Freshwater Biology

Freshwater Biology (2011) **56,** 1017–1029 doi:10.1111/j.1365-2427.2010.02542.x

The evolution of redd site selection in brook charr in different environments: same cue, same benefit for fitness*

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SUMMARY

1. Despite the great interest in characterising fish reproductive habitat, the relationship between the selection of a given spawning site and individual fitness has not been experimentally tested.
2. In this study, we used an *in situ* experimental approach to determine (i) the relative contribution of substrate characteristics as well as hydrological and physicochemical variables to small-scale redd site selection by brook charr, *Salvelinus fontinalis* (Mitchill) and (ii) if hatching and emergence success, used as a surrogate of fitness, are improved in selected compared to non-selected sites in both lake and stream habitats.
3. Our results show that upwelling groundwater flow was always significantly higher in selected than in non-selected sites in both lake and stream habitats. We found no significant difference in the mean geometric substrate diameter and no consistent differences in substrate composition between selected and non-selected sites. Oxygen concentration was higher (significantly so in three of four comparisons) and conductivity tended to be lower in selected than in non-selected sites, while temperature showed no significant or consistent variations. We found a significant positive relationship between the selection of a given spawning habitat and hatching and emergence success in these systems.
4. These results show that the main cue that brook charr use to select their spawning sites is upwelling groundwater in lake and stream habitats, and that active selection of these sites increases individual fitness. This suggests that natural selection acted on the same cues in lentic and lotic environments; this could have been highly adaptive in a species that used both habitats as colonisation routes after the last glaciation.

Keywords: emergence success, evolution, groundwater flow, habitat selection, hatching success, spawning ground, substrate

Introduction

Suitable spawning habitats are not evenly distributed in the environment, as shown by the patchy distribution of many fishes during their reproductive period. In this context, the preference for high-quality spawning sites probably results from natural selection acting on embryo survival. Since the seminal paper of Fretwell & Lucas (1970), habitat selection models have assumed that individuals can assess the relative

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*Contribution to the Fondation pour la sauvegarde de la truite mouchetée.

quality of different habitats and thus select those that maximise their fitness. Selection of the best habitats in heterogeneous environments should ideally be based on cues closely reflecting habitat quality and thus are related to the realised fitness of individuals (Arlt & Pärt, 2007). Although a tremendous amount of work has been published on fish reproductive habitat, explicit experimental tests on the relationship between spawning habitat selection and individual fitness are still lacking. Like many salmonids, brook charr, *Salvelinus fontinalis* (Mitchill), actively select their spawning sites in streams and lakes (see references below), and thus represent a good model to test this relationship.

Many studies have shown that the presence of upwelling groundwater influences redd site selection by brook charr (Curry & Noakes, 1995; Blanchfield & Ridgway, 1997; Essington, Sorenson & Paron, 1998). Circulation of groundwater in the substrate could stabilise the thermal, chemical, and hydrological properties of the redd (Sowden & Power, 1985; Chapman, 1988; Curry, Noakes & Morgan, 1995). It could also carry oxygen to embryos and metabolic wastes away from them (Silver, Warren & Doudoroff, 1963; Sowden & Power, 1985), thus potentially increasing their survival. In the absence of upwelling groundwater, Bernier-Bourgault & Magnan (2002) and Curry & MacNeill (2004) observed that redds were located in areas of fast water velocities; however, these observations were made in atypical spawning habitats in both cases (artificial managed spawning grounds and heavy sediment loads in agricultural zones, respectively).

Redd site selection and spawning success of brook charr could also be influenced by the availability of a suitable substrate. For example, large proportions of fine sediments in the substrate reduce the inflow of oxygenated water to embryos (Witzel & MacCrimmon, 1983a; Sowden & Power, 1985; Chapman, 1988) and restrict the movement of free embryos (Dill & Northcote, 1970), with potential consequences for their survival. Even though upwelling groundwater and substrate composition seem to be key factors in determining salmonid fitness, we know of no study designed to determine their independent effects on embryo survival in the field.

In this study, we used an *in situ* experimental approach to determine (i) the relative contribution of substrate characteristics as well as hydrological and physicochemical variables to small-scale redd site selection by brook charr and (ii) if hatching and emergence success, used as a surrogate of fitness, are improved in selected compared to non-selected sites in both lake and stream habitats. A better knowledge of the relative contributions of these factors is important for understanding potential drivers of salmonid evolution in both lakes and streams as well as for developing efficient conservation practices. Habitat characteristics and reproductive success were studied with the same experimental design, which consisted of a comparison of sites either selected or not selected by spawning individuals in two streams and one lake. The basic assumption of this design is that spawning fish use key characteristics of the sites (i.e. substrate, hydrological and physicochemical variables) as cues for site selection. Finally, the active selection of spawning site is expected to provide higher reproductive success, as assumed by current habitat selection models.

Methods

Study areas

Stream habitat The study was done on two natural spawning grounds: the outlet of Lake Les Étangs (hereafter called Les Étangs spawning ground), northeast of Québec City, Québec, Canada (47°29′33″N, 70°44′46″W), in 2001–2002, and the outlet of Lake Lafond, Dickerman sector (hereafter called Dickerman spawning ground), Réserve Mastigouche, north of Trois-Rivières, Québec, Canada (46°43′50″N, 73°18′45″W), in 2002–2003. Les Étangs exhibited a typical substrate for brook charr spawning (gravel from 0.5 to 5 cm in diameter; Quinn, 1995; Blanchfield & Ridgway, 1997) while Dickerman exhibited atypical substrate (mostly sand) at both selected and non-selected sites (see Results section).

Lake habitat The spawning grounds were located in the littoral zone of Lake St-Michel, 120 km northeast of Québec City, Québec, Canada (47°17′N, 71°55′W). The lake is a typical oligotrophic temperate zone lake (mean depth = 4.6 m, surface area = 220 ha, pH = 5.6, O_2 = 11.8 mg L^{-1}, and conductivity = 7.8) and also contains pearl dace, *Semotilus margarita* (Cope). The study was done in 1997–1998 and 1998–1999.

Localisation and selection of the spawning sites

Stream habitat We identified eight sites selected by spawning individuals and eight other sites that had not been selected (hereafter referred to as 'selected sites' and 'non-selected sites') in each stream. A selected site was retained when two or more individuals were observed over a redd for at least two consecutive days. Non-selected sites were arbitrarily located within 3 m of each selected redd at depths and substrate compositions similar to the selected sites. Each pair of selected and non-selected sites (separated by ≤ 3 m) was considered as a 'station' for statistical analysis. No spawning fish or redds were observed on the non-selected sites over the whole spawning period. Sites were between 30 and 75 cm in depth (mean ± SD: 32.7 ± 7.7 cm in 2001–2002; 52.6 ± 9.5 7 cm in 2002–2003).

Lake habitat The sites selected by spawning individuals were identified in the first 2 m depth of the littoral zone during the night from a boat propelled by an electric motor. A bathyscope and underwater lights allowed us to locate individuals on the spawning grounds. A selected site was retained when two or more individuals were observed over a 1 m diameter area for at least two days. Six selected and six non-selected sites, similar on the basis of their substrate composition, were studied in 1997–1998 whereas 10 selected and 10 non-selected sites were studied in 1998–1999, without any consideration for substrate composition. Site depths were between 35 and 110 cm (66.1 ± 13.7 cm in 1997–1998; 91.1 ± 8.3 cm in 1998–1999). Each pair of selected and non-selected sites (separated by ≤ 20 m along the same depth contour) was considered as a 'station' for statistical analysis.

Substrate analyses

Stream and lake habitats Substrate was sampled in a homogeneous section of each site using a 15 cm diameter × 50 cm length McNeil sampler (McNeil & Ahnell, 1960). In selected sites, samples were taken within or just beside the redd. After processing the dry samples through a stack of 25, 16, 8, 4, 2 and < 1 mm^2 sieves, the proportion (%) of each particle size class was dried and estimated by weight (± 0.1 g). The geometric mean diameter of particles (Dg) was calculated following Lotspeich & Everest (1981) as:

$$\mathrm{Dg} = (d_1^{W1} \times d_2^{W2} \times \ldots \times d_n^{Wn}),$$

where d_n is the median diameter of particles retained by the *n*th sieve and W_n is the decimal fraction of particle weight retained by the *n*th sieve.

Groundwater flow

Stream and lake habitats Repeated measures of groundwater flow were taken at each site with a mini-piezometer (Lee & Cherry, 1978) during the incubation and emergence periods: Lake St-Michel (1997–1998): 16, 22, 29 October, 12 November, 27 January, 9 February, 2, 18 March, and 19, 28 May; Lake St-Michel (1998–1999): 6 October (at egg incubation) and 25 May (at the end of the experiment); Les Étangs (2001–2002): 24 October, 2, 9, 28 November, and 31 May; Dickerman (2002–2003): 1, 14, 28 November, and 8, 15 May. Two mini-piezometers were inserted at each site amid the three incubators (see below). They consisted of polyethylene tubes (9.6 mm o.d., 6.4 mm i.d.) whose ends were perforated by seven holes (4 mm^2) along a section of 100 mm and covered with 1 mm Nitex®. The mini-piezometers were inserted into the substrate according the procedure described by Lee & Cherry (1978) to sample water between 5 and 15 cm into the sediment (depth of egg incubation). The groundwater flow was calculated using Darcy's formula (Lee & Cherry, 1978):

$$Q = A\frac{\mathrm{d}h}{\mathrm{d}l}K$$

where Q is the groundwater flow (cm^3 s^{-1}), A the area through which flow occurs (cm^2), dh/dl the hydraulic gradient (the difference in water levels between water under pressure coming from the piezometer [dh] and from the water column [dl]; unitless) and K the substrate permeability (cm s^{-1}; the time needed for water added to the piezometer to flow through a vertical distance by gravity). In streams, surface water velocity (m s^{-1}) was also measured at the same time using a Price-type mini current meter (model 1205).

Physicochemical variables

Stream and lake habitats The temperature (°C), dissolved oxygen (mg L^{-1}; YSI model 57), and conductivity (μS cm^{-1}; YSI model 33) of interstitial water were measured at the same time as groundwater flow, although conductivity was not measured at Lake St-Michel in 1997–1998. We used a Teflon device to hold the oxygen or conductivity meter probes that allowed us to pump water from the substrate (Guillemette, 2001) to measure these variables. Teflon is an inert material and does not influence oxygen or conductivity measurements. The bottom of the Teflon device tapers to a perforated point that is covered with 1 mm mesh Nitex®. The point was inserted from 5 to 15 cm into the substrate (the depth where eggs were incubated), and water was pumped until temperature, dissolved oxygen, and conductivity values were stable.

Egg incubation

In both the lake and stream experiments, ripe individuals were captured with a seine (10 m × 1.5 m × 1 cm mesh size) near the experimental area. Males and females were kept in separate enclosures until artificial fertilisation using the dry method (Piper *et al.*, 1982). On each site, we placed three incubators that each contained 100 fertilised eggs. Each of these three incubators had a different type of substrate: (i) Astro-turf™, (ii) substrate collected at the selected site and (iii) substrate collected at the non-selected site of a given station. Astro-turf™ is an artificial substrate that maximises egg survival (Lachance, Bérubé & Lemieux, 2000). The purpose of this experimental design was to evaluate the relative contributions of the physicochemical and hydrological, and substrate variables on egg survival. Due to the experimental nature of our study, we assumed that any bias related to the incubators used in the stream and lake habitats (see below) had the same relative effect on hatching and emergence success between selected and non-selected sites.

Stream habitat The incubators used in these experiments are described in Bernier-Bourgault *et al.* (2005). They are cylindrical (12.3 cm height × 8.1 cm diameter) and made of a polyvinyl chloride (PVC) grid (slots of 20 mm × 1.5 mm) that allows water to flow through from all directions. A fry trap (10.0 cm height × 8.1 cm diameter) is fixed over the incubator to allow sampling of the emergent larvae. The incubators were inserted into the substrate to a depth of ~ 15 cm in a hole dug with a small shovel. The removed substrate was used as the incubation substrate in the incubators. Egg incubation began on 11 October 2001 and 15 October 2002 on the Les Étangs and Dickerman spawning grounds, respectively, and incubators were removed on 4 June 2002 and 16 May 2003. Hatching success was estimated by comparing the number of eggs incubated with the number of live eggs found in the incubators and the number of larvae found in the emergence trap (percent hatching) at the end of the experiment. Similarly, emergence success was estimated from the number of larvae found in the emergence trap (percent emergence).

Lake habitat Because the incubators used in the stream experiments were not efficient in still water (based on the 1997–1998 trials), we built incubation boxes to incubate eggs in the various substrates. These incubators were 11 cm long × 8 cm wide × 5 cm deep, made with a PVC plastic grid (1 mm width, 20 mm length; the same as the incubators designed by Bernier-Bourgault *et al.*, 2005). The incubators were inserted into the ground to a depth of 5 cm in a hole dug with a small shovel. Egg incubation began on 6 October 1998 and incubators were removed on 25 May 1999.

Statistical analyses

The geometric particle diameter and mean proportion of particles in each size class were compared between selected and non-selected sites with a paired student *t*-test (*t*) or a Wilcoxon signed rank sum test (S), depending on the normality of the data and the homogeneity of variances. Data were arcsin transformed before analysis. Surface water velocity and groundwater flow were compared between selected and non-selected sites (site effect, a fixed effect) while controlling for both the sampling period (time effect, a fixed effect with repeated measures) and the block effect related to the sampling stations (station effect, a random effect) with a mixed model approach (MIXED procedure of SAS 9.1.3; 2002 SAS package). Mean dissolved oxygen, temperature and conductivity in interstitial waters were compared between selected and non-selected sites (site effect, a fixed effect) and among sampling periods (time effect, a fixed effect with repeated measures) with a two-way mixed model also taking into account the block effect related to the sampling station (station effect, a random effect). These designs allowed us to avoid pseudoreplication by properly handling the block and repeated measures effects. When the main test was significant, we used post-hoc pairwise comparisons of adjusted values (i.e. least square means). The effects of substrate (Astro-turf™, selected or non-selected) and site (selected or non-selected) on hatching and emergence success were investigated with a two-way mixed model followed by post-hoc pairwise comparisons of adjusted values. The interaction terms including fixed factors and the time effect were also included in the models if their inclusion improved their fit, as indicated by the Akaike Information Criterion corrected for small samples (AICc; Burnham & Anderson, 2002). AICc was also used to choose the best covariance structure for both random and repeated factors (Littell *et al.*, 1996; Verbeke & Molenberghs, 2000). For random factors, we tested four possible covariance structures: (i) variance components, (ii) compound symmetry, (iii) Huynh–Feldt and (iv) unstructured. For repeated factors, we also tested (*v*) an autoregressive of order one (AR1) covariance structure. For each model, we compared all possible combinations of these covariance structures. The model with the smallest AICc was selected. The same procedure was conducted on log- or rank-transformed data when the data were not normally distributed; a graphical inspection of the residuals was used to select the best transformation. Homogeneity of variances was tested with the Levene test for one-way models or evaluated graphically for more complex ones (mixed models). Since we were interested here in fixed factors related to the main hypotheses and not in temporal or block effects, the results related to these latter effects are not presented. All statistical analyses were performed with the SAS software (version 9.1.3).

Results

Hydrological and substrate characteristics

Les Étangs spawning ground (stream habitat) No significant differences were observed in the mean geometric particle diameter (Dg) between selected and non-selected sites on the Les Étangs spawning ground (Table 1), whereas the mean proportion of particles showed some significant differences for some size classes (Fig. 1). Particles with sizes from 1 to 1.99 mm, 2 to 3.99 mm, and 4 to 7.99 were significantly more abundant in selected than in non-selected sites (1–1.99 mm: $S = -17$, $P = 0.0156$; 2–3.99 mm: $t = -4.32$, $P = 0.0035$; 4–7.99 mm: $S = -18$, $P = 0.0078$; Fig. 1) even though the visual assessment of the substrate had been similar. Particles < 1 mm tended to be significantly more abundant in non-selected than in selected sites (Wilcoxon signed rank sum test: $S = 14$, $P = 0.0547$; Fig. 1). No significant differences were found for the other size classes (8–15.99 mm: $S = -12$, $P = 0.1094$; 16–24.99 mm: $S = -12$, $P = 0.1094$; > 25 mm: $S = 6$, $P = 0.3750$; Fig. 1). The mean surface water velocity showed no significant difference between selected and non-selected sites (site: $F_{1,14} = 4.14$, $P = 0.0543$; Table 2), while the mean upwelling groundwater flow was significantly higher in selected than in non-selected sites (site: $F_{1,8.23} = 6.12$, $P = 0.0377$; Table 2).

Dickerman spawning ground (stream habitat) No significant difference was observed in the mean geometric particle diameter (Dg) between selected and non-selected sites on the Dickerman spawning ground (Table 1). Particle sizes smaller than 1 mm were significantly more abundant in non-selected than in selected sites ($S = 15$, $P = 0.0391$) whereas those from 1 to 1.99 mm were significantly more abundant in selected than in non-selected sites ($S = -15$, $P = 0.0391$) even though visual assessment of the substrate had been similar. No significant differences were found between selected and non-selected sites for any of the other particle size classes (2–3.99 mm: $S = -11$, $P = 0.1484$; 4–7.99 mm: $S = -11$, $P = 0.1484$; 8–15.99 mm: $S = -8$, $P = 0.3125$; 16–24.99 mm: $S = -10$, $P = 0.1953$; > 25 mm: $S = -1.5$, $P = 0.50$;

Table 1 Geometric mean substrate diameter (mm) in selected and non-selected sites in stream (Les Étangs and Dickerman) and lake (St-Michel) habitats. Data are mean ± SD with sample size in parentheses

Location (period)	Selected substrate size (mm)	Non-selected substrate size (mm)	Statistic	*p*
Les Étangs (2001–2002)	3.7 ± 0.7 (8)	4.57 ± 1.6 (8)	1.24	0.269
Dickerman (2002–2003)	2.1 ± 1.0 (8)	1.9 ± 0.7 (8)	0.35	0.732
St-Michel (1997–1998)	2.5 ± 5.8 (6)	2.1 ± 0.4 (6)	-6.5*	0.219
St-Michel (1998–1999)	5.2 ± 2.6 (10)	2.9 ± 3.4 (10)	-18.5*	0.065

*Indicates the *S* statistic for the Wilcoxon signed rank test; otherwise the statistic is a Student's *t*.

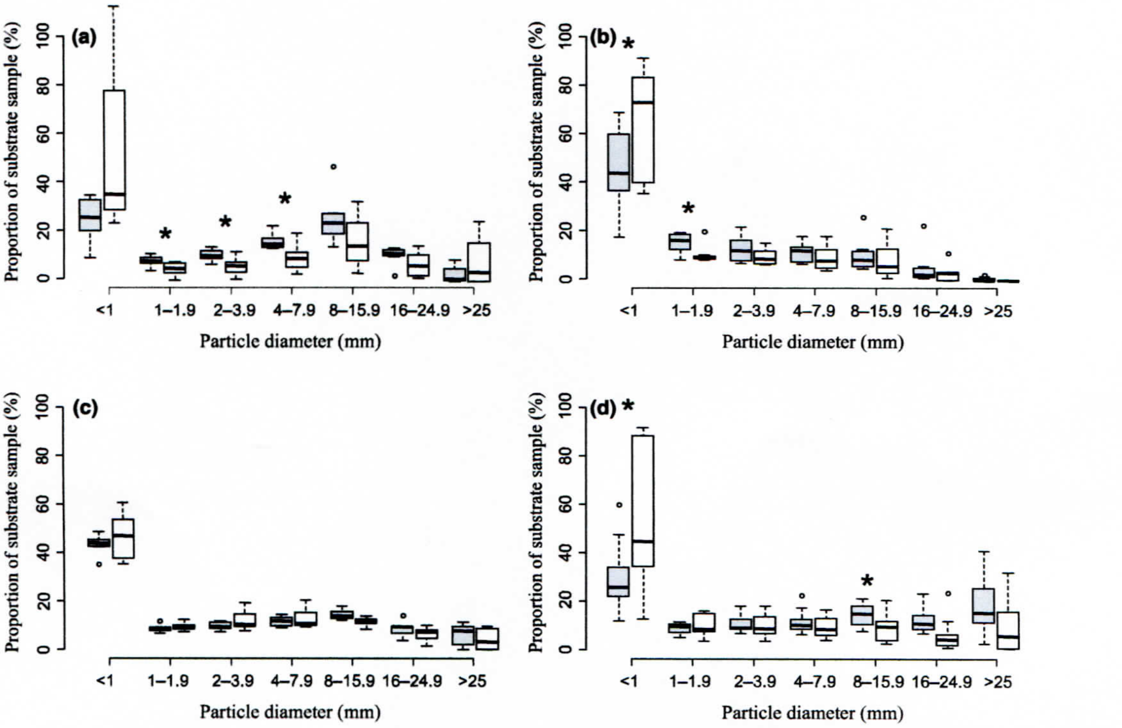

Fig. 1. Mean proportions of particle size diameters (mm) in selected (gray bars) and non-selected (white bars) sites of the Les Étangs (a), Dickerman (b), and Lake St-Michel (c: 1997–1998; d: 1998–1999) spawning grounds. Number of replicates were 8, 8, 6, and 10 in (a), (b), (c), and (d), respectively. Bars are means with SD. For each particle size class, data with asterisks are significantly different ($P < 0.05$). See text for details.

Table 2 Surface water velocity (m s^{-1}; stream habitat only) and upwelling groundwater flow (ml min^{-1}) in selected and non-selected sites in stream (Les Étangs and Dickerman) and lake (St-Michel) habitats. Data are mean ± sd with sample size in parentheses. For a given variable (surface water velocity or upwelling groundwater flow), means with different letters are significantly different as determined by a two-way mixed model testing for the effects of site, time, and their interactions ($P < 0.05$)

Location (period)	Variable	Selected	Non-selected
Les Étangs (2001–2002)	Surface water velocity	0.127 ± 0.158 (40)a	0.133 ± 0.164 (40)a
	Upwelling groundwater flow	3.222 ± 1.403 (37)a	2.228 ± 1.600 (36)b
Dickerman (2002–2003)	Surface water velocity	0.113 ± 0.095 (16)a	0.192 ± 0.106 (16)b
	Upwelling groundwater flow	3.530 ± 1.136 (31)a	2.299 ± 0.988 (31)b
Lake St-Michel (1997–1998)	Upwelling groundwater flow	4.348 ± 4.227 (6)a	1.762 ± 3.333 (6)b
Lake St-Michel (1998–1999)	Upwelling groundwater flow	4.720 ± 1.167 (10)a	0.000 ± 0.000 (10)b

Sample size represents the total number of measures per site. These repeated measures were accounted for in the mixed model (see text).

Fig. 1). The mean surface water velocity was significantly higher in non-selected than in selected sites (site: $F_{1,22} = 33.9$, $P < 0.0001$; Table 2), while the mean upwelling groundwater flow was significantly higher in selected than in non-selected sites (site: $F_{1,14.1} = 8.11$, $P = 0.0129$; Table 2).

Lake St-Michel spawning ground (lake habitat) No significant differences were observed in the mean geometric particle diameter (Dg) between selected and non-selected sites in either study year (Table 1) or in the mean proportion of particles in each size class ($P > 0.05$) on the St-Michel spawning ground in 1997–1998. Only the mean percent of particles < 1 mm and those from 8 to 15.99 mm were significantly different between selected and non-selected sites in 1998–1999 ($S = 21.5$, $P = 0.0273$; $S = -23.5$, $P = 0.0137$, respectively; Fig. 1). The mean upwelling groundwater flow was significantly higher in selected than in non-selected sites in both years (1997–1998, site: $F_{1,61.3} = 26.4$, $P < 0.0001$; 1998–1999, site: $F_{1,9} = 164$, $P < 0.0001$; Table 2).

Physicochemical characteristics

Les Étangs spawning ground (stream habitat) Dissolved oxygen of interstitial water was significantly higher in selected than in non-selected sites ($F_{1,58.9} = 16.8$, $P < 0.001$; Table 3), whereas neither temperature nor conductivity differed significantly between the two types of sites ($F_{1,13.6} = 0.25$, $P = 0.627$ and $F_{1,58.8} = 0.27$, $P = 0.614$, respectively; Table 3).

Dickerman spawning ground (stream habitat) Temperature and conductivity of interstitial water were, respectively, significantly higher and lower in selected than in non-selected sites ($F_{1,4.93} = 10.4$, $P = 0.0237$ and $F_{1,6.93} = 7.15$, $P = 0.0325$, respectively; Table 3). In contrast, dissolved oxygen did not differ ($F_{1,14} = 0.00$, $P = 0.961$; Table 3).

Lake St-Michel spawning ground (lake habitat) In 1997–1998, interstitial water temperature did not differ significantly between selected and non-selected sites ($F_{1,74.7} = 0.54$, $P = 0.464$; Table 3) while dissolved oxygen was significantly higher in selected sites ($F_{1,84.6} = 21.33$, $P < 0.001$; Table 3). Conductivity was not measured in 1997–1998 in Lake St-Michel. Both temperature ($F_{1,9} = 5.48$, $P = 0.044$; Table 3) and dissolved oxygen ($F_{1,18} = 7.61$, $P = 0.0129$; Table 3) were significantly higher in selected sites in 1998–1999. Conductivity did not differ between the two types of sites in 1998–1999 ($F_{1,9} = 1.29$, $P = 0.286$; Table 3).

Table 3 Physicochemical variables in interstitial water of selected and non-selected sites: O_2 = dissolved oxygen (mg L^{-1}); T = temperature (°C); Cond = conductivity ($\mu S\ cm^{-1}$). Data are mean ± SD with sample size in parentheses. For a given variable (O_2, T, Cond), means with different letters are significantly different as determined by a two-way mixed model testing for the effects of site, time, and their interactions ($P < 0.05$)

Location (period)	Variable	Selected	Non-selected
Les Étangs (2001–2002)	O_2	10.35 ± 1.94 (37)a	8.81 ± 2.06 (35)b
	T	1.96 ± 3.78 (37)a	5.00 ± 4.10 (35)a
	Cond	29.53 ± 37.59 (37)a	33.55 ± 37.59 (35)a
Dickerman (2002–2003)	O_2	9.83 ± 0.99 (40)a	9.71 ± 1.16 (40)a
	T	4.93 ± 2.55 (40)a	4.94 ± 2.94 (40)b
	Cond	20.0 ± 6.97 (16)a	30.54 ± 14.71 (16)b
Lake St-Michel (1997–1998)	O_2	9.23 ± 3.43 (108)a	8.27 ± 4.15 (106)b
	T	3.68 ± 4.35 (101)a	3.81 ± 4.28 (100)a
	Cond	—	—
Lake St-Michel (1998–1999)	O_2	5.94 ± 1.26 (10)a	3.46 ± 2.35 (10)b
	T	12.19 ± 0.90 (10)a	11.62 ± 0.99 (10)b
	Cond	11.07 ± 3.83 (10)a	13.11 ± 4.53 (10)a

Sample size represents the total number of measures per site. These repeated measures were accounted for in the mixed model (see text).

Hatching and emergence success

Les Étangs spawning ground (stream habitat) The two-way mixed model revealed significant effects of site and substrate on hatching success (site: $F_{1,35} = 6.32$, $P = 0.017$; substrate: $F_{2,35} = 6.18$, $P = 0.005$; site × substrate: $F_{2,35} = 2.93$, $P = 0.067$; data log-transformed) and emergence success (site: $F_{1,35} = 5.62$, $P = 0.023$; substrate: $F_{2,35} = 5.93$, $P = 0.006$; site × substrate: $F_{2,35} = 2.27$, $P = 0.118$). Hatching and emergence success were significantly higher in selected than in non-selected sites (Table 4). Furthermore, hatching and emergence success were significantly higher in Astro-turf™ than in selected substrates, whereas non-selected substrates showed intermediate values for both variables (but not significantly different between Astro-turf™ and Selected substrate; Table 4).

Dickerman spawning ground (stream habitat) The two-way mixed model revealed significant effects of site and substrate on hatching success (site: $F_{1,34.2} = 45.94$, $P < 0.0001$; substrate: $F_{2,34.2} = 9.38$, $P = 0.0006$; site × substrate: $F_{2,34.2} = 4.30$, $P = .021$; data log-transformed) and emergence success (site: $F_{1,34.1} = 44.16$, $P < 0.0001$; substrate: $F_{2,34.1} = 11.82$, $P = 0.0001$; site × substrate: $F_{2,34.1} = 6.27$, $P = 0.0048$). Hatching and emergence success were significantly higher in selected than in non-selected sites (Table 4). Furthermore, hatching and emergence success were significantly higher in Astro-turf™ and selected substrates than in non-selected substrates (Table 4).

Lake St-Michel spawning ground (lake habitat) The two-way mixed model revealed significant effects of site and substrate on hatching (site: $F_{1,40.8} = 12.4$, $P = 0.0011$; substrate: $F_{2,41.3} = 9.05$, $P = 0.0005$; site × substrate: $F_{2,40.6} = 0.33$, $P = 0.7178$; data log-transformed). Hatching success was significantly higher in selected than in non-selected sites (Table 4).

Table 4 Mean percent hatching and emergence success (± SD) in selected and non-selected sites, and in Astro-turf™, selected, and non-selected substrates in the Les Étangs (2001–2002), Dickerman (2002–2003) and Lake St-Michel (1998–1999) spawning grounds. Emergence was not assessed in Lake St-Michel (see text). For a given factor (site or substrate), means with different letters are significantly different as determined by a two-way mixed model followed by post-hoc multiple comparisons tests ($P < 0.05$)

		Site		Substrate		
	(%)	Selected	Non-selected	Astro-turf™	Selected	Non-selected
Les Étangs	hatching	16.7 ± 10.0 (24)a	13.6 ± 12.8 (24)b	22.1 ± 11.4 (16)a	9.4 ± 9.0 (16)b	13.9 ± 10.5 (16)ab
	emergence	12.6 ± 7.9 (24)a	10.3 ± 9.5 (24)b	16.9 ± 8.6 (16)a	6.9 ± 6.3 (16)b	10.6 ± 8.5 (16)ab
Dickerman	hatching	29.1 ± 29.5 (24)a	4.8 ± 16.2 (24)b	33.3 ± 35.1 (16)a	15.1 ± 20.7 (16)a	2.4 ± 4.5 (16)b
	emergence	24.0 ± 26.2 (24)a	3.0 ± 12.3 (24)b	28.3 ± 31.0 (16)a	10.8 ± 16.1 (16)a	1.3 ± 3.0 (16)b
St-Michel	hatching	78.2 ± 16.3 (27)a	62.3 ± 18.7 (28)b	60.1 ± 24.0 (20)a	81.4 ± 13.9 (19)b	69.2 ± 8.4 (16)ab
	emergence	—	—	—	—	—

Three incubators with three different substrate types were placed in each site. Les Étangs, Dickerman and St. Michel = 8, 8, and 10 replicates per selected and non-selected sites, respectively (excluding missing data).

Furthermore, hatching success was significantly higher in selected sites than in Astro-turf™ whereas non-selected substrates showed intermediate values (but not significantly different between Astro-turf™ and Selected substrate; Table 4).

Discussion

The results of this study show that sites selected by spawning individuals clearly differ from non-selected ones. The most striking difference is the higher upwelling groundwater in selected than in non-selected sites in both lake and stream habitats. The other studied variables showed some – but not consistent – differences between selected and non-selected sites. These results suggest that the main cue that brook charr use to select their spawning site is upwelling groundwater. Our results also show that there is a positive relationship between the selection of a given spawning habitat and the individual fitness in these systems. Although many studies have investigated the role of habitat characteristics on spawning site selection of fish, we know of none that were designed to experimentally determine the effect of spawning site selection on reproductive success *in situ*. This relationship is the main assumption of current habitat selection models, and it is important to better understand what factors drive the evolution of fish in these systems.

Redd site selection

Three mechanisms are currently hypothesised to explain redd site selection in brook charr and related salmonids: the use of (i) substrate composition, (ii) groundwater flow and (iii) physicochemical gradients between interstitial and surface water as cues for spawning site selection. However, very few studies have used an experimental approach to test these hypotheses and to separate the contribution of substrate from the other components (groundwater flow and physicochemical characteristics of ambient water).

Substrate composition hypothesis Many studies characterised the substrate composition of salmonid redds, and some of these suggested that substrate could be involved in spawning site selection (Witzel & MacCrimmon, 1983b; Essington *et al.*, 1998; Soulsby *et al.*, 2001). However, the few studies examining substrate composition at the beginning of the spawning period found no significant differences between selected and non-selected sites (Young, Hubert & Wesche, 1989; Curry *et al.*, 1995; Essington *et al.*, 1998). Similarly, we found no significant difference in mean geometric substrate diameter and no consistent differences in substrate composition between selected and non-selected sites of our studied lake and streams, with the exception of the Dickerman (stream habitat) and St-Michel (1998–1999; lake habitat) study sites, both of which exhibited a significantly higher proportion of fine sediments (< 1 mm diameter) in non-selected redds. Fine sediments were found to be detrimental to egg and larva survival, time to emergence, and emergence in brook charr (Hausle & Coble, 1976; Witzel & MacCrimmon, 1983a; Curry & MacNeill, 2004) and other salmonids (Dill & Northcote, 1970; Witzel & MacCrimmon, 1981; Levasseur *et al.*, 2006).

However, in Les Étangs (stream habitat) and Lake St-Michel (lake habitat; 1997–1998), brook charr built their redds in sites where the proportion of fine sediments did not differ from that of non-selected sites (note that in Lake St-Michel, we positioned the non-selected sites in areas with a substrate composition similar to that of selected sites in 1997–1998). Even if fine sediment can have a negative impact on the reproductive success of individuals, this factor does not seem to be involved in spawning site selection at these sites.

Groundwater flow hypothesis Previous studies have shown that many salmonid species select zones with groundwater sources when establishing spawning sites, although some also spawn in areas without groundwater flow (*S. fontinalis*: Webster & Eiriksdottir, 1976; Carline, 1980; Fraser, 1982, 1985; Witzel & MacCrimmon, 1983b; Snucins, Curry & Gunn, 1992; Curry & Noakes, 1995; Curry *et al.*, 1995; Blanchfield & Ridgway, 1997; Essington *et al.*, 1998; *S. alpinus* (L.): Cunjak, Power & Barton, 1986; *S. confluentus* (Suckley): Baxter & Hauer, 2000; *Salmo trutta* L.: Hansen, 1975; Witzel & MacCrimmon, 1983b; *Oncorhynchus mykiss* (Walbaum): Sowden & Power, 1985; *O. tshawytscha* (Walbaum): Geist, 2000; *O. nerka* (Walbaum): Lorenz & Eiler, 1989). Our results clearly show that upwelling groundwater flow was always significantly higher in selected than in non-selected sites in both lake and stream habitats. Our results and those of Blanchfield & Ridgway (1997) also suggest that brook charr spawn solely at sites with upwelling groundwater. Curry & Noakes (1995) found no statistical differences in groundwater flow with distance from redds in their five study sites. However, they observed that brook charr spawning was always associated with areas of upwelling groundwater and that mean specific discharge declined with distance from the redd. These authors set the significance levels to 0.01 in their statistical analyses to reduce type I errors resulting from multiple testing (Curry & Noakes, 1995). Although we recognise that type I errors are an important issue (Peres-Neto, 1999), we did not attempt to correct probability values for multiple tests given that well-established standard corrections such as the Holm's sequential Bonferroni correction can be extremely conservative (i.e. increase type II errors; Moran, 2003). Therefore, we cannot rule out that the results of Curry & Noakes (1995) are biased toward an inflated type II error. Blanchfield & Ridgway (1997) found that upwelling groundwater flow was significantly higher at spawning sites than at random unused sites in a Canadian Shield lake. Similarly, Witzel & MacCrimmon (1983b) and Essington *et al.* (1998) found that brook charr strongly preferred sites with upwelling groundwater compared to brown trout, which spawned in a wide range of flows in small streams.

Additional evidence that upwelling groundwater is an important cue for individuals when selecting spawning sites was provided by the experiment of Webster & Eiriksdottir (1976). These authors presented suitable gravel containing an artificially controlled aquifer of about 1% of the area of a 1.9 m^2 circular tank to female brook charr and observed that individuals selected spawning sites that were either close or adjacent to the upwelling water in 21 out of 22 trials. Finally, Webster & Eiriksdottir (1976), Fraser (1982) and Blanchfield & Ridgway (1997) observed that lacustrine brook charr spawned successfully in a wide variety of atypical substrates (sandy and silted substrates, waterlogged sticks, and woody debris), but always over areas of upwelling groundwater. We found that brook charr from Dickerman (stream habitat) and St-Michel (1997–1998; lake habitat) selected sites having more than 40% of fine sediments (median values), which is very high compared to the typical substrate composition for this species (Witzel & MacCrimmon, 1983a). However, these sites provided significantly higher upwelling groundwater flow than non-selected ones. The selection of spawning sites by brook charr over such a wide range of substrates suggests that upwelling groundwater is more important than substrate composition in redd site selection (Fraser, 1982; Witzel & MacCrimmon, 1983b; Blanchfield & Ridgway, 1997).

Chemical gradient hypothesis Many authors have suggested that physicochemical gradients created by upwelling water mixing groundwater with surface water could act as cues for salmonids when selecting spawning sites (Lee & Hynes, 1977; Blanchfield & Ridgway, 1997; Geist, 2000). To be effective, such a mechanism requires that physicochemical characteristics differ between selected and non-selected sites. Selected sites are generally characterised by higher (i) oxygen concentration (Curry *et al.*, 1995; Geist, 2000), (ii) temperature (Benson, 1953; Curry *et al.*, 1995) and

(iii) conductivity (Curry & Noakes, 1995; Blanchfield & Ridgway, 1997) than non-selected sites. However, Geist (2000) observed that conductivity of the hyporheic discharge was lower in sites frequented by spawning than non-spawning chinook salmon (*O. tshawytscha*) in streams of the Hanford Reach, the last impounded section of the mainstem Columbia River (U.S.A.). In our system, the physicochemical variables showed some differences between selected and non-selected sites. The oxygen concentration was higher (significantly so in three of four comparisons) and conductivity tended to be lower in selected than in non-selected sites while temperature showed no significant or consistent variations. In this context, it is possible that gradients in oxygen concentration and conductivity could provide cues for adult brook charr to locate their spawning sites, as suggested by Blanchfield & Ridgway (1997) and Geist (2000). However, no study (including ours) was able to discriminate the independent effects of the physicochemical gradient because it was always confounded with groundwater flow. Only a controlled experiment could allow one to disentangle the effects of the physicochemical gradient from that of groundwater flow.

Relationship between redd site selection and individual fitness

Although it is not yet possible to determine the independent contributions of upwelling groundwater and physicochemical gradient to redd site selection in brook charr (and in other salmonids), our study demonstrated that selected spawning sites result in higher individual fitness. Both hatching and emergence success were significantly higher in selected than in non-selected sites in both lake and stream habitats when the incubation substrate was accounted for in the statistical analyses. As we found no consistent difference in the hatching and emergence success between selected and non-selected incubation substrates nor any significant site × substrate interactions, site was the main effect explaining hatching and emergence success in our experiment, suggesting a determinant role for upwelling water. The emergence and hatching success were on average 19% higher in selected than non-selected sites in Les Étang (stream habitat) and St-Michel (lake habitat) and 86.5% higher in Dikerman (stream habitat). The much lower emergence and hatching success observed in non-selected sites in Dickerman were probably due to the higher proportion of fine sediments in this stream; this idea is supported by the fact that the substrate effect between selected and non-selected sites was significant only in this stream.

In this study, we used Astro-turf™ as an incubation substrate to investigate the role of hydrological factors on both hatching and emergence success of brook charr because this material allows egg incubation with no sediments (Lachance *et al.*, 2000). Surprisingly, the hatching and emergence success in the Astro-turf™ was comparable to selected and non-selected sites. Hatching and emergence success tended to be higher in Astro-turf™ than in incubators containing substrate in the stream habitat, but these differences were not significant. This result suggests a negative effect of natural substrate in streams on developmental processes but would need further investigation to be explicitly tested. In contrast, we observed a lower hatching success in Astro-turf™ than in natural substrates in the lake habitat, probably because of the accumulation of fine sediment in the incubators (F. Guillemette and P. Magnan, personal observations). This supports the interpretations of Curry *et al.* (1995) and Blanchfield & Ridgway (1997) that groundwater flow would be more important in lakes than in streams because there is much less water movement in lake habitats during the incubation period.

Curry *et al.* (1995), who monitored brook charr emergence with traps in five redds equipped with mini-piezometer, found that the lowest survival rate was observed in the redd with the least groundwater discharge, supporting our conclusions. Similarly, Curry & MacNeill (2004), who studied emergence success of brook charr at six sites with heavy sediment loads (Prince Edward Island, Canada), found that survival to emergence was the highest at sites with the highest upwelling groundwater. Although they support our results, these works did not allow a comparison of hatching success of selected vs. non-selected sites or a determination of the independent contribution of substrate from the other components (groundwater flow and physicochemical gradient). For example, our results showed that upwelling groundwater was observed everywhere except in the non-selected sites from St-Michel (1998–1999), suggesting that a minimum specific discharge is required to have a positive effect on hatching and emergence success.

Hatching and emergence success were low in the two streams. However, Bernier-Bourgault *et al.* (2005) reported that the incubators used in the present study provided emergence success comparable to other similar incubators used for salmonids. For example, Cunjak *et al.* (2002) observed egg-to-emergence success varying between 0 and 85% for brook charr and between 0 and 56% for Atlantic salmon embryos (mean < 15% for both species) incubated in ten incubators (Bardonnet & Gaudin, 1990) filled with natural substrate. Rubin (1995) observed egg-to-fry survival ranging from 0 to 75% (mean ± SD: 25.9% ± 27.8; estimated from their Table 4) for brown trout incubated in modified MacCrimmon, Gots & Witzel (1989) experimental boxes. This suggests that values observed in the present study are within the expected range of emergence in the field.

Different mechanisms have been suggested to explain the higher hatching and emergence success in spawning sites selected by salmonids. Upwelling groundwater could provide stable and suitable oxygen and thermal regimes during incubation (Sowden & Power, 1985; Chapman, 1988; Curry *et al.*, 1995). As also observed by Curry *et al.* (1995), the upwelling groundwater persisted throughout the incubation periods in the brook charr redds in all our study sites and remained within the range of suitable conditions (results not shown here). Upwelling groundwater could also remove metabolic wastes from the incubation environment (Silver *et al.*, 1963; Sowden & Power, 1985) and prevent fine sediment accumulation on the egg surface, thus allowing oxygen exchange between the egg and ambient water (Curry & MacNeill, 2004). Finally, upwelling groundwater could play a crucial role in protecting the redds from cold surface waters and freezing during winter (Fraser, 1985; Gunn, 1986; Curry *et al.*, 1995). However, more specific experimental studies will be needed to determine the exact mechanism responsible for the higher individual fitness in selected sites.

In conclusion, the results of the present study demonstrate the importance of upwelling groundwater on small-scale redd site selection by brook charr in both lake and stream habitats, and that the active selection of these sites increases individual fitness. This suggests that natural selection acted on the same cues in lentic and lotic environments, which could have been highly adaptive in a species that used both habitats as colonisation routes after the last glaciation.

Acknowledgments

We thank M. Audet, C. Baril, M. Baril, J. Bergeron, S. Bouliane, M.-F. Côté, Y. Branchaud, S. Garceau, S. Labrie, and P. Tanguay for their field assistance, P. East and M. Lapointe for their invaluable logistic support, and L. Devine for her comments on an earlier version of this manuscript. We also thank Mr David Craig, founder of the Fondation pour la sauvegarde de la truite mouchetée, for his great dedication and support throughout this research program. This study was primarily supported by the Fondation pour la sauvegarde de la truite mouchetée. Secondary funds were provided by the Canada Research Chair Program and the Natural Sciences and Engineering Research Council (NSERC) of Canada to P. Magnan.

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(Manuscript accepted 4 November 2010)