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Factors affecting redd site selection, hatching, and emergence of brook charr, *Salvelinus fontinalis*, in an artificially enhanced site

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Synopsis

We measured microhabitat characteristics, hatching and emergence success of brook charr, *Salvelinus fontinalis,* in a series of sites selected and not selected by individuals spawning in an artificially enhanced lake outlet. Differences between the physico-chemistry of surface and interstitial water were small and did not suggest the presence of groundwater seepage. The mean surface water velocity was significantly higher in selected than non-selected sites during the incubation and emergence periods. Differences in interstitial water flow were not detected. Overall, selected substrate was coarser and contained a lower proportion of fine particles than non-selected substrate, as determined by the geometric mean diameter of particles, the proportion of fine particles (<1 mm), and the Fredle index. The proportion of fine particles was correlated with sediment loading in incubators. A two-way ANOVA showed no significant effect of sites (selected versus non-selected) but did show a significant effect of the incubation substrate (Astro-turf™, selected substrate, non-selected substrate) on both the hatching and emergence success; the percentages of hatching and emergence were significantly higher in Astro-turf™ than in non-selected substrate, with selected substrate being intermediate. The results of this study suggest that redd site selection by brook charr is based on surface water velocity and substrate characteristics (granulometry and proportion of fine particles) that in turn affect egg survival. It is possible that the lower proportion of fine particles in selected sites (and incubators) is related to their higher water velocity, which could carry away fine particles that reduce the availability of oxygenated water to the embryos. In the same way, higher water velocity could act as a proximate cue in the absence of groundwater seepage or interstitial water flow for individuals to select suitable sites for spawning and egg incubation.

Introduction

Various studies have shown that the presence of groundwater seepage is important in redd site selection by brook charr, *Salvelinus fontinalis* (e.g. Webster & Eiriksdottir 1976, Fraser 1982, 1985, Witzel & MacCrimmon 1983a, Snucins et al. 1992, Blanchfield & Ridgway 1997, Essington et al. 1998). Circulation of groundwater in the substrate would stabilize the thermal, chemical, and hydrologic properties of the redd (Gunn 1986, Snucins et al. 1992, Curry et al. 1995). It would also carry oxygen to embryos and metabolic wastes away from them (Sowden & Power 1985). In streams, these functions could be carried out by water currents in the substrate (Stuart 1953). Curry & Noakes (1995) reported that discharging groundwater may influence brook charr homing to spawning areas in lakes and creeks of the Canadian Shield, but that it does not influence the selection of individual redd sites.

The availability of suitable substrate can also influence redd site selection and spawning success of brook charr. Even though gravel is the most suitable substrate, brook charr have been observed spawning on atypical substrates in the presence of seeping groundwater (Fraser 1982). However, a large proportion of fine sediments in the substrate reduces the inflow of oxygenated water to the embryos (Witzel & MacCrimmon 1983b, Chapman 1988). Essington et al. (1998) reported that the presence of existing redds was an important component of redd site selection. Redd reuse and superimposition were observed in salmonids and could be due to a limitation in suitable sites (McNeil 1967, Blanchfield & Ridgway 1997). Blanchfield & Ridgway (1997) observed that spawning females were readily replaced when experimentally removed from their redd, suggesting that redd sites are a limiting resource and that certain sites are preferred.

In 1987, an artificial habitat was created in Lake St-Michel, Charlevoix (Québec), Canada, to increase the availability of spawning ground for brook charr (Craig & Dulude[1]). This habitat consisted of a new outlet connecting to the original one, which is not used by spawning brook charr because it is too steep and flows on bedrock. A 0.5 m gravel layer (15–30 mm diameter) was deposited over the existing sand and silt substrate, on a section extending 150 m from the lake outlet. In 1988 and 1989, 150–200 spawning individuals were seined in a small inlet of Lake St-Michel and transferred to the enhanced site to initiate the use of this site and eventually homing. Since 1990, the site has been actively used by spawning brook charr (D. Craig personal communication). Using a counting fence, Baril & Magnan (2002) estimated the spawning stock to be 745 and 1148 individuals in 1995 and 1996 respectively. Despite the intensive use of this site by spawning brook charr and the apparent homogeneity of the substrate in the managed habitat, the redds are patchily distributed within the spawning area. In this context, it is of interest to determine why individuals select a given area to build their nest and spawn, and not an adjacent site a few meters away. Such information is not only of interest for fisheries management: from an evolutionary perspective, it is interesting to determine if factors influencing redd site selection, which have evolved in natural environments, are the same in artificial habitats.

[1] Craig, D. & P. Dulude. 1995. Historique de l'aménagement d'une frayère pour la truite mouchetée au Lac St-Michel. Rapport technique, Club du Manoir Brulé, Stoneham. 10 pp.

The objectives of this study were thus to investigate the physical and chemical factors contributing to redd site selection as well as the hatching and emergence success of brook charr within this enhanced site. We measured the relative importance of surface water velocity, groundwater flow, granulometry, and physicochemistry of water as well as the hatching and emergence success of brook charr in a series of sites selected and non-selected by spawning individuals. We predicted that (i) physical and chemical factors would differ between selected and non-selected sites and (ii) hatching and emergence success of brook charr would be higher in selected than non-selected sites.

Materials and methods

Study site

The experiments were conducted from 1997 to 1999 in the outlet of Lake St-Michel, Charlevoix (Québec), Canada (47°10′N, 71°02′W), at 840 m of altitude. Lake St-Michel has a surface area of 220 ha. The length of the managed section is 150 m, its width varies from 4 to 9 m, and its depth from 0.20 to 1.5 m in summer. Brook charr and pearl dace, *Semotilus margarita*, are the only known species in Lake St-Michel, but charr is the only species in the outlet during spawning season (personal observation). Intensive brook charr stocking (fingerlings) was stopped in 1986 and sport fishing is carefully controlled by the resort managing this territory (Gesti-Faune Inc). Lake St-Michel has supported a sport fishing exploitation of 3000 brook charr per year since 1992 without any stocking.

Experimental design

In 1997 and 1998, we incubated eggs at 16 sites selected by spawning individuals and 16 other sites that had not been selected. A selected site was retained when two or more individuals held their position over a redd. The non-selected sites were situated within 3 m of each selected redd. No spawning fish or redds were observed on the non-selected sites during the spawning period. Each pair of selected and non-selected sites, which we judged visually to be composed of similar substrate, was considered as a station. To determine the relative contributions of the substrate and the hydrological factors, 100 eggs were incubated in selected and non-selected sites on (i) Astro-turf^{TM}, (ii) selected substrate collected at the station, and (iii) non-selected substrate collected at the same station. Astro-turf™ is an artificial substrate that has been used to maximizes egg survival (Lachance et al. 2000).

Egg incubation

The incubators used in our experiments are described in Bernier-Bourgault (2000). The incubators are cylindrical (12.3 cm height × 8.1 cm diameter) and made of a PVC grid (slots of 20 mm × 1.5 mm) that allows water to flow through from all directions. To catch the emergent alevin, a 'fry trap' was set on the top of each incubator. The PVC traps (10.0 cm height × 8.1 cm diameter) were fixed over the incubator with a coupler. A funnel inside the trap guides the emergent alevin into the trap. In the laboratory, the egg-to-emergence success was comparable in Astro-turf™ alone (75.1%) and in the incubators with Astro-turf™ (72.9%) (Bernier-Bourgault 2000). Due to the experimental nature of our study, we assumed that any bias related to these incubators would be the same on the response variables between selected and non-selected sites.

In 1997, ripe individuals were captured with a seine (10 m × 1.5 m × 1 cm) in a pool located in a tributary of Lake St-Michel. Males and females were kept in separate enclosures until artificial fertilization using the dry method (Piper et al. 1982). In 1998, the spawning period lasted only a few days. This unusual situation led to a lack of sexual products for our experiments. Therefore, for three stations we had to use embryos from another lake situated 45 km from Lake St-Michel (Lake Banville, Réserve faunique des Laurentides, Québec, Canada [47°37′N, 71°16′W]). As selected and non-selected sites were always paired within a station, we assumed that any bias due to the use of eggs from an outside source in these three stations would be the same for all response variables (i.e. additive effect). The incubators were inserted into the ground at about 15 cm depth after a hole had been dug with a small shovel. The removed substrate was used as the incubation substrate in the incubators. The eggs were incubated on 29 September 1997 and 5 October 1998 and the incubators were removed on 28 May 1998 and 12 June 1999. The hatching success was estimated by comparing the number of eggs incubated and the number of live eggs found in the incubators + the number of embryos found in the emergence trap (percent hatching) at the end of the experiment. Similarly, the emergence success was estimated from the number of alevin found in the emergence trap (percent emergence).

Water physico-chemistry

Dissolved oxygen (mg l^{-1}) and water temperature (°C) were measured in the surface water and in the substrate (5–15 cm) with a YSI oxygen meter (model 57) and conductivity ($\mu S\,cm^{-1}$) was measured with a YSI conductivity meter (model 33). For the substrate measurements, the probes were placed in a Teflon pipe with a pointed and perforated end that allowed water to enter (Guillemette 2001). Teflon is an inert material and it does not influence oxygen measurements. The pipe was inserted to a depth of 5–15 cm into the substrate, the depth at which eggs were incubated in the incubators. The interstitial water was hand pumped into the pipe to assure that the water close to the probe was coming from the desired depth and not from surface water.

Hydrological characteristics

Surface water velocity was measured at 10 cm from the bottom with a Price-type mini current meter (model 1205). The groundwater flow was measured with two mini-piezometers inserted at each site amid the three incubators. The mini-piezometers consisted of slotted polyethylene tubes (10 cm long, 9.6 mm o.d., 6.4 mm i.d.) wrapped with 1 mm nitex screen to prevent infiltration of fine particles (Curry & Noakes 1995). In 1997, the mini-piezometers were inserted into the substrate following the procedure described by Lee & Cherry (1978) to sample water between 25 and 35 cm in the sediment (as Curry & Noakes 1995). Based on the 1997 results (i.e. absence of significant differences in inerstitial flow between selected and non-selected sites at incubation and emergence periods; see results section), we adjusted the 1998 sampling to between 5 and 15 cm in depth (i.e. depth of eggs in the incubators). The groundwater flow in the substrate was calculated using Darcy's formula:

$$Q = A\frac{dh}{dl}K, \tag{1}$$

where Q is the flux of groundwater ($cm^3\,s^{-1}$), A is the area through which flow occurs (cm^2), dh/dl is the hydraulic gradient (unitless), and K is the hydraulic conductivity of the substrate ($cm\,s^{-1}$). These hydrological properties were calculated following the procedures of Lee & Cherry (1978).

Substrate analysis

At each site, the substrate was sampled with a 15 cm diameter × 50 cm length McNeil sampler (McNeil & Ahnell 1960). Three sieves with mesh sizes of 1 cm, 500 μm, and 100 μm were superimposed at one end of the tube. The sampling occurred in a homogeneous section of each site. In sites selected by spawning individuals, samples were taken in the redd or beside it but not in the egg pocket. Young et al. (1989) noted that sampling the substrate with a shovel or a McNeil sampler does not allow the detection of significant differences in substrate composition outside and within redds (excluding egg pockets). We thus assumed that substrate sampled beside or within the redds in selected sites was representative of substrate before spawning. After processing the dry samples through a stack of 25, 16, 8, 4, 2, and 1 mm sieves, the percent of fine particles (<1 mm) was estimated by weight (± 0.1 g). Particles with a diameter greater than 48 mm were excluded from samples for reasons of weight bias as discussed by Adams & Beschta (1980). The geometric mean diameter of particles (Dg) was calculated following Lotspeich & Everest[2] as:

$$Dg = (d_1^{w1} \times d_2^{w2} \times \cdots \times d_n^{wn}), \quad (2)$$

were d_n is the median diameter of particles retained by the n^{th} sieve and w_n is the decimal fraction of the particle weight retained by the n^{th} sieve.

The Fredle index was also calculated following Lotspeich & Everest (1981) as:

$$f_i = Dg\, S_o^{-1}, \quad (3)$$

where Dg is geometric mean diameter of particles (described above) and $S_o = (d_{75}/d_{25})^{1/2}$, that is, the particle diameters at the 75^{th} and 25^{th} percentiles of the cumulative substrate sample weight. Particles accumulated in the Astro-turf™ at the end of the experiment were dried and weighed (±0.1 g) to estimate the sediment loading during the incubation period.

Statistical analyses

Mean dissolved oxygen, water temperature, and conductivity were compared between surface and interstitial water with Student's paired t-tests (Sokal & Rohlf 1981). Surface and interstitial water velocity, depth, proportion of particle diameter, and geometric mean particle diameter were compared between selected and non-selected sites with Student's t-tests. Fredle index, S_o, and sediment loading were compared with Mann-Whitney U-tests (Sokal & Rohlf 1981) because the variances of these parameters were too heterogeneous. The effects of substrates (Astro-turf™, selected, and non-selected) and sites (selected and non-selected) were investigated with a two-way analysis of variance followed by Tukey comparison tests (Sokal & Rohlf 1981). The homogeneity of variances was tested with an F_{max}-test (Sokal & Rohlf 1981); when variances were heterogeneous, data were log(x) transformed while percent data were arcsine transformed. Even after transformation, the variance of some data sets were heterogeneous. We assumed that these departures from the assumption of homogeneity of variance had no marked effect on the significance level of t-tests and ANOVA (see Sokal & Rohlf 1981). All statistical analyses were performed with SYSTAT software (version 8.0).

Results

Site characteristics

No significant differences were observed in mean temperature, dissolved oxygen, or conductivity between selected and non-selected sites ($p > 0.05$). However, the mean temperature was significantly higher in the surface than in the interstitial water during the incubation and emergence periods but not during the spawning period (spawning period: $t = 0.69$, $p > 0.05$; incubation period: $t = 3.22$, $p < 0.01$; emergence period: $t = 2.75$, $p < 0.01$; Table 1). Dissolved oxygen in the surface water was significantly higher than in the interstitial water for all periods (spawning period: $t = 5.33$, $p < 0.001$; incubation period: $t = 5.68$, $p < 0.001$; emergence period: $t = 6.69$, $p < 0.001$). Conductivity was significantly higher in surface than in interstitial water during the emergence period only (spawning period: no data available; incubation period: $t = 1.53$, $p > 0.05$; emergence period: $t = 4.70$, $p < 0.001$). The mean surface water velocity was significantly higher in selected than in non-selected sites during the incubation and emergence periods but not during the spawning period (spawning period: $t = 1.52$, $p > 0.05$; incubation period: $t = 4.85$, $p < 0.001$; emergence period: $t = 4.37$, $p < 0.001$; Table 2).

[2] Lotspeich, F.B. & F.H. Everest. 1981. A new method for reporting and interpreting textural composition of spawning gravel. U.S. For. Serv. Res. Note PNW-369.

Table 1. Mean temperature, dissolved oxygen, and conductivity of surface and interstitial water during spawning, incubation, and emergence periods. Data are means ± SD with sample size in parentheses. For each period and parameter, data with different letters are significantly different as determined by a paired t-test ($p < 0.05$).

	Temperature (°C)		Dissolved oxygen (mg l^{-1})		Conductivity ($\mu S\ cm^{-1}$)	
	Surface	Interstitial	Surface	Interstitial	Surface	Interstitial
Spawning period	2.9 ± 1.2a (34)	3.4 ± 1.0a (34)	11.8 ± 1.1a (43)	9.8 ± 2.1b (43)	ND	ND
Incubation period	0.8 ± 0.3a (62)	0.7 ± 0.3b (62)	12.1 ± 2.0a (58)	10.4 ± 2.5b (58)	7.7 ± 0a (20)	8.2 ± 1.5a (20)
Emergence period	12.7 ± 1.8a (36)	12.6 ± 1.7b (36)	8.7 ± 1.2a (36)	7.3 ± 1.4b (36)	7.5 ± 0a (16)	6.5 ± 0.6b (16)

ND = no data available.

Table 2. Mean surface water velocity and depth during the spawning, incubation, and emergence periods at selected and non-selected sites. Data are means ± SD with sample size in parentheses. For each period and parameter, means with different letters are significantly different as determined by a t-test ($p < 0.05$).

	Surface water velocity (cm s^{-1})		Depth (cm)	
	Selected sites	Non-selected sites	Selected sites	Non-selected sites
Spawning period	24.2 ± 19.3a (16)	14.2 ± 17.8a (16)	49.2 ± 11.7a (34)	46.0 ± 13.6a (34)
Incubation period	15.4 ± 6.4a (34)	8.2 ± 5.9b* (33)	37.4 ± 13.6a (34)	36.3 ± 14.4a (34)
Emergence period	46.7 ± 17.5a (30)	28.5 ± 14.7b* (30)	66.0 ± 18.5a (30)	64.3 ± 15.4a (30)

*= $p < 0.001$.

Table 3. Mean interstitial water flow during the spawning, incubation, and emergence periods at selected and non-selected sites in 1997 (sampling depth: 25–35 cm) and in 1998 (sampling depth: 5–15 cm). Data are means ± SD with sample size in parentheses. For each period and parameter, means with different letters are significantly different as determined by a t-test ($p < 0.05$).

	Interstitial water flow (25–35 cm) ($\times 10^{-3}$ cm s^{-1})		Interstitial water flow (5–15 cm) ($\times 10^{-3}$ cm s^{-1})	
	Selected sites	Non-selected sites	Selected sites	Non-selected sites
Spawning period	3.3 ± 2.2a (11)	5.8 ± 3.2b (11)	ND	ND
Incubation period	3.4 ± 3.2a (23)	5.1 ± 3.7a (19)	76.3 ± 11.6a (8)	56.8 ± 17.8b (7)
Emergence period	1.4 ± 1.2a (10)	2.4 ± 1.8a (11)	45.1 ± 25.5a (8)	29.5 ± 17.8a (6)

ND = no data available.

No significant differences were observed between the depth of selected and non-selected sites for any sampling period (spawning period: $t = 1.04$, $p > 0.05$; incubation period: $t = 0.34$, $p > 0.05$; emergence period: $t = 0.38$, $p > 0.05$). In 1997, the mean groundwater flow (measured at 25–35 cm) was significantly higher in non-selected than in selected sites during the spawning period only (spawning period: $t = 2.15$, $p < 0.05$; incubation period: $t = 1.52$, $p > 0.05$; emergence period: $t = 1.55$, $p > 0.05$; Table 3). In 1998, the mean groundwater flow (measured at 5–15 cm) was significantly higher in selected than in non-selected sites during the incubation period only (spawning period: no data available; incubation period: $t = 2.47$, $p < 0.05$; emergence period: $t = 1.35$, $p > 0.05$).

Particles <1 mm, from 1 to 1.99 mm, and from 2 to 3.99 mm were significantly more abundant in non-selected than in selected sites (<1 mm: $t = 3.08$, $p < 0.01$; 1–1.99 mm: $t = 3.33$, $p < 0.01$; 2–3.99 mm: $t = 2.53$, $p < 0.05$; 4–7.99 mm: $t = 0.98$, $p > 0.05$; 8–15.99 mm: $t = 1.24$, $p > 0.05$; 16–24.99 mm: $t = 1.94$, $p > 0.05$; >25: $t = 0.28$, $p > 0.05$; Figure 1). The cumulative percentages of particles finer than 1, 2, 4, and 8 mm were significantly higher in non-selected than in selected sites (<1: $t = 3.08$, $p < 0.01$; <2: $t = 3.29$, $p < 0.01$; <4: $t = 3.28$, $p < 0.01$; <8: $t = 2.90$, $p < 0.01$; <16: $t = 1.54$, $p > 0.05$; <25: $t = -0.06$, $p > 0.05$). The geometric mean diameter of particles (Dg) and the Fredle index were significantly higher in selected than in non-selected substrate (Dg: $t = 2.94$,

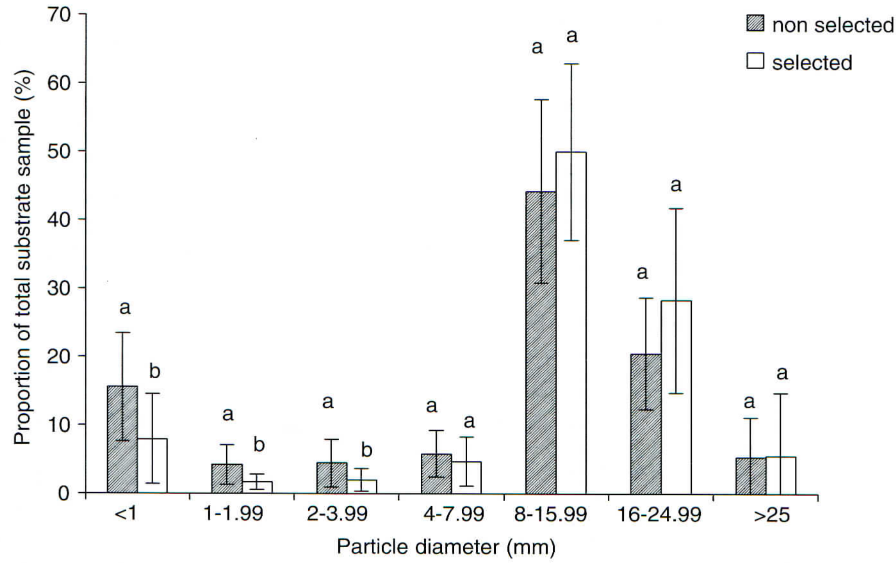

Figure 1. Mean proportion of particle size classes (diameter, mm) at selected and non-selected sites. Bars are means ± SD. For each particle size class, data with different letters are significantly different as determined by a t-test ($p < 0.05$).

Table 4. Geometric mean diameter (Dg), geometric standard deviation (So) of particles, Fredle index of substrate, and sediment loading at selected and non-selected sites. Data are means ± SD with sample size in parentheses. For each parameter, data with different letters are significantly different as determined by a t-test (Dg) and a Mann-Whitney U-test (So, Fredle index, sediment loading) ($p < 0.05$).

	Dg (mm)	So	Fredle index	Sediment loading (g)
Selected sites	11.2 ± 4.0a (16)	1.7 ± 0.3a (16)	6.9 ± 3.3a (16)	75.4 ± 64.7a (9)
Non selected sites	7.7 ± 2.6b* (16)	2.7 ± 1.2b* (16)	3.7 ± 2.4b* (16)	83.3 ± 91.2a (16)
	(16)	(16)	(16)	(9)

* = $p < 0.01$.

$p < 0.01$; Fredle index: $U = 57.00$, $p < 0.01$; Table 4). In contrast, the geometric standard deviation of particles (So) in the substrate was significantly higher in non-selected than in selected substrate ($U = 199.00$, $p < 0.01$). Sediment loading was not significantly different between selected and non-selected sites ($U = 56.00$, $p > 0.05$). However, the sediment loading in the incubators was correlated with the proportion of particles finer than 1 and 2 mm in the substrate (1 mm: $r = 0.49$, $p < 0.05$; 2 mm: $r = 0.45$, $p < 0.05$).

Hatching and emergence success

The two-way ANOVA showed no significant site effect on hatching or emergence success (selected versus non-selected, hatching: $F = 0.62$, $p > 0.05$; emergence: $F = 1.08$, $p > 0.05$) but did show a significant effect of the incubation substrate (Astro-turf™, selected substrate, non-selected substrate) at both the hatching and emergence intervals (hatching: $F = 4.93$, $p < 0.01$; emergence: $F = 3.51$, $p < 0.05$; Table 5). An *a posteriori* Tukey multiple sample comparison test showed that the hatching and emergence percentages were significantly higher in Astro-turf™ than in non-selected substrate with selected substrate being intermediate.

Discussion

Although differences in the physico-chemistry between the surface and interstitial waters were statistically significant, they do not suggest the presence of groundwater seepage. The interstitial water flow is

Table 5. Mean percent hatching and emergence (±SD) at selected and non-selected sites and in Astro-turf and selected and non-selected substrates. For each developmental interval, means with different letters are significantly different as determined by a two-way ANOVA followed by a Tukey multiple sample comparison test ($p < 0.05$).

	Site		Substrate			Sites × incubators
	Selected	Non selected	Astro-turf	Selected	Non selected	
% hatching	12.4 ± 13.2a (41)	17.3 ± 19.5a (44)	22.9 ± 19.9a (25)	13.2 ± 14.8ab (32)	9.8 ± 14.0b* (28)	N.S.
% emergence	8.1 ± 10.0a (41)	12.7 ± 16.8a (44)	16.1 ± 17.5a (25)	8.2 ± 10.6ab (32)	8.1 ± 13.2b (28)	N.S.

* = $p < 0.01$.

rather due to surface water flowing through the substrate in streams (Stuart 1953, White 1990). This kind of water supply offers less stable conditions for the eggs because temporal variations in surface water temperatures are larger than those in groundwater (Gunn 1986, Snucins et al. 1992, Curry et al. 1995). For example, Curry et al. (1995) observed temperatures ranging from 2.0°C to 6.2°C and from 2.7°C to 8.0°C in redds with groundwater discharge in Dickson and Meach lakes (Ontario, Canada). At the same time, surface water ranged from −1.5°C to 6.4°C, and from 0°C to 7.9°C, respectively. In December, they observed a temperature of 4.7°C in redds with groundwater discharge compared to 0.2°C in surface water. In July, Fraser (1982) observed a temperature of 11.4°C in groundwater compared to 18.8°C in surface water in a Canadian Shield lake. Interstitial water temperature ranged from 0.5°C to 14.5°C in our study.

Water depth did not appear to be a determinant in the spawning site selection. This may be due to the fact that non-selected sites were chosen close (<3 m) to selected ones and that other factors related to micro habitat were more important. In contrast to depth, surface water velocity was significantly higher in selected than in non-selected sites during the incubation and emergence periods but not during the spawning period. It is possible that high variance combined with low sample size ($n = 16$) did not allow us to detect a significant difference during the spawning periods. In a study at the same site, Baril (1999) found that surface water velocity was significantly higher ($p < 0.005$) at selected ($18.5 \pm 11.5\,cm\,s^{-1}$, $n = 42$) than at non-selected ($11.5 \pm 12.1\,cm\,s^{-1}$, $n = 36$) sites during the spawning period of 1996.

The mean depth (49.18 ± 11.65 cm) and surface water velocity ($24.21 \pm 19.29\,cm\,s^{-1}$) selected by brook charr were relatively deeper and higher compared to values reported in other studies. Smith (1973) observed brook charr redds at a mean depth of 24.9 cm (±47.0 cm) and with a mean water velocity of $11.2\,cm\,s^{-1}$ ($\pm 27.7\,cm\,s^{-1}$). Recently, Essington et al. (1998) observed brook charr redds at depths ranging from 36 to 46 cm and surface water velocity ranging from 13 to $21\,cm\,s^{-1}$ in a section of Valley Creek (Minnesota) containing both brook charr and brown trout, *Salmo trutta*, redds. The difference between these values and those we observed may be explained by the fact that brook charr is the only species in our study area. The selection of a redd site is thus not influenced by competitive pressure. The mean depth and water velocity selected by brook charr in our study ensure that water will flow over redds during the incubation period. Other shallower sites may freeze or allow frazil accumulations from top to bottom during winter.

Observed differences in interstitial water flow between selected and non-selected sites were not consistent and did not exhibit clear relationships. Webster & Eiriksdottir (1976) suggested that thermal and chemical gradients produced by discharging groundwater can be detected by brook charr. When thermal and chemical gradients do not exist, as in the present study, only a physical gradient can be detected. Our results may indicate that the discharge of interstitial water was not determinant in the selection of a spawning site or that the minimum criteria were satisfied in the spawning area. In such situations, Curry & Noakes (1995) suggested that redd site selection may be made using visual or tactile stimuli like substrate composition.

We found the proportion of fine sediments to be a determinant of redd site selection. Their proportions were significantly higher at non-selected than selected sites and they were correlated with sediment loading in incubators. It has been documented that fine sediments reduce oxygen delivery to embryos and thus reduce survival (Hausle & Coble 1976, Witzel & MacCrimmon 1983b, Sowden & Power 1985). The smaller proportion of fine particles in selected substrate resulted in a higher geometric mean particle diameter (Dg) and a higher substrate Fredle index; i.e. selected substrate was coarser and more homogenous than non-selected substrate, which is more favorable for successful reproduction (Lotspeich & Everest[2], Snucins et al. 1992). However, substrate selected by brook charr in the Lake St-Michel outlet was coarser than has been observed in other studies. For example, Witzel & MacCrimmon (1983a) measured a geometric mean diameter of 5.71 mm ($\pm$2.31 mm) in redds used by brook charr in streams of Ontario, which is half the diameter measured in this study. Furthermore, the geometric mean particle diameter (Dg) and the Fredle index measured at selected sites were respectively 4.7 and 7.7 times higher than those measured at redd peripheries (0–20 cm layer) by Snucins et al. (1992). The non-selected sites exhibited even coarser substrate than those measure at redd peripheries in Chikanishing Creek, with Dg and Fredle index respectively 3.2 and 4.1 times higher. These differences from other studies may be due to the fact that the diameter of particles used to enhance the spawning ground of the Lake St-Michel outlet ranged from 15 to 30 mm.

The results presented above suggest that surface water velocity and substrate characteristics (granulometry and proportion of fine particles) were involved in redd site selection by brook charr. However, other factors may also be involved. Essington et al. (1998) found that females exhibited a preference for spawning on existing redd sites that was not related to habitat availability. Results on hatching and emergence success indicate that egg survival is more closely associated with substrate than with other site characteristics. The hatching and emergence percentages were significantly higher in Astro-turf™ than in non-selected substrate with selected substrate being intermediate.

In conclusion, the results of this study suggest that redd site selection by brook charr is based on surface water velocity and substrate characteristics (granulometry and proportion of fine particles) that in turn have an effect on egg survival. The substrate of selected sites was coarser, contained a lower proportion of fine particles, and had higher hatching and emergence success than non-selected substrate. It is possible that the lower proportion of fine particles in selected sites is related to the higher water velocity observed in these sites during the spawning (Baril 1999), incubation, and emergence (present study) periods. Higher water velocity could carry away fine particles that could reduce the inflow of oxygenated water to the embryos (Witzel & MacCrimmon 1983b, Chapman 1988). In addition, higher water velocity could act as a proximate cue for individuals to select suitable sites for spawning and egg incubations in the absence of groundwater seepage or interstitial water flow, as was the case in the present study. From an evolutionary point of view, the selection of zones with higher water flow (such as higher interstitial water flow or water velocities in streams and groundwater seepage in lakes) may have been a selected behaviour in the evolution of brook charr and other salmonids. Spawning ground enhancement should thus focus on the attainment of specific water velocities during the spawning periods (about 18–25 cm s^{-1}; Baril 1999, present study) and substrate characteristics to reduce sediment loading during the incubation period.

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