found in pool sections (20 m^2) of Édouard (migrant-resident) and Épinette (resident-only) stream was 1·9 and 3·5, respectively (Fig. 1). In riffles, juvenile brook trout were found at densities of 2·8 and 2·1 per 20-m^2 in Édouard and Épinette, respectively. A two-way ANOVA revealed significant differences in pool and riffle use between Édouard and Épinette (habitat type $*$ stream, $P = 0{\cdot}002$). As predicted, Épinette had a greater density of juvenile trout in pools than in riffles ($t = 3{\cdot}4$, $P = 0{\cdot}002$). In contrast, there was no difference in the pool and riffle use of juvenile brook trout in the migrant-resident stream (Édouard), although there was a tendency towards a higher riffle use ($t = -1{\cdot}8$, $P = 0{\cdot}085$). Interestingly, pool densities of the resident-only stream (Épinette) were 1·8 times higher than the migrant-resident stream (Édouard).

In the migrant-resident stream (Édouard), Atlantic salmon occurred at densities of 0·17–1·7 per 20-m^2 pool and riffle section, respectively (Fig. 1). As expected, Atlantic salmon used riffle habitats more than pools ($t = -4{\cdot}89$, $P < 0{\cdot}001$). Overall, a greater proportion of fish utilized riffle habitats in the migrant-resident stream (Édouard), which contrasts that observed in the resident-only stream (Épinette) where a greater proportion of fish utilize pool habitats.

2. *YOY brook trout*. The mean number of YOY brook trout found in pool sections of Édouard (migrant-resident) and Épinette (resident-only) stream was 2·2 and 1·3 per 20 m^2, respectively (Fig. 1). YOY brook trout were found in riffles at densities of 1·0 and 0·06 per 20 m^2 section, in the migrant-resident and resident-only streams, respectively. More YOY brook trout were found in pools than in riffles in both streams (ANOVA: $P = 0{\cdot}002$), although the relative difference between pool and riffle densities in Édouard was lower than in Épinette. In addition, the migrant-resident stream (Édouard) had a higher density of YOY in riffles (ANOVA: $P = 0{\cdot}009$). As pool densities were higher than riffle densities in both streams, the occupancy (number of habitat-specific sections with at least 1 YOY/total number of habitat-specific sections) of pools and riffles by YOY was measured. Only 1 (6%) riffle section in the resident-only stream contained YOY, thus YOY were virtually absent from riffle habitats (Fig. 2). In contrast, 72% and 56% of pools and riffles, respectively, contained YOY in the migrant-resident stream. YOY thus exploit at a high proportion both types of habitats.

General stream habitat use across migrant-resident and resident-only streams

No significant differences were found between the different methods (mean of beginning and end of section vs. random velocity measurements within section) for describing mean section velocity in either Édouard (paired $t = -0{\cdot}46$, d.f. = 18, $P = 0{\cdot}65$) or Épinette (paired $t = -1{\cdot}21$, d.f. = 18, $P = 0{\cdot}24$). The method of taking velocities at the beginning and end of each section was thus considered adequate for describing mean section velocity.

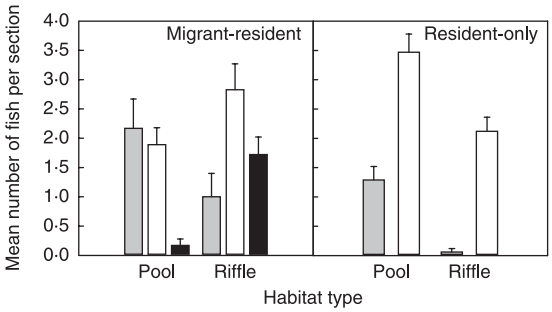

Fig. 1. The mean number of fish captured per 20 m^2 section in pool and riffle habitats of Édouard (migrant-resident, AR; 18 pool and riffle sections) and Épinette (resident-only, RO; 17 pool and riffle sections). Shaded, open and closed bars indicate YOY brook trout (AR: $n = 59$; RO: $n = 23$), juvenile brook trout (AR: $n = 85$; RO: $n = 95$) and Atlantic salmon (AR: $n = 34$), respectively. Error bars represent +1 SE.

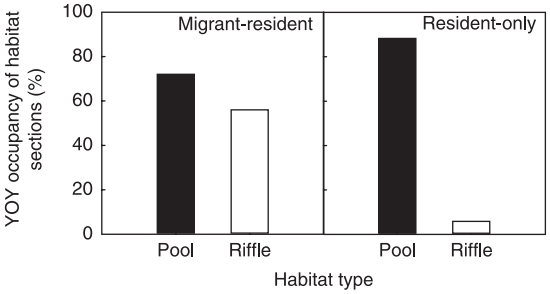

Fig. 2. Young-of-the-year (YOY) brook trout occupancy (ratio of number of habitat-specific sections that contained at least 1 YOY to total number of habitat-specific sections) of pool (closed bars) and riffle habitat sections (open bars) from Édouard (migrant-resident; 18 pool and riffle sections) and Épinette streams (resident-only; 17 pool and riffle sections).

Table 2. Mean velocity (± 1 SE) and sample size (*n*) of habitat, juvenile brook trout and Atlantic salmon samples in migrant-resident and resident-only streams

Stream type	Stream		Mean velocity ($m\ s^{-1}$)	*n*
Migrant-resident	Édouard	Habitat	0·20 ± 0·007	210
		Brook trout	0·17 ± 0·008	252
		Atlantic salmon	0·21 ± 0·006	343
	Morin	Habitat	0·21 ± 0·015	40
		Brook trout	0·18 ± 0·012	44
		Atlantic salmon	0·21 ± 0·007	231
	Allaire below	Habitat	0·24 ± 0·013	38
		Brook trout	0·23 ± 0·008	106
		Atlantic salmon	0·25 ± 0·010	80
	Portage below	Habitat	0·27 ± 0·028	32
		Brook trout	0·22 ± 0·036	18
		Atlantic salmon	0·30 ± 0·011	210
Resident-only	Épinette	Habitat	0·17 ± 0·011	40
		Brook trout	0·14 ± 0·008	90
	Allaire above	Habitat	0·22 ± 0·015	34
		Brook trout	0·18 ± 0·009	96
	Portage above	Habitat	0·21 ± 0·021	16
		Brook trout	0·18 ± 0·018	23

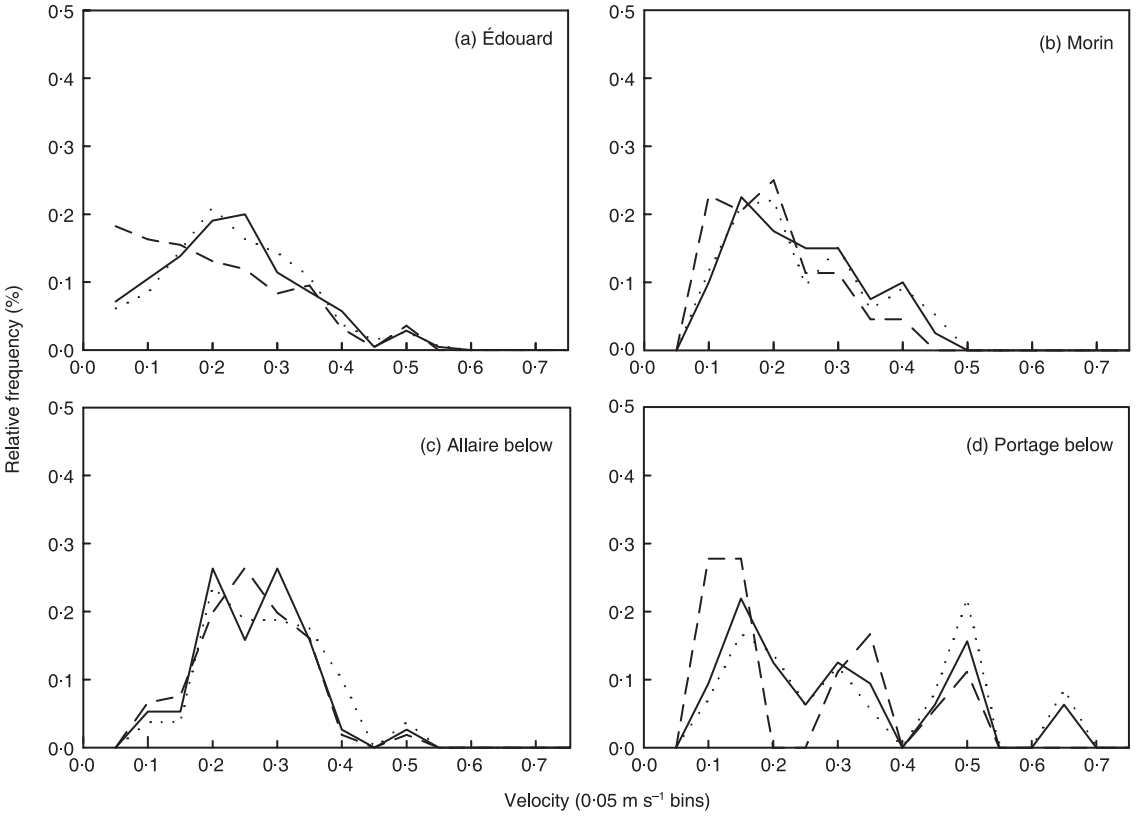

Fig. 3. Relative frequency distributions of velocity measurements of habitat (solid line), trout (dashed) and salmon (dotted line) sampled in four migrant-resident streams: (a) Édouard, (b) Morin, (c) Allaire below, and (d) Portage below.

Mean available habitat velocities varied between 0·20 m s^{-1} and 0·27 m s^{-1} in migrant-resident streams (Table 2). The mean velocities occupied by brook trout and Atlantic salmon varied between 0·17–0·22 m s^{-1} and 0·21–0·30 m s^{-1}, respectively.

General stream habitat use by fish in comparison with the habitats available in migrant-resident streams varied depending on the stream (Fig. 3). In Édouard, brook trout occupied slower velocities than the average available in the stream ($D = 0{\cdot}20$, $P < 0{\cdot}005$) and those occupied by Atlantic salmon ($D = 0{\cdot}23$, $P < 0{\cdot}005$), which exploited velocities more or less in the same proportion to their availability in the stream ($D = 0{\cdot}044$, $P = 0{\cdot}96$). In Morin, brook trout ($D = 0{\cdot}18$, $P = 0{\cdot}47$)

and Atlantic salmon ($D = 0{\cdot}062$, $P = 1{\cdot}0$) occupy the same velocities as those available in the habitat. There was also no difference in habitat use between brook trout and Atlantic salmon ($D = 0{\cdot}19$, $P = 0{\cdot}17$). Brook trout ($D = 0{\cdot}085$, $P = 0{\cdot}99$) and Atlantic salmon ($D = 0{\cdot}11$, $P = 0{\cdot}91$) velocities did not differ from those available in the habitats in the lower sections of Allaire. There was also no difference in habitat use between brook trout and Atlantic salmon ($D = 0{\cdot}12$, $P = 0{\cdot}54$). In the lower section of Portage stream, brook trout ($D = 0{\cdot}25$, $P = 0{\cdot}45$) and Atlantic salmon ($D = 0{\cdot}10$, $P = 0{\cdot}93$) also occupied all available habitats, although the sample size for brook trout was very low ($n = 18$). Atlantic salmon tended to occupy slightly faster velocities than brook trout but the difference was not significant ($D = 0{\cdot}32$, $P = 0{\cdot}062$).

When all migrant-resident streams were pooled, other than Édouard which was sampled much more intensively than the others, brook trout ($D = 0{\cdot}10$, $P = 0{\cdot}57$) and Atlantic salmon ($D = 0{\cdot}094$, $P = 0{\cdot}40$) occupied velocities in the same proportion as to those available in the stream. However, as expected, salmon utilized faster velocities than brook trout ($D = 0{\cdot}19$, $P < 0{\cdot}005$).

In resident-only streams, mean habitat velocities ranged between 0·17 and 0·22 m s^{-1} (Table 2). Brook trout had mean velocities that varied between 0·14 and 0·18 m s^{-1}.

Brook trout in resident-only streams generally occupied habitats slower than the average velocities available in the streams, although the pattern was not significant in all streams (Fig. 4). In Épinette, brook trout occupied slower current velocities than those available in the habitat ($D = 0{\cdot}26$, $P = 0{\cdot}047$). Brook trout captured in the upper section of Allaire exploited similar current velocities as those available in the habitat ($D = 0{\cdot}20$, $P = 0{\cdot}24$), although 41% of the fish were found between 0 and 0·15 m s^{-1}, compared with 24% of habitats exhibiting these velocities. In Portage, 57% of brook trout were found between 0 and 15 m s^{-1}, compared with 31% of habitats exhibiting these velocities. Although it seems that brook trout occupied slower velocities than those available, the difference is not significant ($D = 0{\cdot}25$, $P = 0{\cdot}53$). This is most likely the result of a small sample size as only 75 m of stream was sampled and only 23 trout were captured. When all resident-only streams were pooled, brook trout occupied slower current velocities than those found in the habitat ($D = 0{\cdot}21$, $P = 0{\cdot}009$).

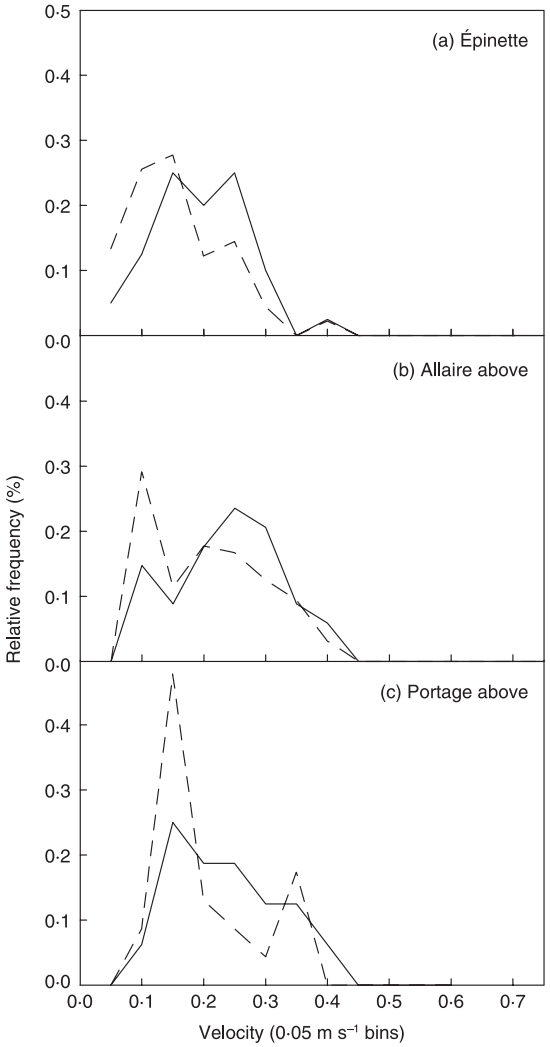

Fig. 4. Relative frequency distributions of velocity measurements of habitat (solid line) and trout (dashed line) sampled in three resident-only streams: (a) Épinette, (b) Allaire above, and (c) Portage above.

Discussion

HABITAT USE OF FISH IN MIGRANT-RESIDENT AND RESIDENT-ONLY STREAMS

Overall, the data corroborate expected patterns of wider habitat occupancy when a population is comprised of different metabolic forms (future migrants and residents) compared with a population composed of only resident phenotypes. The sampling of pool and riffle habitats as dichotomous surrogates of current velocity showed that brook trout occupied both habitat types in a migrant-resident stream (Édouard), and riffles tended to have higher densities than pools, albeit not significant. Similarly, observations across several migrant-resident streams showed that brook trout generally exploited all velocities in the same proportion as those available in the habitat. In contrast, juvenile brook trout from a resident-only stream (Èpinette) were found at higher densities in pools than in riffles, differing significantly from that observed in Édouard Stream. Brook trout thus exploited faster currents at a lower proportion than slow ones, even though there were no other species to compete with, suggesting a preference for slower flowing water. These findings were also supported by the general habitat use patterns observed across resident-only streams where, with all streams combined, trout exploited slow velocities at a greater proportion than those available in the habitat.

Interestingly, the differences in habitat use between stream types could be observed as early as at age 0+. As expected with small fish, densities of YOY were highest

in pools compared with riffles in both migrant-resident and resident-only streams, although the migrant-resident stream had higher YOY densities in riffles compared with the resident-only stream. Specifically, pools in Épinette had YOY densities 20 times higher than those in riffles, whereas in Édouard, pool densities were only two times greater the riffle densities. In addition, YOY occupancy of pool and riffle habitats, that is, the proportion of habitat-specific sections containing at least one YOY, revealed that over 50% of the sampled riffle habitat sections were occupied by YOY in the migrant-resident stream, compared with less than 6% (one section out of 17) of the riffles in the resident-only stream (Épinette). In contrast, 90% of the sampled pools contained YOY in Épinette (migrant-resident). The results thus clearly demonstrate that YOY in resident-only streams prefer pool habitats to riffle habitats, even though pool habitats are more densely populated with juvenile trout than riffle habitats. In addition, the finding that YOY exploit both riffle and pool habitats (wider habitat use distribution) concurs with habitat use expectations of migrant-resident streams as YOY in such streams comprise both resident and migrant phenotypes, the latter migrating as early as age 1+ (Lenormand 2003; Thériault & Dodson 2003).

The observations we report assume that the differences in habitat use persist over time, i.e. habitat switching between pools and riffles is not occurring on a frequent basis. Stable isotope analysis supports this because differences between migrants and residents can be detected (Morinville & Rasmussen 2003; Morinville 2005). In addition, young salmonids occupying lotic systems are generally sedentary, defending their feeding territory from a central position (Grant, Noakes & Jonas 1989; Keeley & Grant 1995).

It is accepted that Atlantic salmon use faster, more costly habitats than resident brook trout (Gibson 1966, 1973; Gibson *et al*. 1993), leading to their higher consumption rates but higher metabolic costs (Tucker & Rasmussen 1999). Our results clearly demonstrated this preferred use of fast currents. Similarly, it has been demonstrated that migrant brook trout also have higher consumption rates than resident brook trout stemming from higher metabolic costs (Morinville & Rasmussen 2003). However, unlike the case of the resident brook trout and Atlantic salmon dichotomy, we cannot conclude from the results of this study that the YOY and juvenile trout captured in faster current velocities in migrant-resident streams are indeed future migrants as they were captured in the summer prior to the following spring migration. It may be migrants, possessing higher metabolic rates, that are pushing residents into faster currents, as metabolism has been linked to dominance and aggression behaviours in salmonids (Metcalfe *et al*. 1995; Cutts *et al*. 1998, 1999). However, the alternative hypothesis, that migrants occupy faster velocities than residents, is better supported.

First, migrants have higher consumption rates than residents (Morinville & Rasmussen 2003) and food delivery is higher in fast current velocities (Grant & Noakes 1987). Trout from resident-only streams were indeed found to occupy slower velocities (mean trout velocity = 0·17 m s^{-1}) than trout from migrant-resident streams (mean trout velocity = 0·20 m s^{-1}). Secondly, given the general acceptance that fish morphology is tightly linked to habitat use and swimming (Riddell & Leggett 1981; Webb 1984; Bisson *et al*. 1988), migrant brook trout are more streamlined than resident brook trout of the same stream and thereby possess a low drag morphology (Morinville 2005). In addition, trout from migrant-resident streams are also more streamlined than trout from resident-only streams, supporting the between stream-type habitat use observations. The morphological attributes are distinct, allowing the correct classification of individuals as either being migrant-like or resident-like using a linear discriminant function (Morinville 2005).

Furthermore, applying the linear discriminant function to YOY from a migrant-resident stream (Morin), classified about 60% of YOY as future migrants over 2 years. A large proportion of YOY in migrant-resident streams thus comprise future migrants, and observations in habitat use may thus reflect the ratio of migrants and residents in the system. YOY predicted as future migrants do have more negative $\delta^{13}C$ signatures (indicative of feeding in fast currents) than predicted residents, consistent with previously reported signatures for known migrants and residents captured in the spring (Morinville & Rasmussen 2003; Morinville 2005). As stable isotopes integrate long-term feeding information (Peterson & Fry 1987), the signatures of trout captured in spring reflect the previous summer's feeding. All of this evidence, although circumstantial, favours migrants as exploiting faster currents than residents.

It is important to mention that additional mechanisms to explain the observed patterns in habitat use could be involved, including density-dependent effects (Bult *et al*. 1999; Young 2004). Previously reported salmonid densities of streams of the Ste. Marguerite River system range from 0·3 to 44 fish·100 m^{-2} (Tucker 1998; Tucker & Rasmussen 1999; Lenormand 2003) and are typical of the range observed in other salmonid streams (Mills & Tomison 1985; Kennedy 1988; Mills 1989; Gibson *et al*. 1993). Our densities, extrapolated to an area of 100 m^2 and assuming a 50% capture rate from one pass fishing, are also consistent with previous reports in the system. Densities below 15 fish per 100 m^2 are considered marginal to poor. The densities reported for brook trout in Édouard pools (*c*. 18 per 100 m^2) could also be considered marginal, and thus not likely contributing to strong intraspecific interactions. However, Épinette trout densities were almost twice as high (*c*. 35 per 100 m^2) as those in Édouard, and possibly leading to agonistic interactions. This could explain the observation of trout in riffle habitats of Épinette, where dominant fish in pools push weaker fish into faster and less preferred habitats. Indeed, higher trout densities and poorer growth has been consistently reported in Épinette compared

with migrant-resident streams (Lenormand 2003). This provides support to the idea that trout inhabiting resident-only streams have lower metabolic requirements than those inhabiting migrant-resident streams.

Furthermore, given the higher consumption rates and maintenance rations (minimum amount of energy required to maintain zero growth) of Atlantic salmon and anadromous brook trout compared with resident brook trout (Tucker & Rasmussen 1999; Morinville & Rasmussen 2003), in addition to the observation that Édouard (migrant-resident) contained more than twice the density of fish in riffles than those found in Épinette (resident-only), invertebrate drift may be depleted more rapidly in riffles of migrant-resident than resident-only streams. Indeed, at equal densities, communities dominated by Atlantic salmon depress invertebrate drift densities much more rapidly than those dominated by resident brook trout (J.B. Rasmussen, unpublished data). It is thus quite likely that the lower pool fish densities observed in Édouard (migrant-resident) may also be the outcome of reduced levels of invertebrate drift entering the pools. This further supports the idea that brook trout from resident-only streams exploit slower habitats than those from migrant-resident streams.

Importantly, in the migrant-resident streams, in which we presume brook trout to prefer faster currents than resident-only streams, salmon were always present. Gibson *et al*. (1993) found that when Atlantic salmon were introduced to streams above waterfalls where previously only resident brook trout were present, that brook trout selected slower velocity regimes than prior to the salmon introduction. Atlantic salmon are more aggressive and territorial than brook trout, such that they are normally able to obtain the best feeding sites and defend them, limiting trout to slower velocities (Gibson 1973). This could imply that migratory brook trout prefer even faster velocity regimes than those we report because of their coexistence with salmon. The difference in the preference of velocities between anadromous and resident brook trout may thus be even greater.

JUVENILE HABITAT USE, METABOLIC COSTS AND LIFE-HISTORY STRATEGIES

This study, for the first time, links juvenile habitat use to anadromous migrations that occur later in life, the results being consistent with previously reported bioenergetic differences between migrant and resident brook trout, where the latter exhibits lower growth efficiencies than the former (Morinville & Rasmussen 2003). The observed differences in both habitat use (this study) and energy allocation (Morinville & Rasmussen 2003) are detectable as early as in the first year of life and persist throughout the juvenile stages, indicating that the life-history variation is expressed early in life and is not simply adopted in the year in which migration occurs.

Some important issues arise from the results of this study and the earlier published bioenergetic study (Morinville & Rasmussen 2003). First, the finding that brook trout in resident-only streams (above impassable waterfall or culvert) exploit slower current velocities suggests a selection for fish with high growth efficiency (low metabolic rates) and a high level of local adaptation. This is necessary for the maintenance of such a population because the opposite scenario would result in an outflow of fish because fish exhibiting low growth efficiency would ultimately migrate from a system, never to return for spawning. In contrast, fish having an open access to a wider range of environments can be selected for lower growth efficiency (high metabolic rates). These fish have the opportunity of satisfying their higher demands by migrating to new habitats when they become food limited because they possess the energetic scope required to exploit large-scale environmental heterogeneity, without losing the opportunity to return.

Habitat selection in salmonids generally involves a trade-off between the costs (swimming and foraging) and benefits (prey availability) acquired by occupying certain velocities leading to a spectrum of habitat preferences (Smith & Li 1983; Fausch 1984). Because different species of salmonids vary in their metabolic capacity for swimming in currents and distribute themselves accordingly (Facey & Grossman 1990; Hansson *et al*. 1997; Peake *et al*. 1997; McDonald *et al*. 1998), it is likely that such patterns can also be observed within a species.

Whether elevated metabolic costs in migrants would be expected to result in them selecting faster currents where they could capitalize on higher food flux, would likely depend on whether SMR (fixed costs) were elevated, or whether metabolic costs were only elevated when migrants were utilizing fast water habitats (variable costs elevated). Under the scenario of elevated SMR we would expect that migrant fish would have sufficient energetic scope to utilize the entire spectrum of velocity ranges in the stream, but starve in slow water/low food flux sites. Migrants will then outperform residents in food-rich environments because they will exploit this more effectively, whereas residents will outperform migrants in food-poor environments because their maintenance rations are lower and they are more efficient. Thus, under this simple trade-off we should expect migrants always to prefer fast water and residents always to prefer slow water habitats. On the other hand if migrants experienced increased metabolic costs only when swimming in fast current and were not metabolically different from residents when using slow currents, then we might expect habitat selection by migrants to depend on competition/density. Thus, in the absence of competition there would be no reason to expect migrant fish to select fast and food-rich environments; however, under competitive pressure from residents they might be expected to show such a preference, as fast water would provide them with a niche refuge unavailable to residents. Such preference would be even more likely if through feeding in fast water riffles, migrants were able to reduce food renewal rates to slow water habitats. Thus in either case, as migrants have the

metabolic scope to utilize faster water habitats we would expect to see at least a tendency for migrants to utilize a broader range of velocities and, at least when densities are high, select a higher average velocity. Our results cannot, however, shed any light on whether migrants have higher metabolic costs as a result of higher SMR, or higher swimming costs, or whether both are involved. Further work will be needed to explore this question.

Metabolic differentiation between migratory and resident forms has been observed in other fish species. For example, anadromous threespine sticklebacks *Gasterosteus aculeatus* become less fatigued in prolonged swimming tests than freshwater threespine sticklebacks (Taylor & McPhail 1986). Similarly, anadromous sockeye *Oncorhynchus nerka* can also attain greater swimming velocities than nonanadromous kokanee of the same size raised under identical conditions (Taylor & Foote 1991). Both of these studies (Taylor & McPhail 1986; Taylor & Foote 1991) also found morphological differences between the freshwater and anadromous forms, which helped to explain the observed differential swimming capacities. Early variations in morphology (McLaughlin & Grant 1994), developmental rates (Thorpe 1989; Marten 1992) and physiology (SMR-aerobic capacity) (Metcalfe & Thorpe 1992; Metcalfe *et al*. 1995) within a species could thus all be at play, allowing certain individuals to exploit faster waters than others, and ultimately leading to individuals adopting either a migrant or resident strategy. Interestingly, morphological variations between morphs have been found to be both heritable and related to physiological performance (Proulx & Magnan 2002, 2004). Therefore, fish possessing an energetically inefficient morphology may avoid fast currents while those possessing the metabolic capacity and morphology may seek out faster currents. This is not to say that less efficient swimmers will never enter fast water, but rather that they will utilize fast currents only on a limited basis.

In summary, this study provides some useful insights into the adaptive trade-offs that may underlie the evolution of anadromy in salmonids. On the basis of this study that shows differences in habitat utilization between migrant (anadromous) and resident brook trout, and our previous study showing bioenergetic differences, we hypothesize that the 'pure' resident brook trout do not have the energetic scope to persist in fast currents but that migrant brook trout do. Migrants express their greater energetic scope both in their use of faster water habitats with greater food supply rates as juveniles, and as adults, in the larger scale over which they complete their life cycle and the larger marine prey types that they are able to access. Thus, while they grow larger and return as more fecund adults, there is a cost to this greater energetic scope. This cost includes low growth efficiency in small streams and when migration is not possible due to fragmentation (waterfalls and impassable culverts), the migrant phenotype will not prosper. We also suggest that river systems containing only residents will tend to express local adaptations only and exhibit poor ability to adapt to large-scale climate variations in time and space.

Importantly, the study also demonstrates that in systems containing both anadromous and resident species, all habitats are exploited, leaving few, if any, unused niches compared with streams only containing resident species where many habitats are left unexploited. This should be of important concern for fishery managers as streams containing many empty niches may be at greater risk of being invaded by exotic species and may create further constraints on native species. In addition, this study indicates that the presence of barriers, such as culverts, not only results in the loss of anadromous forms, but also results in changes in the overall upstream habitat use. Furthermore, it supports the idea that fish will not risk employing energetically costly habitats if benefits, on the long term, are impossible to achieve due to the presence of a barrier. Understanding the specific habitat requirements of fish is thus crucial for species conservation and attaining sustainable management practices.

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