

The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine brook trout (*Salvelinus fontinalis*)

Paul J. Blanchfield and Mark S. Ridgway

Abstract: Egg losses for female salmonines primarily occur through competition for egg incubation sites (i.e., redds) and the differences in quality among these sites. Through detailed observations and an experiment linking egg survival to groundwater flow, we estimated the relative influence of redd superimposition and habitat quality on female reproductive success for a population of lake-spawning brook trout (*Salvelinus fontinalis*). Three quarters of all spawning sites were reused by multiple females; however, brood loss was much less (28%–38%) because large females spawned earlier and constructed deeper nests. The relationship between groundwater flow rate and egg survival was not linear, with consistent egg survival occurring only at sites with flows over 20 mL·m⁻²·min⁻¹. Varying scenarios of redd superimposition and habitat-related egg survival resulted in an estimated 4%–21% of deposited eggs surviving to emergence and greatly reduced the size-related advantages of larger females owing to fecundity. Limited numbers of high-quality spawning sites and overall low survival of eggs resulted in habitat being the dominant route of egg loss. In the absence of female competition, spawning habitat alone accounted for egg losses of 67%–91% and points to the importance of physical habitat features in the maintenance of brook trout populations.

Résumé : Les pertes d'oeufs chez les femelles des salmoninés se produisent à cause de la compétition pour les sites d'incubation des oeufs (i.e. nids) et des différences de qualité de ces sites. Des observations détaillées et une expérience mettant en relation la survie des oeufs et l'écoulement des eaux souterraines nous ont permis d'estimer l'importance relative de la superposition des nids et de la qualité de l'habitat sur le succès reproductif des femelles dans une population d'ombles de fontaine (*Salvelinus fontinalis*) qui se reproduisent en lac. Trois-quart de tous les sites de ponte sont utilisés successivement par plusieurs femelles; cependant, les pertes des masses d'oeufs sont moins importantes (28–38 %) parce que les grosses femelles pondent plus tôt et construisent des nids plus profonds. La relation entre le taux d'écoulement de l'eau phréatique et la survie des oeufs n'est pas linéaire et il ne se produit de survie uniforme des oeufs qu'au sites ayant un écoulement supérieur à 20 mL·m⁻²·min⁻¹. Divers scénarios de superposition des nids et de survie des oeufs en fonction de la qualité de l'habitat nous amènent à estimer que 4–21 % des oeufs pondus survivent jusqu'à l'émergence, ce qui réduit considérablement les avantages reliés à la taille chez les grosses femelles à fécondité plus élevée. Les nombres limités de sites de ponte de grande qualité et la survie globale faible des oeufs ont comme conséquence que l'habitat est la cause principale de la perte des oeufs. En l'absence de compétition entre les femelles, l'habitat de ponte à lui seul explique 67–91 % des pertes d'oeufs, ce qui démontre l'importance des caractéristiques de l'habitat physique dans le maintien des populations d'ombles de fontaine.

[Traduit par la Rédaction]

Introduction

The theoretical limit of reproductive success in female salmonines is defined by the power function relating fecundity to body size. Achieving this limit is compromised by competition among females for access to spawning sites and differences in the physical characteristics of spawning sites.

Competition among females for spawning sites can be intense and superimposed redds (sequential use of a spawning site by more than one female salmonine) can limit reproductive success and recruitment (McNeil 1964; Essington et al. 2000; Hendry et al. 2001). Spawning site quality is largely defined by substrate composition and particle size, as well as water depth and flow (Reiser and Wesche 1977; Crisp and

Received 15 October 2004. Accepted 29 June 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 27 October 2005.
J18358

P.J. Blanchfield.^{1,2} Department of Biology, York University, 4700 Keele St., Toronto, ON M3J 1P3, Canada, and Harkness Laboratory of Fisheries Research, Ontario Ministry of Natural Resources, Aquatic Ecosystem Science Section, 3rd Floor North, 300 Water St., Peterborough, ON K9J 8M5, Canada.

M.S. Ridgway. Harkness Laboratory of Fisheries Research, Ontario Ministry of Natural Resources, Aquatic Ecosystem Science Section, 3rd Floor North, 300 Water St., Peterborough, ON K9J 8M5, Canada.

¹Corresponding author (e-mail: BlanchfieldP@dfo-mpo.gc.ca).

²Present address: Fisheries and Oceans Canada, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

Carling 1989; Bjorn and Reiser 1991). These physical features singly or in combination directly affect embryo survival in many salmonines (Chapman 1988). As a result of these factors, embryo survival can be low (16%–32%, McNeil 1966; 7%–20%, Godin 1982; Bradford 1995) and clearly below the limits defined by the relationship between body size and fecundity.

Observations of redd superimposition point to spawning site selection based on certain characteristics of habitat and highlight the possibility that spawning habitat is generally a limiting resource in this group of fishes. Certainly, observations associating specific habitat features (the trinity of water depth, flow, and substrate particle size) with redd distribution in the field are common (e.g., Hoopes 1972; Knapp and Vredenburg 1996) and support the idea that production of age-0 fish is a function of the supply of spawning habitat (Knapp et al. 1998). Despite the apparent linkage between spawning habitat characteristics and redd distribution, only recently have models of physical spawning habitat successfully predicted use in the field (Knapp and Preisler 1999; Geist 2000; Geist et al. 2000).

Some have cautioned against assuming that body size alone is a strong measure of reproductive success in this group of fishes because of the potential for reproductive success to be affected by competition among females and spawning habitat quality (Holtby and Healey 1986; McPhee and Quinn 1998). In one study on coho salmon (*Oncorhynchus kisutch*), redd superimposition accounted for greater losses of egg biomass than did habitat quality, with larger females losing proportionately less of their reproductive investment relative to smaller females (van den Berghe and Gross 1989). The exponential relationship between female size and egg biomass in the coho study was lowered as a result of the effects of both competition and habitat quality (gravel size and interstitial area for egg survival) but the general pattern remained unchanged; large females clearly had a reproductive advantage over smaller females in a manner similar to the power function relating fecundity to female body size (van den Berghe and Gross 1989).

The mating system of brook trout (*Salvelinus fontinalis*) in lakes provides a unique opportunity to quantify the influence of female reuse of spawning sites and habitat quality on the survival of young. Female brook trout compete for access to spawning sites where upwelling groundwater is present (Blanchfield and Ridgway 1997). The importance of groundwater for maintaining brook trout populations has been known for some time (Latta 1965), and in lakes, the presence of groundwater flow is thought to be the primary criterion for the selection of spawning sites by females (Fraser 1982; Curry and Noakes 1995; Blanchfield and Ridgway 1997). The flow of groundwater at spawning sites increases the survival from egg to emergence by providing a stable environment and removing metabolic wastes from developing embryos (Sowden and Power 1985; Curry et al. 1995). Groundwater sites also shorten the time required for development to a free-swimming stage because groundwater is generally warmer than ambient water temperatures during the incubation period (Embrey 1934).

In this study, we extend our previous observations of a brook trout mating system (Blanchfield and Ridgway 1997, 1999; Blanchfield et al. 2003) to examine the key factors

limiting female reproductive success in a lake population. Extensive reuse of spawning sites, as well as rapid replacement of females during removal experiments, indicate that spawning sites can be limiting (Blanchfield and Ridgway 1997). The spatial distribution of spawning is highly skewed, with half of all spawning activity occurring at fewer than 20% of sites used (Blanchfield and Ridgway 1997). Breeding observations over 4 years have demonstrated that repeated use of specific redd sites is related to the rate of groundwater flow, with spawning activity occurring every year only at sites with higher seepage rates (Ridgway and Blanchfield 1998). The objective of this study was to determine the relative influence of female competition (redd superimposition) and habitat quality (groundwater seepage rate) on reproductive success of female brook trout. Reproductive success of females was not directly observed in the field but inferred when data on redd site use by females, female fecundity, and egg survival as a function of groundwater flow rate were combined. We chose this model approach for assessing reproductive success for two reasons. First, it allowed us to scope the range of egg survival based on variation in factors such as redd depth as a function of female size and egg survival as a function of groundwater flow. Second, the breeding adult population in Scott Lake is small (~70–190 individuals; Blanchfield and Ridgway 1997), so direct estimates of offspring production could potentially disrupt a relatively large proportion of adult spawners as well as a new cohort of brook trout. We also use these data to model, at the population level, the overall production of young after partitioning the main sources of egg mortality under natural breeding conditions.

Materials and methods

Study site

Scott Lake is a small, deep headwater lake (27.6 ha; maximum depth 25 m) located within Algonquin Park, Ontario (45°29'N, 78°43'W). The fish community is composed of *Culea inconstans*, *Pimephales promelas*, and *Phoxinus* spp. in addition to brook trout. The location of the spawning area and description of the site are provided in earlier publications (Blanchfield and Ridgway 1997; Ridgway and Blanchfield 1998; Blanchfield et al. 2003). The spawning area is somewhat more dispersed and individual redd sites are more distinct than observed in other brook trout lakes (Fraser 1985; Ridgway and Blanchfield 1998). The total spawning area is 829 m² and consists of six adjacent areas, each with a concentration of redds, with an overall redd density of 5.7 redds·100 m⁻².

Observations of female reproductive activity

Brook trout were captured and tagged in the middorsal area with t-tags, as well as numbered vinyl disk tags, to facilitate individual recognition of fish (see Blanchfield and Ridgway (1997) for details). Fish were initially captured using a 1.5-m trap net just prior to spawning (early October) and later with dip nets used by swimmers (with mask and snorkel) after spawning began. Fish were anaesthetized with tricainemethane sulfonate (MS 222) prior to tagging and fork length (millimetres) and weight (grams) for each fish were recorded. Most females in the spawning population

were marked (~80%) and their reproductive activities were documented on a daily basis during the breeding seasons. For fish that were not captured, or lost their tag during the breeding season, we estimated fork length (to within 5 cm) based on the size of other marked individuals that were in close proximity.

To monitor reproductive activities, we conducted a census of the spawning area four times daily (weather permitting) once spawning activity commenced (10 October in each year) until fish were no longer present on the spawning grounds (6 December 1994) or the lake surface was frozen (24 November 1995). During each census, the position of each female within the spawning area and its tag number were recorded on underwater slates by swimmers. Females were recorded as being on a redd site and spawning based on behavioural criteria. These criteria included digging behaviour for redd construction, guarding the redd from intrusion by other females before or after spawning, covering behaviour in which the female uses her caudal fin to cover the eggs deposited in the redd, and spawning behaviour (Blanchfield and Ridgway 1999). Collectively, these behaviours were interpreted as evidence of spawning at a particular redd site.

Redd superimposition and brood loss

Estimates of brood loss through redd superimposition were based on the depth of redds and the overlap that occurs in the construction of subsequent redds. The difference between the edge (unexcavated) and deepest part of an excavated redd in relation to the top of the water column was determined for 23 spawnings, each at a unique spawning site and by a different female (Steen and Quinn 1999). A regression of redd depth on female body size (fork length) was used to predict the egg burial depth of all females.

We recorded the number of spawnings that occurred at a specific site, the order in which they occurred, and the size of each female. Other studies that estimated the number of eggs sequentially deposited by females in a series of nests showed that there was reduction in eggs deposited in the last redds relative to egg deposition in the first redd (Maekawa and Hino 1990; Fleming 1996). We were unable to count the number of eggs deposited at each spawning, so we assumed that eggs were distributed equally among spawning events for females that spawned multiple times. Few data exist to resolve this assumption. In Atlantic salmon (*Salmo salar*), only marginal declines in the number of eggs deposited per nest were observed for females spawning in their first three redds (Fleming 1996). Female brook trout in Scott Lake spawn, on average, 2.7 times during the breeding season (Blanchfield and Ridgway 1997), so we have assumed that this does not result in declines in eggs per nest with each spawning. The redd depth criterion was used to determine whether the eggs deposited during individual spawning events were completely lost owing to multiple use of a single site by different females (van den Berghe and Gross 1989). Because we were not able to measure the size of every spawning female at Scott Lake, and therefore had to estimate size for some fish, we took two approaches to model egg loss owing to site reuse. We assumed a complete loss of one brood to superimposition for every spawning by later-

spawning females that were (i) larger or equal in size than earlier-spawning females and (ii) larger, equal, or <5 cm smaller in size than earlier-spawning females. Thus, only female size and corresponding digging depth were used to model egg losses owing to superimposed redds.

Estimates of habitat quality

Habitat quality in this study was the groundwater seepage rate at redd sites. Measurements of groundwater flow at spawning sites, as well as randomly chosen sites within the spawning area, were made prior to the start of the 1994, 1995, and 1996 breeding seasons using seepage meters (Blanchfield and Ridgway 1996, 1997; Ridgway and Blanchfield 1998). We included flow rates from 1996 to increase our sample size from which to model groundwater flow at sites that we did not measure in previous years. We used the mean rate of groundwater flow from all 3 years combined in our estimation of habitat quality because flow rate did not differ among years for 14 sites measured annually (repeated-measures analysis of variance: $F = 0.69$, $p = 0.51$). Based on the mean rates of groundwater flow at spawning and random sites within the breeding area ($n = 53$), an inverse distance weighting (IDW) interpolation method was used to predict rates of groundwater flow for all spawning sites ($n = 92$; Ridgway and Blanchfield 1998). IDW interpolation determines cell values using a linearly weighted combination of a set of sample points (ArcView software; Environmental Systems Research Institute 1992). By this method, an interpolated 1-m resolution raster grid of groundwater flow values was produced for the entire spawning area. The average of cell values within 1 m of each spawning site (i.e., the surrounding eight cells) was then calculated as the groundwater flow at that site.

Egg survival experiment

To determine the effect of groundwater flow (i.e., habitat quality) on egg survival at Scott Lake, we conducted an experiment using egg hatchboxes (Whitlock-Vibert; described in Garrett and Bennett 1996) during the 1997 breeding season. We measured groundwater flow using seepage meters (described above) at nine previously used spawning sites and at one random site located close (<2 m) to other spawning sites. We made separate crosses of the eggs of three ripe females (37.4–41.1 cm fork length) using two males, all anaesthetized lightly with MS 222. Eggs were incubated overnight in the lake, and the following day, 100 living eggs were placed in each hatchbox. Three hatchboxes, each containing 100 eggs of a different female, were buried in each of the spawning sites (~10 cm depth) and a mesh cover was placed over the buried egg boxes to prevent any disturbance from site reuse by spawning females. There were not equal numbers of eggs available from all females; thus, each set of three boxes did not always contain eggs from all three females ($n = 2$), and one box contained only 57 eggs (not included in analysis). Egg survival did not differ among females for the eight sites in which the eggs of all three females were present (analysis of variance: $F = 0.35$, $p = 0.71$). Egg boxes were left for a period of 88 days prior to retrieval, at which point the eggs were counted and scored as to survival and developmental stage. We considered missing

eggs as young that had emerged only if there were yolk sac fry (i.e., the stage just prior to emergence) present (alive or dead) in the hatchboxes. Egg survival was equal to the number of eggs alive in addition to the number of emerged young relative to the total number of eggs placed in the hatchboxes at the start of the experiment. Temperature was recorded hourly (Ryan TempMentors™, Ryan Instruments, Redmond, Washington) at six of the buried egg boxes to determine lake water temperatures during the incubation period.

Determination of female reproductive success

We did not sample the Scott Lake population to acquire a size–fecundity relationship because of the low numbers of adult females (~50–60 adult females; Quinn et al. 1994; Blanchfield and Ridgway 1997). Instead, we relied on the fecundity relationship of Vladykov (1956) ($Y = 30.487 \exp(0.01X)$, where Y is the number of eggs and X is female fork length in millimetres) to estimate egg numbers for female brook trout of different size. The additional question of egg size and survival has been addressed in other studies but was not part of this analysis.

Loss of eggs was inferred in the following way. Numbers of eggs deposited in redds was based on female size and the assumption of equivalent egg deposition per spawning for individual females that spawned multiple times. Our daily coverage of the spawning area captured whether or not female brook trout spawned at more than one site and if they spawned repeatedly at a single site (Blanchfield and Ridgway 1997). After accounting for egg loss owing to superimposition, the proportion of remaining eggs assumed surviving as a function of habitat quality (i.e., groundwater seepage rate) was determined based on the inferred flow of groundwater at spawning sites derived from the IDW model and the results from the egg survival experiment. Tag loss during the spawning season, late arrival of females onto the spawning grounds, and some breeding at night prevented an exact estimate of reproductive success for all females (Blanchfield and Ridgway 1997). A subset of females retained their individual tags throughout the spawning season and allowed us to estimate reproductive success for individuals of different size. Reproductive success was estimated for 31 females in 1994 (66% of all tagged females) and 29 females in 1995 (62% of all tagged females), which represents over half of the total estimated female spawning population in both years.

Population-level loss of eggs

Swimming the entire spawning area of Scott Lake four times daily over periods of 57 days (1994) and 45 days (1995) provided an opportunity to model the distribution of eggs among redds in a fully sampled mating system, that is, a mating system in which all spawning sites are known, as well as their frequency of use and the approximate size of females spawning in those sites. Population-level patterns of egg deposition and loss owing to habitat quality were based on two kinds of data. First, the distribution of seepage rates at all sites was derived from observed measurements using seepage meters and inferred values from the IDW model. Second, daily surveys of the spawning area and all redd sites

provided data for mapping female spawning on redds and the estimated number of eggs deposited in redds based on female size. The behavioural criteria described above for assigning spawning activities were also used in the spawning area survey. Egg loss was inferred at each redd based on the relationship between groundwater seepage rate and egg survival in the hatchbox experiment. Female identity was based on observed tags or previous sightings based on location, body size, and markings. In this mating system, not all females are active on a given day and the number spawning was always a subset of the female population (Blanchfield and Ridgway 1997).

Results

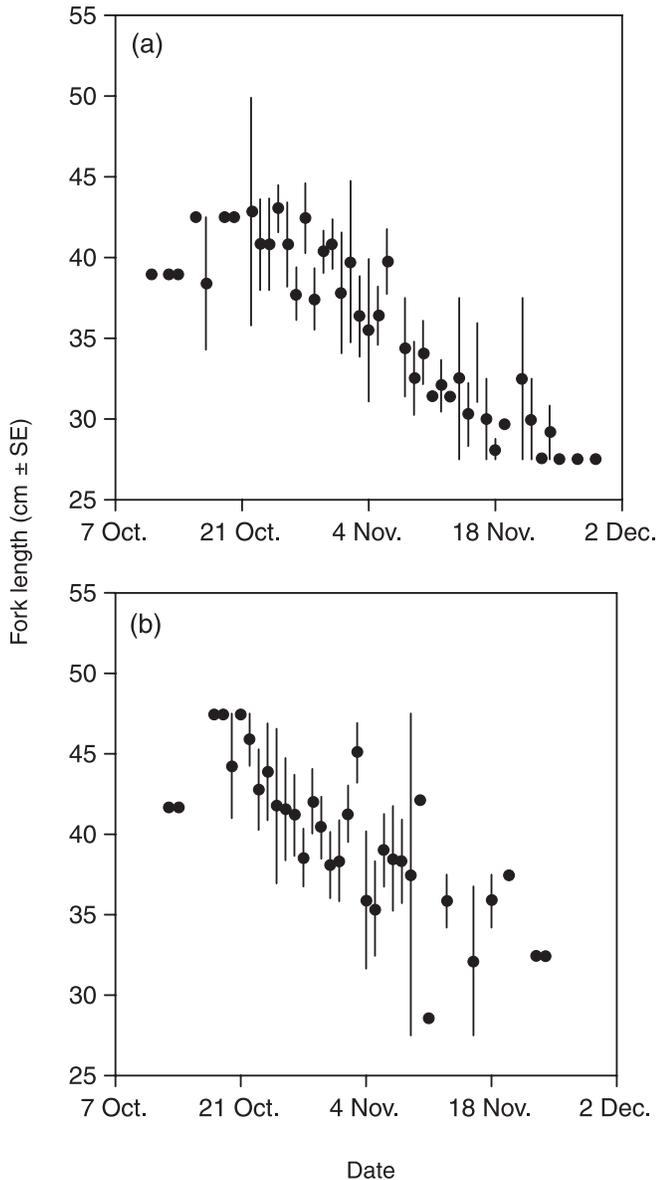
Seasonal timing of spawning, redd depth, and frequency of redd site reuse

The range in body size of spawning female brook trout was approximately 25 cm in both years (1994: 26.5–51.5 cm fork length; 1995: 26.5–51.9 cm fork length). Daily monitoring of the breeding activities at Scott Lake revealed that the size of spawning female brook trout decreased throughout each breeding season (1994: $F_{[1,161]} = 114.2$, $R^2 = 0.41$, $p < 0.001$; 1995: $F_{[1,173]} = 16.2$, $R^2 = 0.09$, $p < 0.001$) (Fig. 1). The residence time of large females (>40 cm fork length) on the spawning area is approximately 10–20 days (Blanchfield and Ridgway 1997) and therefore, the seasonal decline in size of spawning females represents a slow turnover in females as the season progresses. The depth at which female brook trout buried their eggs increased with body size ($Y = -0.97 + 0.23X$, where Y is nest depth and X is female fork length in centimetres; $F_{[1,21]} = 6.0$, $R^2 = 0.22$, $p = 0.022$) such that the largest females constructed redds that were, on average, twice the depth of redds of the smallest females in this population (Fig. 2). Overall, there was extensive reuse of redd sites in this mating system with spawning by multiple females occurring at roughly three quarters of redd sites (78% and 72% in 1994 and 1995, respectively) (Fig. 3). More than half of all redd sites were used by three or more spawning females. Owing to the earlier breeding by larger females and the positive relationship between nest depth and female body size (Fig. 2), the extensive reuse of sites resulted in a smaller fraction of brood loss stemming from superimposition. Nest destruction owing to superimposition was estimated at 28% (1994) and 30% (1995) of all spawnings that occurred during the two breeding seasons if later-spawning females at a given site were of equal or greater fork length. Our alternate estimate, in which we allowed for additional brood loss by later-spawning females that were smaller (by <5 cm) than earlier-spawning females, resulted in a greater incidence of nest destruction (38% for both breeding seasons).

Egg emergence experiment

After 88 days, little or no emergence occurred from redds with groundwater flows less than or equal to $20 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ (Fig. 4a). Eggs that were buried at redds with flow rates above $20 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ showed increasing emergence with flow rate. The proportion of brook trout embryos that emerged from within the buried hatchboxes reached a maxi-

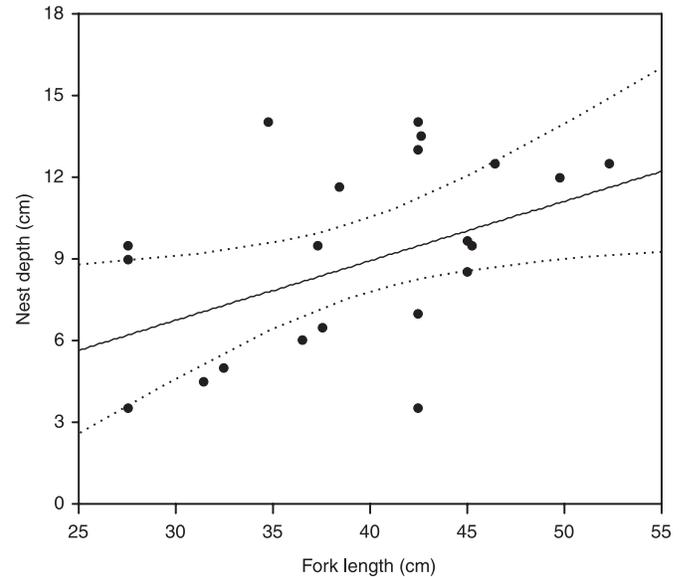
Fig. 1. Daily mean size of spawning female brook trout (*Salvelinus fontinalis*) during the (a) 1994 and (b) 1995 breeding seasons.



mum of 0.28 at the highest flow rate ($\sim 35 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$) (Fig. 4a).

The survival of eggs was also related to groundwater flow rates in redds. Survival of eggs at low flow rates was very low or nonexistent, while survival at flow rates equaling or exceeding $20 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ was consistent and did not increase with increasing groundwater flow rate (Fig. 4b). Comparing the patterns of emergence and survival as a function of groundwater flow rate points to the role of water temperature as a factor in affecting developmental timing and survival. For eggs that were buried at sites with a flow rate of approximately $20 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$, emergence after 88 days was low (Fig. 4a), but survival of brook trout embryos was similar to hatchboxes located at redds with higher flow rates (Fig. 4b). For brook trout embryos to emerge after

Fig. 2. Relationship between female body size and nest depth (solid line; $Y = -0.97 + 0.23X$) with 95% confidence intervals (dotted lines) for Scott Lake brook trout (*Salvelinus fontinalis*).



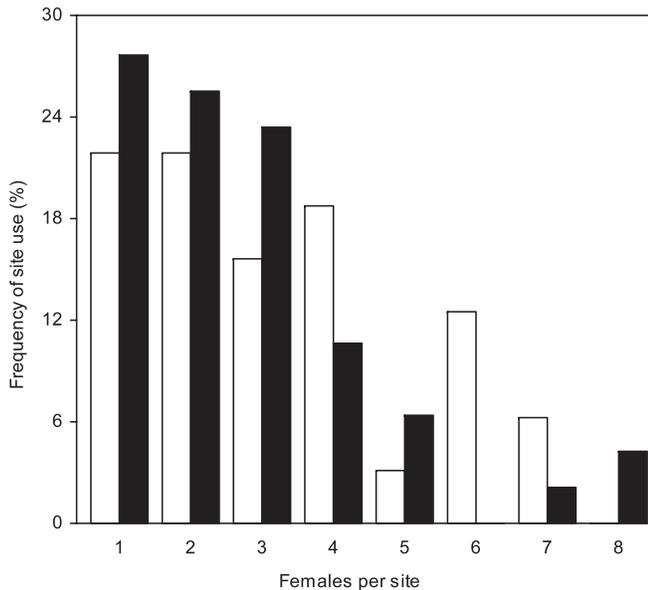
88 days, the mean daily temperature in the egg pockets would have to have been $5.6 \text{ }^\circ\text{C}$ (Embrey 1934) ($Y = 183.16 \exp(-0.132X)$, where Y is days to emergence and X is temperature). Mean lake water temperature at redd sites during the incubation period was $3.4 \text{ }^\circ\text{C}$ (range: $1.8\text{--}7.1 \text{ }^\circ\text{C}$), suggesting that groundwater was at least several degrees warmer than lake water during the incubation period. For redd sites with groundwater flow above $20 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$, mean survival was relatively constant at 37% (95% confidence interval CI: 28%–46%). The overall egg to alevin survival at the nine sites in which we had previously observed brook trout spawning was 20% (95% CI: 12%–29%).

Female reproductive success

The results from the egg survival experiment were used to model the egg losses at redd sites with different seepage rates (Fig. 4b). Because territory quality was not continuous, we classified spawning sites based on the rate of groundwater flow. Sites of low quality ($<11.2 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$) were classified as having no survival (0) (Fig. 4b, line section *i*). We assigned all sites with groundwater flow equaling or exceeding $20.6 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ an egg survival rate of 0.366, the mean from observed data (Fig. 4b, line section *ii*). We used three different scenarios to model egg survival as a function of groundwater flow for sites of groundwater flow between 11.2 and $20.6 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ (Fig. 4b). We inferred maximum egg survival (scenario A), a linear relationship ($Y = -0.484 + 0.043X$, where X is groundwater flow in $\text{mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$) (scenario B), and minimum egg survival (scenario C) (Fig. 4b). Together, these scenarios provided a range of modeled egg survival for spawning sites with intermediate rates of groundwater flow (Fig. 4b).

The power function relating fecundity to female body size represents the theoretical limit of reproductive success for females of different size. Subsequently, egg loss resulting from superimposed redds reduced fecundity and accounted

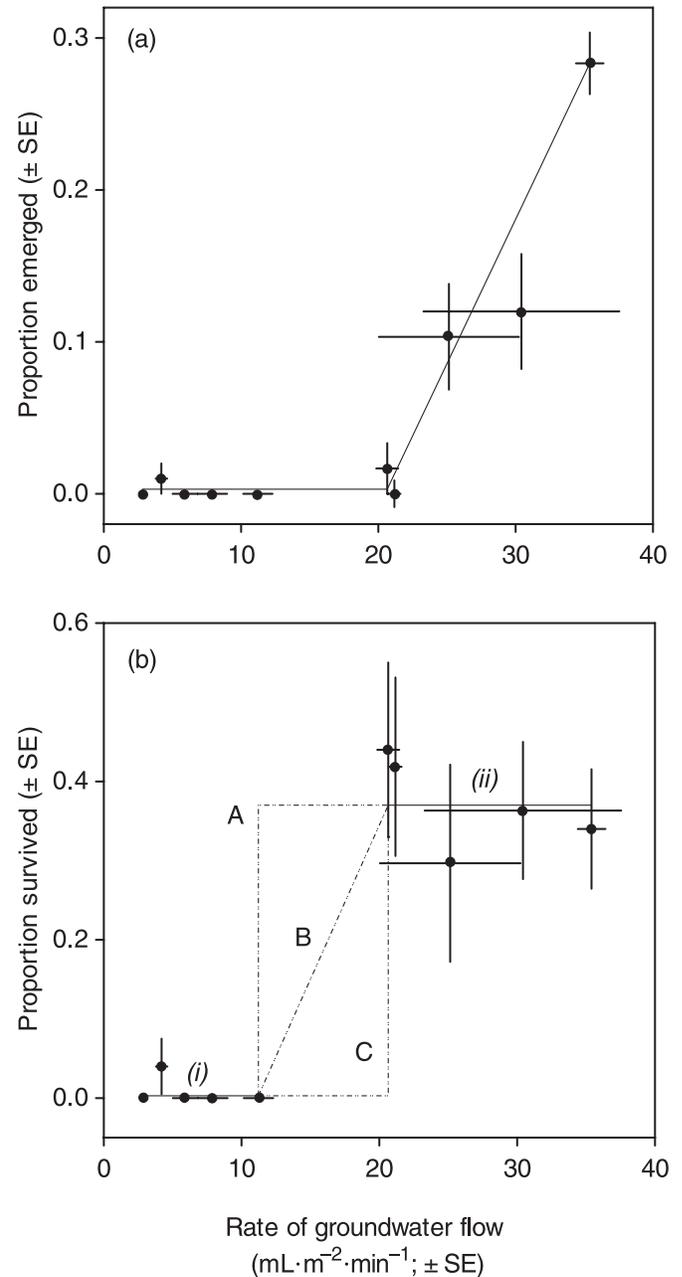
Fig. 3. Frequency of spawning site use by female brook trout (*Salvelinus fontinalis*) for the 1994 breeding season (open bars) and 1995 breeding season (solid bars).



for mean losses of 34% (95% CI: 19%–50%) and 27% (95% CI: 14%–41%) of eggs deposited in the 1994 and 1995 breeding seasons, respectively, assuming that spawning females lost one brood to every later-spawning female of equal or greater fork length at a given site (Figs. 5a and 5b). Deposited eggs that survived site reuse by females suffered further mean egg losses of 68%–93% depending on the scenario used to describe the relationship between egg survival and habitat quality (i.e., groundwater flow rate). Mean egg survival for female brook trout after accounting for losses to superimposition and habitat quality ranged from 6% to 21% (1994: scenario A, 21%, 95% CI: 15%–27%; scenario B, 12%, 95% CI: 8%–16%; scenario C, 6%, 95% CI: 2%–11%; 1995: scenario A, 21%, 95% CI: 16%–27%; scenario B, 11%, 95% CI: 7%–16%; scenario C, 6%, 95% CI: 1%–11%) (Figs. 5a and 5b).

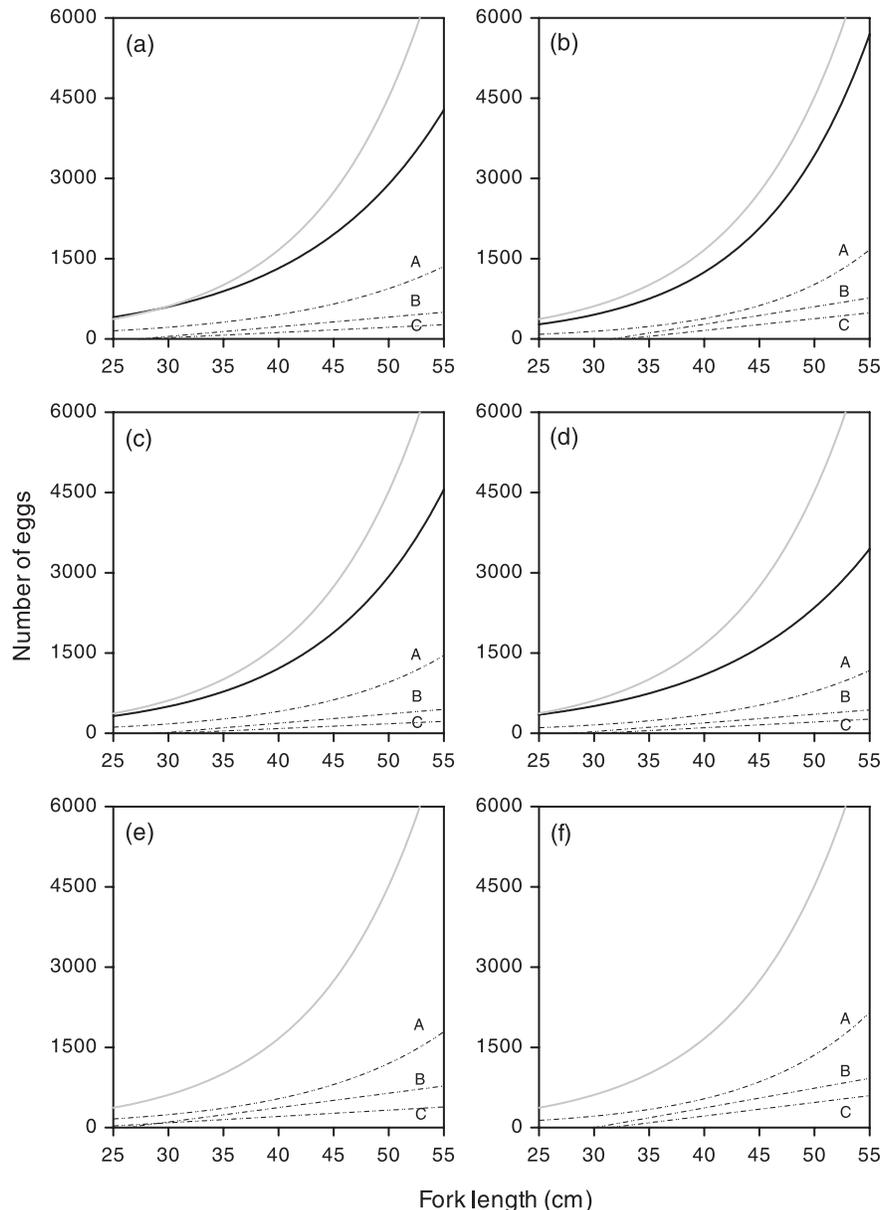
Loosening our criterion to also include nest destruction by later-spawning females that were less than 5 cm smaller in fork length than earlier-spawning females increased our estimate of egg loss owing to superimposition by less than 10% (1994: 43%, 95% CI: 28%–59%; 1995: 33%, 95% CI: 20%–47%) (Figs. 5c and 5d). The additional egg loss from superimposition owing to relaxing our body size criterion was slightly greater in 1994 (9%) than in 1995 (6%). However, the exponential relationship between female size and number of eggs remaining after losses through nest destruction was similar in 1994 (Figs. 5a and 5c) because most additional egg loss was incurred by medium-sized females ($n = 7$; range: 31.4–42.3 cm fork length). In contrast, the additional egg loss owing to superimposition that occurred in the 1995 breeding season was limited to much larger females, including the largest females in this population ($n = 5$; range: 44.5–51.9 cm fork length). As a result, the relationship between female size and number of eggs surviving nest destruction was markedly lower between these two scenarios of brood loss in 1995 (Figs. 5b and 5d). Overall, the greater

Fig. 4. Influence of groundwater flow on the (a) proportion of emerged fry and (b) egg survival for eggs held in hatchboxes and buried at brook trout (*Salvelinus fontinalis*) spawning sites. Each point is the mean of three hatchboxes per site, each containing the eggs of a different female (see text for exceptions). Egg survival was estimated to be (i) 0 when groundwater flow was $<11.2 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ and (ii) constant at 0.366 at groundwater flows $>20.6 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$. Three scenarios (A, B, and C) described egg survival as a function of groundwater flow for spawning sites between 11.2 and 20.6 $\text{mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$. Scenario B is a linear relationship ($Y = -0.4361 + 0.0389X$).



egg loss owing to superimposed redds by smaller females made little difference in mean egg survival to emergence once egg loss owing to spawning habitat quality was included, 4%–19% (1994: scenario A, 18%, 95% CI: 12%–

Fig. 5. Number of eggs per spawning female brook trout (*Salvelinus fontinalis*) (top line in all panels) in relation to body size determined from Vladykov (1956). Modeled estimates of the number of eggs surviving after accounting for egg loss through brood superimposition (solid line) and the combined loss of eggs through superimposition and territory quality (scenarios A, B, and C in Fig. 4b) (broken lines) are shown in relation to female body size (1994: $n = 31$; 1995: $n = 29$). Egg loss through superimposition by later-spawning females of equal or greater size and subsequent loss to habitat quality scenarios is shown for (a) 1994 and (b) 1995. Egg loss through superimposition by later-spawning females of larger, equal, or smaller (by <5 cm) size with the combined loss to habitat quality is shown for (c) 1994 and (d) 1995. Egg loss owing solely to habitat quality scenarios is shown for (e) 1994 and (f) 1995. Fecundity and the modeled number of remaining eggs after losses to superimposition and combined egg loss to superimposition and habitat quality scenario A were best described by exponential relationships. The numbers of eggs remaining after combined losses to superimposition and habitat quality scenarios B and C were best fit with a linear model.



23%; scenario B, 9%, 95% CI: 6%–13%; scenario C, 4%, 95% CI: 1%–8%; 1995: scenario A, 19%, 95% CI: 14%–25%; scenario B, 10%, 95% CI: 6%–14%; scenario C, 5%, 95% CI: 0%–9%) (Figs. 5c and 5d).

In the absence of nest destruction from female competition, modeled outcomes of egg loss owing solely to habitat quality resulted in reductions of 67%–91% of egg numbers from the relationship between body size and fecundity for female brook trout (Figs. 5e and 5f). Modeled egg survival

was 33% (95% CI: 30%–37%), 21% (95% CI: 16%–25%), and 13% (95% CI: 7%–19%) in 1994 for habitat quality scenarios A, B, and C, respectively (Fig. 5e). Similar levels of egg survival after accounting for losses owing solely to habitat quality were estimated for females during the 1995 breeding season (scenario A, 31%, 95% CI: 27%–35%; scenario B, 17%, 95% CI: 12%–22%; scenario C, 9%, 95% CI: 3%–15%) (Fig. 5f). We examined the relationship between female body size and the groundwater flow at sites chosen

for egg deposition. For each female, we chose the site of greatest flow where eggs were deposited because female brook trout can spawn at multiple sites. There were no size-related patterns in choice of sites by habitat quality (Spearman rank correlation: 1994, $r_s = -0.033$, $p = 0.86$, $n = 31$; 1995, $r_s = 0.23$, $p = 0.23$, $n = 29$).

After partitioning the major sources of egg loss in our scenarios, habitat quality reduced the potential reproductive output of female brook trout by 1.5–3.4 times that of redd superimposition through female competition for spawning sites. The difference in the mean percentage of modeled egg loss through the combined effects of female competition and habitat quality (Figs. 5a–5d) and that from habitat quality alone (Figs. 5e and 5f) ranged from 3% to 16% and became increasingly diminished as estimates of habitat quality worsened (range in mean differences pooled for year and level of superimposition: scenario A, 10%–15%; scenario B, 6%–11%; scenario C, 3%–8%).

Population-level egg loss

Spawning habitat quality, modeled by groundwater seepage rate, appeared to have the strongest effect on egg survival, and therefore, we estimated the losses of eggs at the population level as a function of groundwater seepage rate based on observations of spawning at all redd sites. Survival estimates associated with different redds were based on the approach used in estimating survival of eggs outlined above when determining the reproductive success of females of different size (Fig. 4b, scenarios A, B, and C).

The observed distribution of eggs deposited among redds in both years matched the frequency distribution of redds of different seepage rates (Kolmogorov–Smirnov test: 1994, $D_{0.05,14} = 0.36$, $p > 0.05$; 1995, $D_{0.05,14} = 0.29$, $p > 0.05$) (Fig. 6). Thus, spawning habitat use by females, as reflected in projected egg deposition (Figs. 6c and 6d), matched habitat availability at the population level (Figs. 6a and 6b). However, modeled differences in survival resulting from site differences in seepage rates reduced the total number of eggs available for production with full loss occurring at seepage rates below $11.6 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ for all scenarios of habitat quality (Figs. 6e and 6f). The projected percent loss of total eggs deposited at or below this seepage rate was 14% of eggs in 1994 and 13% of eggs in 1995. Redds below this threshold represent 27% of all spawning sites observed in Scott Lake. At the threshold of $20.6 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ and above this rate of groundwater flow, redds provide a consistent survival rate of 0.366 for all habitat quality scenarios (Figs. 6e and 6f). This category of redds was the least common in Scott Lake (20%) but provided between 36% and 100% of surviving eggs depending on habitat quality (1994 and 1995: scenario A, 36%–48%; scenario B, 59%–73%; scenario C, 100%) (Figs. 6e and 6f). The balance of egg production for the 1994 and 1995 cohorts appears to be derived from redd sites representing a transition from sites that provide no survival to sites that provide consistent survival (11.2 – $20.6 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$). These redd sites represent 53% of all redds used for egg deposition and produced 0%–64% of surviving eggs. At the population level, habitat quality resulted in a 68%–89% reduction in egg survival for Scott Lake brook trout (1994 and 1995: scenario A, 68%–69%; scenario B, 79%–81%; scenario C, 85%–89%) (Figs. 6e and 6f).

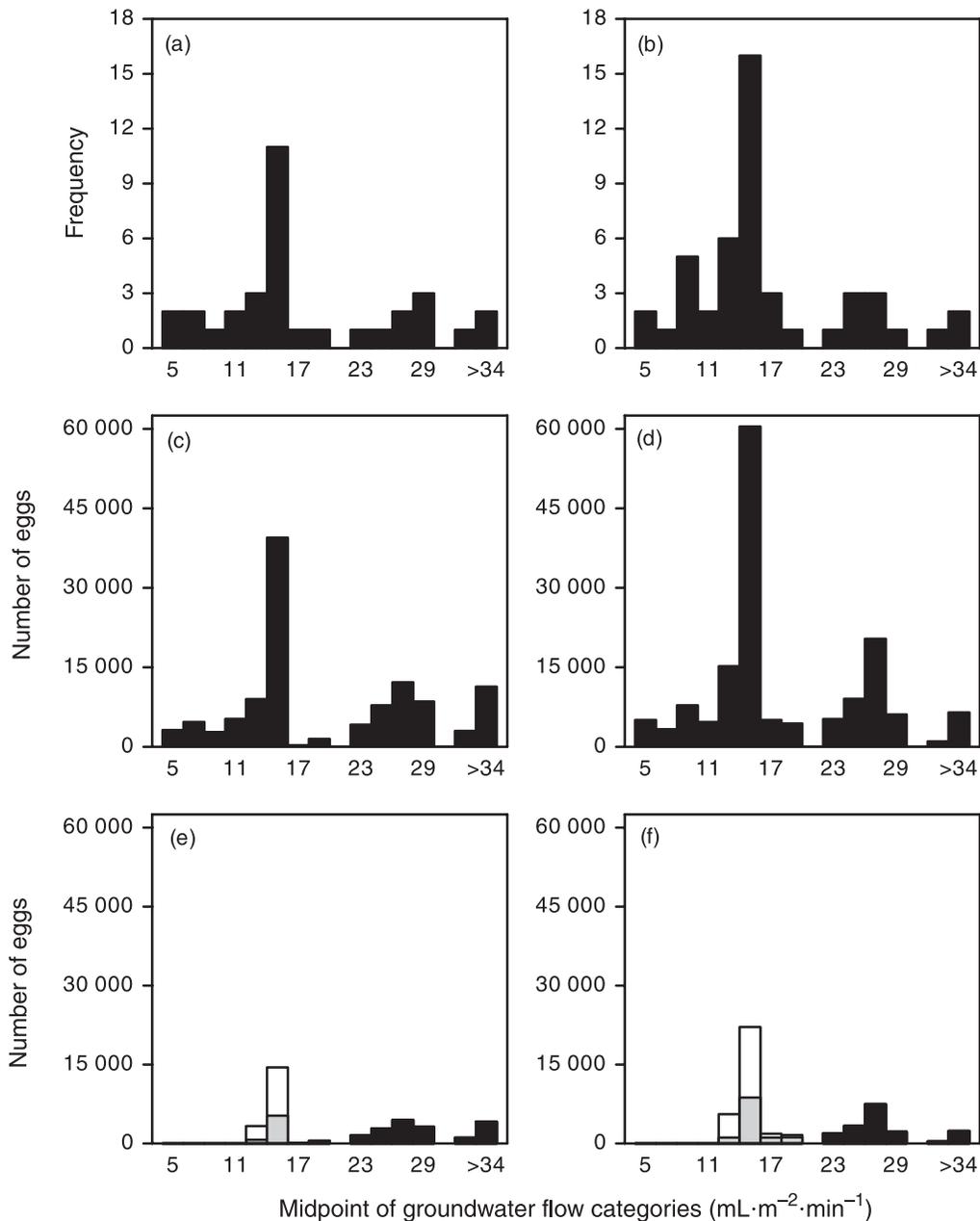
Discussion

Habitat quality, measured as groundwater seepage rate, had a stronger influence on the reproductive success of female brook trout than competition for spawning sites. Egg incubation experiments clearly indicated a threshold effect of groundwater seepage rate on the emergence and survival of young brook trout. The fecundity of lake-spawning brook trout as a function of size was greatly reduced when the effects of both habitat quality and redd superimposition were modeled. However, habitat quality alone resulted in such significant egg mortality that larger female brook trout, because of their greater fecundity, retained only a slight relative advantage in effective or operational fecundity over smaller females. Our model of changes in the effective fecundity of female brook trout stemming from competition and site quality points to the importance of physical habitat in the maintenance of brook trout populations.

Ranking competition for redds ahead of habitat quality appears to be the general outcome of most salmonine studies examining the relationship between spawner abundance and offspring production (e.g., Fukushima et al. 1998; Essington et al. 2000). For example, reproductive success in coho salmon appears to be controlled primarily by competition for spawning sites and only secondarily by redd habitat quality (van den Berghe and Gross 1989). In coho salmon, redd superimposition lowers but does not fundamentally alter the power function from the theoretical limit of female reproductive success (Fig. 7 in van den Berghe and Gross 1989). In contrast, the power function relating fecundity to body size for lake-spawning brook trout is essentially flattened as a result of habitat quality differences among redd sites. The difference in the relative strength of the site quality – site competition dichotomy in determining egg survival may reflect a gradient in the strength of density-dependent mortality during the egg stage in salmonine mating systems. In many salmonine mating systems such as Pacific salmon, redd superimposition in large, dense populations of spawning fish likely represents a significant source of density-dependent mortality for eggs as female competition for sites increases with spawning population size. Pacific salmon appear to adjust their seasonal timing of reproduction to minimize egg loss under these conditions (Morbey and Ydenberg 2003). The effect of habitat quality on egg survival is likely a rather weak density-dependent mechanism affecting egg survival relative to superimposition. In the case of brook trout observed in Scott Lake, the seasonal timing of spawning by females of different size occurs over a protracted period and may reflect an adaptive response by small females for minimizing density-dependent egg loss by waiting for large females to complete spawning in the limited number of groundwater sites.

The effects of redd superimposition can be particularly acute for small female salmonines. Experimental studies of Pacific salmon show that small (or hatchery) females attempting to breed at the same time as large females incurred greater displacement from territories (van den Berghe and Gross 1989; Foote 1990) or suffered greater delays in the onset of breeding, resulting in a decreased ability to spawn all eggs before death (Fleming and Gross 1993, 1994). Suitable spawning sites appear to be a limiting feature of this brook trout mating system. In Scott Lake, three quarters of

Fig. 6. Distribution of spawning sites used by brook trout (*Salvelinus fontinalis*) in (a) 1994 and (b) 1995, the corresponding numbers of eggs deposited in (c) 1994 and (d) 1995, and the estimated numbers of eggs surviving in those sites in relation to groundwater flow scenarios (A, B, and C in Fig. 4b) for the (e) 1994 and (f) 1995 breeding seasons at Scott Lake. Modeled egg survival was least in habitat quality scenario C (solid bars), with additional numbers of eggs surviving under scenarios B (shaded bars) and A (open bars).



all spawning sites were subsequently reused by a different female. The extensive redd superimposition, however, resulted in a realized frequency of redd destruction of about half of this amount (27%–43%) because large females constructed deeper redds and tended to spawn prior to small females. Somewhat higher levels of redd superimposition than observed for this brook trout population have been recorded for other salmonines (e.g., 89%, Hayes 1987; 50%, van den Berghe and Gross 1989; 53%, Essington et al. 1998), as well as low rates of superimposition (4%, Knapp and Vredenburg 1996; 3%–22%, summary in Fleming 1996). In other brook trout populations, high levels of redd superimposition are in-

terpreted as socially facilitated site choice rather than an outcome of spawning site limitation (Essington et al. 1998). Alternatively, others have proposed that redd site choice is a random process (Sorensen et al. 1995). This approach ignores seasonal timing of redd use and crowding effects that can effectively lower the operating density of spawning females on any given day relative to a strict random model of settlement (Blanchfield and Ridgway 1997; Essington et al. 1998).

In Scott Lake, the total number of seepage sites used by spawning brook trout varies among years because peripheral sites with low flow rates increase or decrease in number ap-

parently as a function of rainfall (Ridgway and Blanchfield 1998). Only redd sites with relatively high rates of groundwater flow are used each year (Ridgway and Blanchfield 1998). The effect of redd superimposition on egg survival is therefore likely to vary from year to year depending on the number of redd sites available, the range in flow rates at available sites, and female population size at the time. Female reproductive success in brook trout is not based on a fixed number of redd sites but is an interaction between environmental factors (rainfall and seepage) that affect site availability and competitive interactions among females that vary with year-class size.

Groundwater seepage rate is an essential habitat feature for spawning brook trout in lakes (Fraser 1982; Curry and DeVito 1996; Blanchfield and Ridgway 1997) and an important although not exclusive element for stream-spawning populations (Curry et al. 2002). A single habitat parameter has facilitated our examination of habitat effects on reproductive success as opposed to more commonly used multi-parameter models that typically include water depth, substrate characteristics, and flow patterns. The threshold relationship between groundwater seepage rate and embryo survival in Scott Lake is a pattern observed in other relationships linking environmental parameters and egg survival in salmonines (Bjorn and Reiser 1991). At flow rates of $20 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$ and greater, mean egg survival was relatively constant (37%), while at sites of about half this seepage rate and lower ($<11 \text{ mL}\cdot\text{m}^{-2}\cdot\text{min}^{-1}$), there is essentially no survival of eggs. Low flow patterns observed with the use of piezometers in another lake also resulted in a dramatic reduction in egg survival (6%) relative to redds with relatively high flows (~30%–50% survival; Curry et al. 1995). The limited number of spawning sites with high flow rates at Scott Lake produced a bottleneck to the recruitment of young brook trout that substantially lowered female reproductive success.

Groundwater flow was the dominant route through which female brook trout experienced egg loss in our model such that even in the absence of competition for spawning sites, egg survival to emergence was only 9%–33%. The combined influence of female competition and habitat quality resulted in survival of eggs to emergence of approximately 4%–21% in both years of this study. Comparable survival estimates were observed for an egg incubation study at brook trout spawning sites in a lake inlet stream (mean 8.1%; Bernier-Bourgault and Magnan 2002). These estimates of egg to fry survival are similar to those of various Pacific salmon species over the same life history stage (~7% for *O. gorbuscha*, *O. keta*, and *O. nerka* and ~17% for *O. kisutch* at the lower end of survival estimates; Bradford 1995). The wide range in egg to alevin survival for eggs buried in hatchboxes at Scott Lake (0%–59%) is similar to other estimates of survival for the same life history stage of lacustrine brook trout in this region (3%–38% for preferred spawning sites, Fraser 1985; 6%–68%, Curry et al. 1995). The similarity among these studies suggests that the overall low survival of eggs in Scott Lake was not an artefact of using hatchboxes (see Garrett and Bennett 1996) but rather is typical of brook trout under natural conditions.

An empirically stronger route for estimating female reproductive success, compared with the modeling approach

adopted in this study, would include redd sampling for egg abundance, genotyping females and offspring, and then determining the scope of redd disruption based on offspring production owing to reuse of sites by females. This approach seems impractical for the Scott Lake population. Many redds were located at 1 m depth and distributed among sand and cobble substrates covered with organic deposits. Furthermore, spawning extended over approximately 60 days in each year (Blanchfield and Ridgway 1997). Sampling substrates for egg abundance would have disrupted spawning habitat and disrupted ongoing mating behaviour over a 2-month period, particularly at sites that received repeated spawning activity. Extensive sampling activity would have compromised a unique feature of the Scott Lake site; specifically the ability to observe in full a salmonine mating system in terms of individually identified breeding adults over the entire spawning season and all available sites. Despite some limitations of the modeling approach, we believe that adopting this route has helped demonstrate the dominant role of habitat quality in the determination of female reproductive success, at least for the period of egg to alevin survival, for a lake-spawning brook trout population.

Reproductive success in this study was examined only in terms of habitat quality and superimposed redds. Predation of newly deposited eggs is known to occur in salmonine mating systems (Maekawa and Ozonato 1986), and it occurs in the mating system of brook trout in Scott Lake as well (Blanchfield and Ridgway 1999). Although estimating the loss of eggs owing to predation/cannibalism is difficult for each spawning event, the magnitude of this factor in overall egg loss can be estimated for the population. Egg cannibalism by peripheral males occurred in 24% of observed spawnings in Scott Lake during the same time period of this study and, on average, two peripheral males were present around each spawning pair of brook trout (range: 0–6 peripheral males; Blanchfield and Ridgway 1999). Maekawa and Ozonato (1986) estimated the loss of eggs to cannibalism in the mating system of Miyabe charr (*Salvelinus malma miyabei*) at ~5–10 eggs consumed per cannibalistic male. Thus, based on the observed frequency of egg cannibalism (24%), and assuming that two males each consume 20 eggs during these events, egg losses owing to cannibalism represent less than 2% of total egg deposition in each breeding season for the Scott Lake population. Loss of eggs to cannibalism is likely small in comparison with losses stemming from redd superimposition and habitat quality.

In summary, groundwater discharge is an important feature of spawning habitat in other *Salvelinus* species (e.g., Cunjak et al. 1986; Baxter and McPhail 1999; Power et al. 1999) along with hyporheic exchange of water (Baxter and Hauer 2000). A significant amount of field work has been invested so far in determining the site characteristics of spawning habitat in brook trout and other members of the char group. For brook trout, this work has demonstrated the importance of groundwater as a feature of spawning sites (Curry et al. 1995; Blanchfield and Ridgway 1997; this study) and its absence as an element of spawning sites in other areas (Fiss and Carline 1993; Curry et al. 2002). Whether spawning sites are indeed fed by groundwater or hyporheic exchange, a real need exists for determining the locations of these features at the landscape level (e.g.,

Baxter and Hauer 2000) where resource planning and conservation efforts for brook trout and other *Salvelinus* species can be more operationally effective.

Acknowledgements

We greatly appreciate the field assistance of Kim Hughes, Kim Mandzy, Lori Flavelle, and Scott Milne during the 1994–1997 fall seasons. We thank Greg Betteridge, Doug Brown, and Gary Ridout for advice and help with the hatchbox experiment and Trevor Middel for interpolation of groundwater seepage data. This paper is part of a thesis submitted by P.J.B. in partial fulfilment of a doctoral degree from the Faculty of Graduate Studies, York University, and has been improved with comments from committee members and other reviewers. Support for this work came from a Dean's Academic Excellence Scholarship, York University (P.J.B.), the Ontario Ministry of Natural Resources, and a Natural Sciences and Engineering Research Council of Canada operating grant (M.S.R.).

References

- Baxter, C.V., and Hauer, F.R. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). *Can. J. Fish. Aquat. Sci.* **57**: 1470–1481.
- Baxter, J.S., and McPhail, J.D. 1999. The influence of redd site selection, groundwater upwelling, and over-winter incubation temperature on survival of bull trout (*Salvelinus confluentus*) from egg to alevin. *Can. J. Zool.* **77**: 1233–1239.
- Bernier-Bourgault, I., and Magnan, P. 2002. Factors affecting redd site selection, hatching, and emergence of brook charr, *Salvelinus fontinalis*, in an artificially enhanced site. *Environ. Biol. Fishes*, **64**: 333–341.
- Bjorn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. In *Influences of forest and rangeland management on salmonid fishes and their habitats*. Edited by W.R. Meehan. *Am. Fish. Soc. Spec. Publ.* **19**: 83–138.
- Blanchfield, P.J., and Ridgway, M.S. 1996. Use of seepage meters to measure groundwater flow at brook trout redds. *Trans. Am. Fish. Soc.* **125**: 813–818.
- Blanchfield, P.J., and Ridgway, M.S. 1997. Reproductive timing and redd site use by lake-spawning brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* **54**: 747–756.
- Blanchfield, P.J., and Ridgway, M.S. 1999. The cost of peripheral males in a brook trout mating system. *Anim. Behav.* **57**: 537–544.
- Blanchfield, P.J., Ridgway, M.S., and Wilson, C.C. 2003. Breeding success of male brook trout (*Salvelinus fontinalis*) in the wild. *Mol. Ecol.* **12**: 2417–2428.
- Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. *Can. J. Fish. Aquat. Sci.* **52**: 1327–1338.
- Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Trans. Am. Fish. Soc.* **117**: 1–21.
- Crisp, D.T., and Carling, P.A. 1989. Observations on siting, dimensions and structure of salmonid redds. *J. Fish Biol.* **34**: 119–134.
- Cunjak, R.A., Power, G., and Barton, D.R. 1986. Reproductive habitat and behaviour of anadromous arctic char (*Salvelinus alpinus*) in the Koroc River, Quebec. *Nat. Can. (Que.)*, **113**: 383–387.
- Curry, R.A., and Devito, K.J. 1996. Hydrogeology of brook trout (*Salvelinus fontinalis*) spawning and incubation habitats: implications for forestry and land use development. *Can. J. For. Res.* **26**: 767–772.
- Curry, R.A., and Noakes, D.L.G. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* **52**: 1733–1740.
- Curry, R.A., Noakes, D.L.G., and Morgan, G.E. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* **52**: 1741–1749.
- Curry, R.A., Scruton, D.A., and Clarke, K.D. 2002. The thermal regimes of brook trout incubation habitats and evidence of changes during forestry operations. *Can. J. For. Res.* **32**: 1200–1207.
- Embody, G.C. 1934. Relation of temperature to the incubation period of eggs of four species of trout. *Trans. Am. Fish. Soc.* **64**: 281–289.
- Environmental Systems Research Institute. 1992. ArcView GIS version 3.1 [computer program]. ESRI Limited, Redlands, Calif.
- Essington, T.E., Sorensen, P.W., and Paron, D.G. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Can. J. Fish. Aquat. Sci.* **55**: 2310–2316.
- Essington, T.E., Quinn, T.P., and Ewert, V.E. 2000. Intra- and interspecific competition and the reproductive success of sympatric Pacific salmon. *Can. J. Fish. Aquat. Sci.* **57**: 205–213.
- Fiss, F.C., and Carline, R.F. 1993. Survival of brook trout embryos in three episodically acidified streams. *Trans. Am. Fish. Soc.* **122**: 268–278.
- Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev. Fish Biol. Fish.* **6**: 379–416.
- Fleming, I.A., and Gross, M.R. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecol. Appl.* **3**: 230–245.
- Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution*, **48**: 637–657.
- Foote, C.J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. *Behaviour*, **115**: 283–314.
- Fraser, J.M. 1982. An atypical brook charr (*Salvelinus fontinalis*) spawning area. *Environ. Biol. Fishes*, **7**: 385–388.
- Fraser, J.M. 1985. Shoal spawning of brook trout, *Salvelinus fontinalis*, in a Precambrian shield lake. *Nat. Can. (Que.)*, **112**: 163–174.
- Fukushima, M., Quinn, T.P., and Smoker, W.W. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Can. J. Fish. Aquat. Sci.* **55**: 618–625.
- Garrett, J.W., and Bennett, D.H. 1996. Evaluation of fine sediment intrusion into Whitlock-Vibert boxes. *N. Am. J. Fish. Manag.* **16**: 448–452.
- Geist, D.R. 2000. Hyporheic discharge of river water into fall chinook salmon (*Oncorhynchus tshawytscha*) spawning areas in the Handford Reach, Columbia River. *Can. J. Fish. Aquat. Sci.* **57**: 1647–1656.
- Geist, D.R., Jones, J., Murray, C.J., and Dauble, D.D. 2000. Suitability criteria analyzed at the spatial scale of redd clusters improved estimates of fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat use in the Handford Reach, Columbia River. *Can. J. Fish. Aquat. Sci.* **57**: 1636–1646.
- Godin, J.–G.J. 1982. Migrations of salmonid fishes during early life history phases: daily and annual timing. In *Proceedings of the Salmon and Trout Migratory Behavior Symposium*, 3–5 June

- 1981, Seattle, Washington. Edited by E.L. Brannon and E.O. Salo. University of Washington Press, Seattle, Wash. pp. 22–50.
- Hayes, J.W. 1987. Competition for spawning space between brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*) in a lake inlet tributary, New Zealand. *Can. J. Fish. Aquat. Sci.* **44**: 40–47.
- Hendry, A.P., Berg, O.K., and Quinn, T.P. 2001. Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos*, **93**: 407–418.
- Holtby, L.B., and Healey, M.C. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **43**: 1946–1959.
- Hoopes, D.T. 1972. Selection of spawning sites by sockeye salmon in small streams. *Fish. Bull.* **70**: 447–458.
- Knapp, R.A., and Preisler, H.K. 1999. Is it possible to predict habitat use of spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). *Can. J. Fish. Aquat. Sci.* **56**: 1576–1584.
- Knapp, R.A., and Vredenburg, V.T. 1996. Spawning by California golden trout: characteristics of spawning fish, seasonal and daily timing, redd characteristics, and microhabitat preferences. *Trans. Am. Fish. Soc.* **125**: 519–531.
- Knapp, R.A., Vredenburg, V.T., and Matthews, K.R. 1998. Effects of stream channel morphology on golden trout spawning habitat and recruitment. *Ecol. Appl.* **8**: 1104–1117.
- Latta, W.C. 1965. Relationship of young-of-the-year trout to mature trout and groundwater. *Trans. Am. Fish. Soc.* **94**: 32–39.
- Maekawa, K., and Hino, T. 1990. Spawning tactics of female Miyabe charr (*Salvelinus malma miyabei*) against egg cannibalism. *Can. J. Zool.* **68**: 889–894.
- Maekawa, K., and Ozonato, N. 1986. Reproductive tactics and fertilization success of mature male Miyabe charr, *Salvelinus malma miyabei*. *Environ. Biol. Fishes*, **15**: 119–129.
- McNeil, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. *J. Fish. Res. Board Can.* **21**: 1385–1396.
- McNeil, W.J. 1966. Distribution of spawning pink salmon in Sashin Creek, southeastern Alaska, and survival of their progeny. *U.S. Fish Wildl. Serv. Sci. Rep.* 538.
- McPhee, M.V., and Quinn, T.P. 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. *Environ. Biol. Fishes*, **51**: 369–375.
- Morbey, Y.E., and Ydenberg, R.C. 2003. Timing games in the reproductive phenology of female Pacific salmon (*Oncorhynchus* spp.). *Am. Nat.* **161**: 284–298.
- Power, G., Brown, R.S., and Imhof, J.G. 1999. Groundwater and fish — insights from northern North America. *Hydrol. Processes*, **13**: 401–422.
- Quinn, N.W.S., Korver, R.M., Hicks, F.J., Monroe, B.P., and Hawkins, R.R. 1994. An empirical model of lentic brook trout. *N. Am. J. Fish. Manag.* **14**: 692–709.
- Reiser, D.W., and Wesche, T.A. 1977. Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations. *Comp. Rep. Water Res. Ser. No.* 64.
- Ridgway, M.S., and Blanchfield, P.J. 1998. Brook trout spawning areas in lakes. *Ecol. Freshw. Fish*, **7**: 140–145.
- Sorensen, P.W., Cardwell, J.R., Essington, T., and Weigel, D.E. 1995. Reproductive interactions between sympatric brook and brown trout in a small Minnesota stream. *Can. J. Fish. Aquat. Sci.* **52**: 1958–1965.
- Sowden, T.K., and Power, G. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. *Trans. Am. Fish. Soc.* **114**: 804–812.
- Steen, R.P., and Quinn, T.P. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Can. J. Zool.* **77**: 836–841.
- van den Berghe, E.P., and Gross, M.R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution*, **43**: 125–140.
- Vladykov, V.D. 1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. *J. Fish. Res. Board Can.* **13**: 799–841.