

Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*)

Paul J. Blanchfield and Mark S. Ridgway

Abstract: We provide a detailed description of a salmonine mating system based on daily observations of tagged individuals in a lake-spawning population of brook trout (*Salvelinus fontinalis*) throughout two breeding seasons. Actual spawning occurred over a period of ~50 d. Over 90% of spawning males were present soon after spawning commenced and outnumbered females for the duration of the spawning period. The amount of time males and females remained on the spawning grounds increased with body size; however, males were present over a longer period than females of equivalent size. A distinct seasonal peak in spawning activity (~15 d) accounted for 58 and 84% (1994 and 1995) of all reproduction and was coincident with a decline in water temperature below 11°C and increased rainfall. Selection of redd sites by female brook trout was determined by groundwater flow which was significantly greater than at nonspawning sites. A preference for certain redd sites was observed, with 50% of spawnings occurring at 11 sites. The construction of multiple redds and duration in spawning activity by females increased with body size. Extensive reuse of redd sites and rapid replacement of females during removal experiments indicate that redd sites are a limiting resource.

Résumé : Nous donnons une description détaillée du système d'accouplement de salmonidés fondé sur des observations quotidiennes de poissons marqués dans une population d'ombles de fontaine (*Salvelinus fontinalis*) frayant dans un lac pendant deux saisons de reproduction. Le frai s'est échelonné sur une période d'environ 50 jours. Plus de 90% des géniteurs mâles étaient présents peu après le début du frai et leur nombre a dépassé celui des femelles pendant toute la durée du frai. Le temps passé par les mâles et les femelles dans les aires de frai a augmenté avec la taille corporelle; cependant, les mâles sont demeurés sur les lieux plus longtemps que les femelles de même taille. L'activité de frai a connu un sommet saisonnier très distinct (d'une durée d'environ 15 jours) au cours duquel on a enregistré 58 et 84% de toutes les reproductions en 1994 et 1995 respectivement et qui coïncidait avec un chute de la température en-dessous de 11°C et avec une augmentation des précipitations. La sélection de l'emplacement des nids de frai par les ombles femelles était déterminée par le ruissellement souterrain qui était nettement plus grand que dans les emplacements non utilisés pour le frai. Une préférence pour certains nids de frai a été observée; en effet, 50% des activités de frai se sont déroulées dans 11 sites. La construction de nids multiples et la durée de l'activité de frai des femelles ont augmenté avec la taille corporelle. Une réutilisation intensive des emplacements préférés et le remplacement rapide des femelles enlevées des lieux indiquent que les emplacements pour les nids constituent une ressource limitante.

[Traduit par la Rédaction]

Introduction

Among salmonines (salmons, trouts, and chars), females prepare sites for spawning (redds) and males compete vigorously for access to females (e.g., Keenlyside and Dupuis 1988). Although not all species of salmonines follow this general description (e.g., *Salvelinus namaycush*; Martin 1957), the site-based competitive mating system in this group of fishes is

the most frequently observed pattern of mating behaviour. In this mating system, males develop secondary sexual characteristics that show clear sexual dimorphism and dichromatism during the reproductive season (Quinn and Foote 1994), and in some cases the evolution of alternative mating strategies (Gross 1985).

Pacific salmon (genus *Oncorhynchus*) have become the model system for investigating and describing these mating systems. In Pacific salmon, female preparation of redds is highly synchronous (van den Berghe and Gross 1986; Hendry et al. 1995), with females spawning and then defending one redd for ~9 d (Hartman et al. 1964; van den Berghe and Gross 1986). These mating systems are further characterised by a relatively short reproductive lifespan (7–12 d), limited movement of males among females (Hendry et al. 1995), and terminal investment in reproduction as males and females die soon after spawning (Quinn and Foote 1994).

Direct observations of individuals in these mating systems are difficult, in part because of the size and distribution of the adult population as well as the difficulty of observing behaviour from shore. At a logistical level, not identifying individuals has led to some controversy about the operation of mate choice in coho salmon (*Oncorhynchus kisutch*) (Sargent et al. 1986, 1988; Foote 1988a). At a fundamental level, being unable to

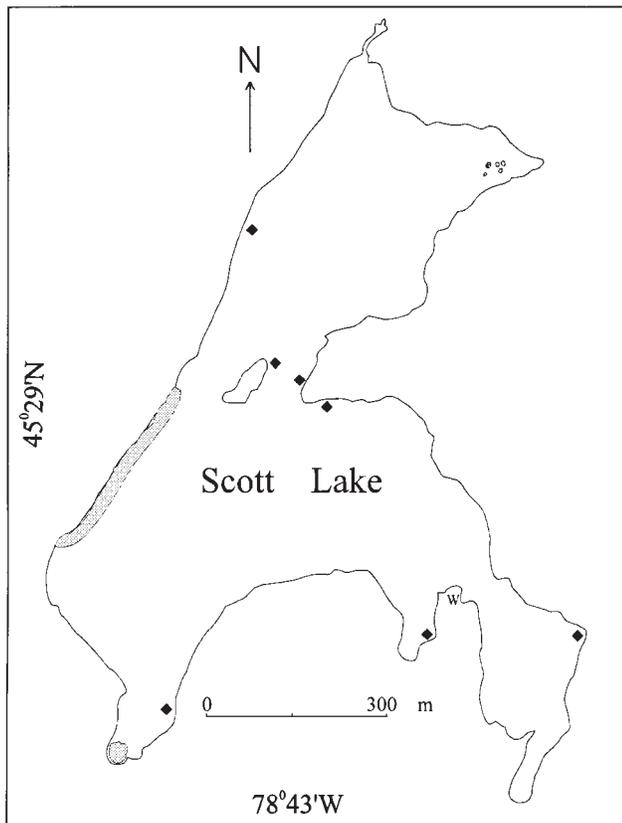
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Fig. 1. Map of study site showing the location of Scott Lake, Algonquin Park, Ontario. The areas where spawning activity occurred are shaded. Random groundwater sampling sites from around the lake (diamonds) and the weather station (W) are shown.



assess the dispersion of the entire breeding population limits the application of patch choice models as a theoretical framework for site or mate choice (Sargent et al. 1986). If breeding adults cannot be fully sampled because of their dispersion, then experiments in enclosures can alleviate this problem to some extent by providing an experimental model of a complete mating system (e.g., Fleming and Gross 1994). However, these manipulations cannot provide all the movement options facing free-ranging fish in a natural mating system. This is particularly true if some individuals, such as males using an alternative mating strategy, are moving throughout the spawning population based on the competitive abilities of other males and size of females at specific redd sites. In any case, it is often difficult to delimit the effective population size in the large stream and lake systems where Pacific salmon spawn.

The purpose of this study is to describe mating in a lake population of brook trout (*Salvelinus fontinalis*) in which the majority of adults are individually tagged and where the entire spawning population can be observed. We present data on the seasonality of redd site use and reproductive behaviour of lake-spawning brook trout. These data provide a strong contrast with the literature on Pacific salmon mating systems as well as one of the most extensive field descriptions of a salmonine mating system based on an iteroparous population.

Information on the reproductive ecology of brook trout is based largely on data collected in stream (e.g., White 1930; Greeley 1932; Hazzard 1932; Smith 1941; Needham 1961)

and laboratory settings. Abiotic factors related to spawning substrate (Fraser 1985; Young et al. 1989), redd selection (Witzel and MacCrimmon 1983), and the requirement of groundwater seepage (Benson 1953; Reiser and Wesche 1977; Curry and Noakes 1995) characterise much of what is known about brook trout reproductive ecology. Laboratory observations have supported the general observation of seepage flow as a preferred element of redd selection (e.g., Webster and Eiriksdottir 1976) and have provided some descriptions of spawning behaviour (Hale 1968; Hale and Hilden 1969; Hokanson et al. 1973). Recent contributions on life history variation and the survival cost of reproduction provide the most current perspective on the reproductive ecology of brook trout (Hutchings 1994).

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) (Fig. 1). Scott Lake tends to be slightly acidic (pH 6.3–6.9), high in dissolved oxygen (8.4–9.6 mg·L⁻¹), with a conductivity of 26.6 μS·cm⁻¹ at 25°C. The fish community of Scott Lake is composed primarily of *Culaea inconstans*, *Pimephales promelas*, and *Phoxinus* spp. Catastomids are absent. Scott Lake supports a self-sustaining brook trout population last stocked with hatchery fish (Hill's Lake strain) in 1959. Despite hatchery plantings, Scott Lake fish closely resemble ancestral lineages, although hatchery influences cannot be completely ruled out (Danzmann and Ihssen 1995).

Adult observations

Brook trout were caught using a 1.5-m trap net just prior to spawning (early October 1994 and 1995) and thereafter were captured with dip nets by swimmers (mask and snorkel). Fish were anaesthetized with tricaine methanesulfonate (MS 222) prior to tagging and measuring. A t-tag (Hallprint Co., Australia) was inserted just below the dorsal fin of the fish and a uniquely coded disc applied to this tag to allow for individual identification. At this time, fish were determined to be ripe if eggs or milt were extruded when gentle pressure was applied along the ventral surface. Fork lengths (FL) were measured to the nearest millimetre and mass recorded to the nearest 10 g (Pesola™, 2.5-kg scale). All other field data were recorded from underwater observations made by swimmers using drysuits, mask, and snorkel.

Spawning was concentrated in one area of the lake (Fig. 1); however, the entire shoreline of the lake was searched on two separate occasions during the spawning period to determine if spawning occurred elsewhere in the lake. Only one redd site was found outside the main spawning area and this was monitored for the rest of the season. We conducted a census of the entire spawning area four times daily (weather permitting) once spawning activity commenced (10 October 1994 and 1995) until fish were no longer present on the spawning grounds (6 December 1994) or the lake surface was frozen (24 November 1995). Three days were missed during the 1995 season due to equipment failure. During each census the position and activity of each fish were recorded on underwater slates by swimmers.

The term "redd" has been used to describe the nest or group of nests that female salmonines prepare in which to spawn (Chapman 1988). This definition more commonly describes the successive nests (or egg pockets) that a stream-spawning female digs and covers as she works her way upstream. In Scott Lake, female choice of redd sites and spawning substrate did not always allow for the construction of contiguous nests; therefore, we considered all noncontiguous nests in which a female spawned to be a separate redd.

The majority of spawnings occurred during the day and were often witnessed either by swimmers or via video camera, but more often the

presence of eggs in the nest or covering behaviour was used to distinguish a spawning act. Spawns were assumed to have occurred if redds that were open the previous evening were covered before our arrival in the morning. If, during the first transect swim, we observed covering behaviour by the same female that was active and present at the redd the previous evening, then we considered the spawning act to have occurred just prior to our arrival. Often, the female that was active and present at a particular redd the previous evening was not found near the redd at which she was formerly active, although the redd was covered. In such instances, we considered the spawning act to have occurred at some time after our departure the previous evening. In the text, these spawning acts are referred to as "early" (before 09:00) and "late" (after 18:00), respectively.

Redd selection

To determine the hydraulic preferences of spawning brook trout, we measured groundwater flow and conductivity at sites where we had observed spawning the previous season (1994, $n = 23$; 1995, $n = 22$) and at random sites (1994, $n = 20$; 1995, $n = 11$). Random sites were located in close proximity (0.5–20 m) to redds where spawning had occurred and were of similar substrate composition. Of the 20 randomly selected sites measured in 1994, 13 sites occurred "within" the spawning area; the remaining seven sites were located elsewhere around the lake (Fig. 1). Measurements of groundwater flow were made using plastic seepage meters just prior to the start of spawning in 1994 and 1995. Measurements of groundwater flow were made in triplicate, lasted 2 h, and used collection bags prefilled to 1 L (see Blanchfield and Ridgway 1996 for full details). A separate collection of groundwater was made without a prefilled bag to measure conductivity (microsiemens per centimetre at 25°C). Two conductivity meters were used during the 1994 season. Groundwater samples were measured with both meters to correct for differences in sensitivity in accordance with the more sensitive meter (Orion™ model 140).

Measurements of depth, area, and distance to shore were taken for all redds after spawning was complete. Estimates were made for four redds that were inaccessible due to freezing in 1994. Area was calculated by measuring the longest axis and the maximum width perpendicular to the long axis for the entire cleared area. Water temperatures were recorded hourly throughout the spawning seasons at six locations within the spawning area using submersible temperature recorders (Ryan TempMentors™). Precipitation was measured continually from a weather station located on Scott Lake (Fig. 1). Precipitation prior to September would have little influence on spawning activities; therefore, only fall precipitation data are included (1 September to 31 October 1994; 1 September to 15 November 1995).

To determine if redd sites were limiting, a female removal experiment was conducted at Stringer Lake (45°26'N, 78°30'W) in Algonquin Park, just following peak spawning, on 7 November 1994. Stringer Lake was used for this experiment, since we did not wish to disturb any of the spawning activity occurring at Scott Lake. An active female was removed from her redd with a dip net by a snorkeller. The removed fish was held in a container onshore while the redd was observed. A female was considered to be replaced if a new female commenced redd construction activities or actively defended the redd against other females. We allowed a period of 1 h for females to be replaced. Seven different females were removed from their redds and the time for each replacement recorded. All confined females were released to the spawning area immediately after their redds were occupied by another female.

Statistical analyses

We compared the onset of ripeness by males and females using a chi-squared test. We used linear regression to analyse the number of days fish were observed in relation to body size (ln transformed). To be consistent between years, we recorded the amount of time male and female brook trout were present on the spawning area starting from

the first day of spawning activity (10 October 1994 and 1995). We compared the duration of time males and females spent on the spawning grounds in each year and within sexes between years using analysis of covariance (ANCOVA). We compared the rate of groundwater flow and conductivity at spawning sites versus unused spawning sites and random sites using the Mann–Whitney U -test (two-tailed). Because data were nonnormal, the number of redds used by individual females and the duration of actual spawning were analysed with a Spearman correlation. We followed a closed sequential test design to determine if redds were reoccupied (Cole 1962). Mean values (± 1 SD) are reported below.

Results

Adult observations

Brook trout were observed on or near the spawning grounds over a 64-d period in 1994 (30 September to 2 December) and a 61-d period in 1995 (25 September to 24 November). Male and female brook trout were first observed congregating around a small inlet creek adjacent to the spawning area; however, no reproductive activity was observed at this time. Only one of the females caught prior to the first observed spawning was ripe. In contrast, 86% ($\pm 16\%$) of the males caught at this time were ripe. From the first day of spawning, but prior to peak spawning, 20% ($\pm 7\%$) of females and 98% ($\pm 3\%$) of males caught were ripe. Throughout both spawning seasons, more males were found to be ripe than females (1994, $df = 1$, $\chi^2 = 21.9$, $P < 0.0001$; 1995, $df = 1$, $\chi^2 = 63.5$, $P < 0.0001$).

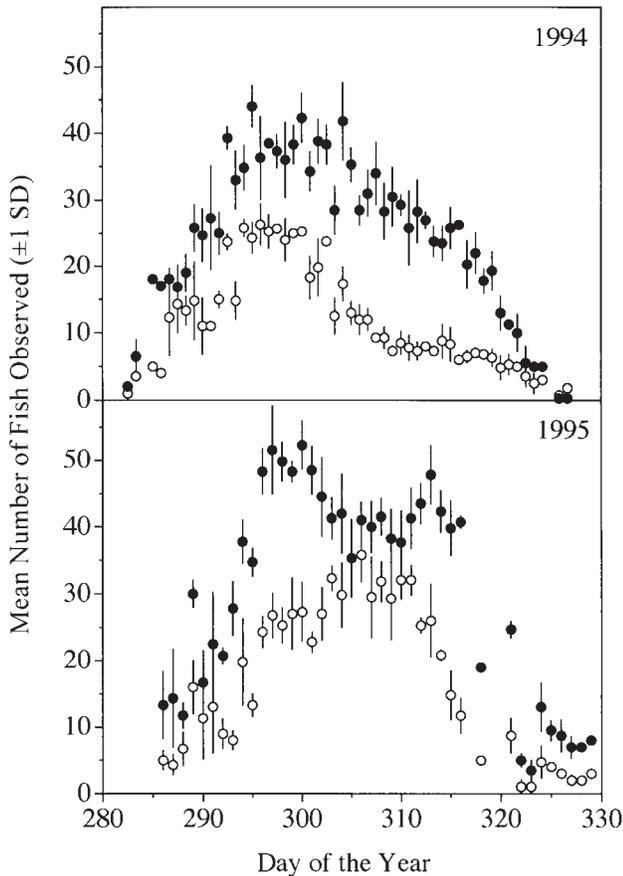
More males occurred on the spawning grounds than females, except for the very end of spawning (Fig. 2). In both years, peak numbers of males and females occurred at approximately the same time, between days 296 and 312 (22 October to 8 November), although a second peak in the number of males occurred in 1995 (Fig. 2). Approximately 90% of all spawning males were present within 14 d following the first day of spawning, while only 60% of the spawning female population was present by this time.

There was a trend for larger fish to remain on the spawning grounds longer than smaller fish (Fig. 3). Increased duration on the spawning grounds with body size was significant for both males ($n = 38$, $r^2 = 0.19$, $F = 8.6$, $P = 0.006$) and females ($n = 45$, $r^2 = 0.27$, $F = 15.9$, $P < 0.001$) during the 1994 season. This trend was not observed for males ($n = 55$, $r^2 = 0.002$, $F = 0.09$, $P = 0.8$) or females ($n = 31$, $r^2 = 0.06$, $F = 1.8$, $P = 0.2$) during the 1995 season. The duration of time spent on the spawning grounds was longer for males in 1994 than in 1995 (31 ± 12 and 22 ± 9 d, respectively; $F = 9.3$, $P = 0.003$), although no difference in duration was observed for females between years (11 ± 6 and 15 ± 7 d, respectively; $F = 2.7$, $P = 0.1$). Males, however, remained on the spawning grounds for a longer period than females during both spawning seasons (1994, $F = 100.8$, $P < 0.001$; 1995, $F = 12.1$, $P < 0.001$).

We observed spawning at all times of the day throughout both seasons, with a distinct peak in activity between 13:00 and 14:00 (Fig. 4). Eighty-nine percent of all spawning took place during the hours of daily observation (09:00–18:00), the remaining spawns occurred either just prior to our arrival ("early", 3%) or sometime after our departure ("late", 8%) (Fig. 4).

The seasonal peak in spawning activity (1994, days 296–310; 1995, days 296–312) (Fig. 5) coincided with peak

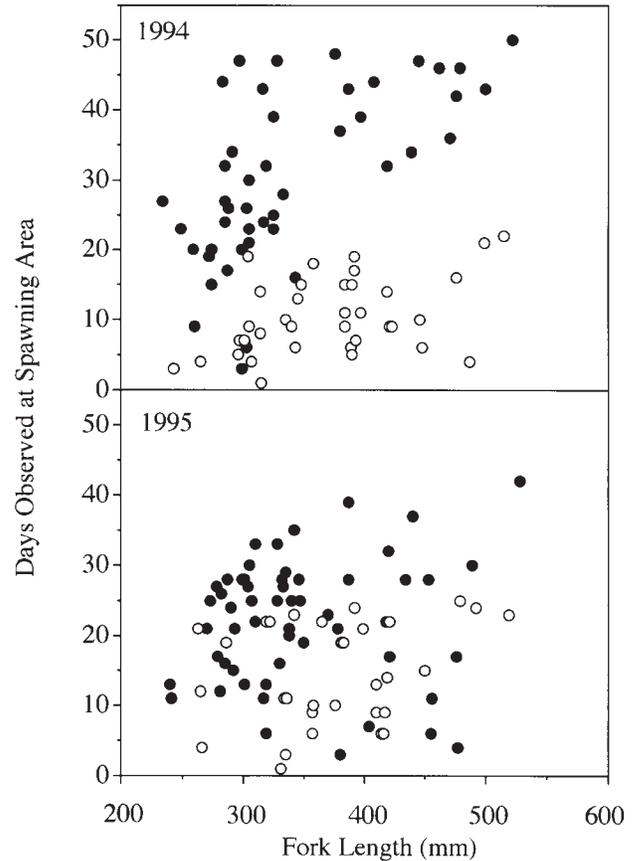
Fig. 2. Mean number (± 1 SD) of male (solid circles) and female (open circles) brook trout observed on the spawning grounds in 1994 and 1995, beginning from the first day of spawning activity (day 283 is 10 October).



counts of males and females (Fig. 2). In 1994 and 1995, peak breeding activity accounted for 58 and 84% of the total spawnings observed during the season, respectively (Fig. 5). During peak spawning periods, water temperature in the spawning area decreased from 11.3 to 8.8°C in 1994 and from 10.3 to 5.9°C in 1995 (Fig. 5). In both years, peak spawning periods were preceded by substantial rainfall events such that 90 mm of rainfall had accumulated (from 1 September) by this time (Fig. 6).

In general, spawning females were longer (1994, $n = 47$, 372 ± 65 mm; 1995, $n = 42$, 376 ± 64 mm) and heavier (1994, $n = 45$, 656 ± 395 g; 1995, $n = 42$, 705 ± 381 g) than spawning males (FL: 1994, $n = 50$, 334 ± 77 mm; 1995, $n = 65$, 337 ± 65 mm; mass: 1994, $n = 48$, 480 ± 407 g; 1995, $n = 63$, 507 ± 351 g), although several small females were not captured. In each year, a very small (≤ 140 mm FL), sexually mature male brook trout was captured on the spawning grounds and is included in the above length data. Two other similar-sized fish (≤ 140 mm FL) were also caught in 1994, but it was not possible to determine their sex. The stomachs of these two fish were full of eggs (P.J. Blanchfield, personal observation). These smaller fish were always seen hiding close to active redds and were never observed as part of the hierarchy formed by males around females. Often, these fish were aggressively attacked by active females.

Fig. 3. Number of days that individual male (solid circles) and female (open circles) brook trout were observed on the spawning grounds during the 1994 and 1995 breeding seasons.

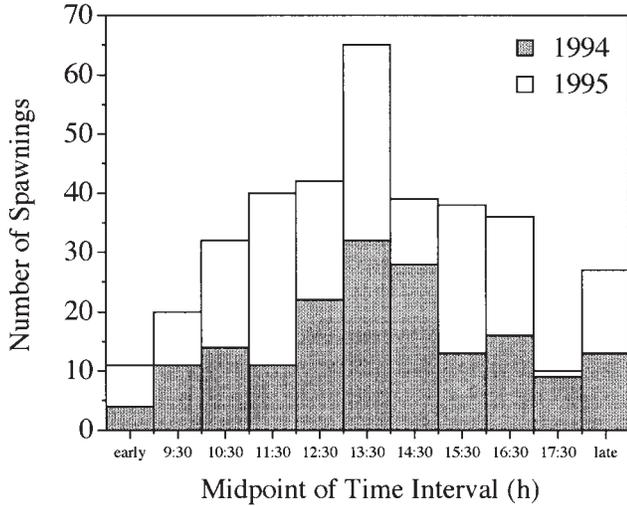


Redd selection

Of the known spawning sites (observed the previous year) that were measured for groundwater flow, 13 and 11 of these sites remained unused during the 1994 and 1995 spawning periods, respectively (Table 1). The flow rates of the unused sites were not lower than at redd sites where spawning occurred (1994, $U_{[13,10]} = 95$, $P = 0.07$; 1995, $U_{[11,11]} = 55$, $P = 0.7$). However, groundwater flow at spawning sites was greater than at random sites located within the spawning area (1994, $U_{[13,10]} = 126$, $P < 0.001$; 1995, $U_{[11,11]} = 11$, $P = 0.001$) and around the lake (1994, $U_{[10,7]} = 70$, $P < 0.001$). The conductivity of groundwater at redds was higher compared with random sites (1994, $U_{[13,10]} = 5$, $P < 0.001$; 1995, $U_{[11,11]} = 26$, $P = 0.02$) (Table 1).

Redds were located in the shallow littoral zone (1994, 1.1 ± 0.4 m; 1995, 1.6 ± 0.5 m) and near shore (1994, 6.6 ± 4.6 m; 1995, 7.8 ± 6.1 m). Redds were less than 1 m² in area (1994, 0.9 ± 0.8 m²; 1995, 0.7 ± 0.7 m²), resulting in a total substrate area of 30 m² in 1994 and 35 m² in 1995. There was evidence of female spawning activity (i.e., clearings) in other areas; however, we observed spawning at only 32 and 47 redd sites in 1994 and 1995, respectively. In total, 60 redd sites were used, of which 19 were used in both years (Fig. 7). Throughout the breeding seasons, there was an unequal distribution of spawning activity among redd sites, with the 11 most used sites accounting for half of the total spawnings (Fig. 7). Female brook trout often constructed more than one redd (1994,

Fig. 4. Daily timing of actual spawning by brook trout observed during the 1994 and 1995 spawning seasons. “Early” refers to spawning estimated to have taken place just prior to 09:00; “late” refers to spawning that occurred sometime after 18:00 (see text for details).



1.4 ± 0.8; 1995, 1.7 ± 0.8) (Fig. 8). The construction of multiple redds by spawning females increased with body size during the 1994 season ($n = 34$, $R = 0.44$, $P = 0.009$), but not in 1995 ($n = 23$, $R = 0.039$, $P = 0.9$) (Fig. 8). In 1994 and 1995, female brook trout spent, on average, 3.6 ± 2.7 and 4.1 ± 2.6 d between their first and last observed spawning, respectively. The number of days between first and last spawning increased with female body size (1994, $n = 34$, $R = 0.43$, $P = 0.01$; 1995, $n = 23$, $R = 0.48$, $P = 0.02$) (Fig. 9). As well, most of the larger females spawned during the period of peak activity, while only smaller females tended to spawn after this time (Fig. 9).

In all seven removal trials, females were replaced within the allotted 1-h time period ($P < 0.001$) (Cole 1962). Active females removed from their redd were quickly replaced by other females (12 ± 7 min). In three trials, more than one female visited the redd prior to establishing dominance on that redd. In three additional trials, a single female was involved in redd replacement. In another trial, the redd was visited twice, but we were unable to determine if this was by the same female. Because they were not individually marked, it was difficult to determine if the replacing females were from neighbouring redds or “floaters”. In one trial, a neighbouring female (A) started defending the unoccupied redd of the removed female (B) against other females. Later, we removed this female (A), and similar behaviour was shown by the initial female (B) after release. In another trial, a neighbouring female inspected a redd from which a female had been removed, but returned to her original redd.

Discussion

We have provided a detailed description of an iteroparous salmonine mating system, which was based on daily observations of the spawning activities of marked individuals throughout two breeding seasons. Male recruitment to the spawning area was abrupt and occurred early in both seasons. In contrast, female recruitment occurred throughout the spawning period

Fig. 5. Daily number of spawnings at Scott Lake in 1994 and 1995. Peak spawning activity occurred over approximately the same period between years. Mean (solid line) water temperature (±1 SD, broken lines) within the spawning area decreased throughout the spawning season.

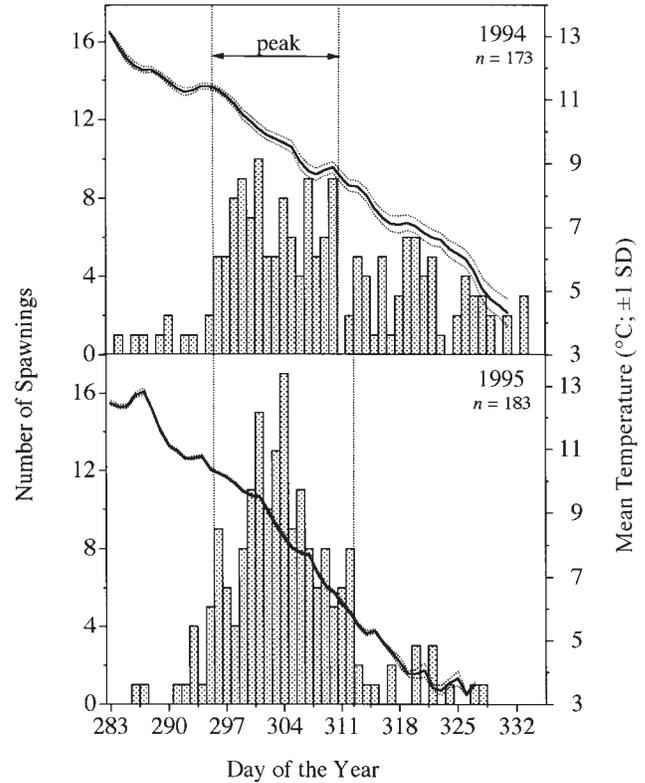
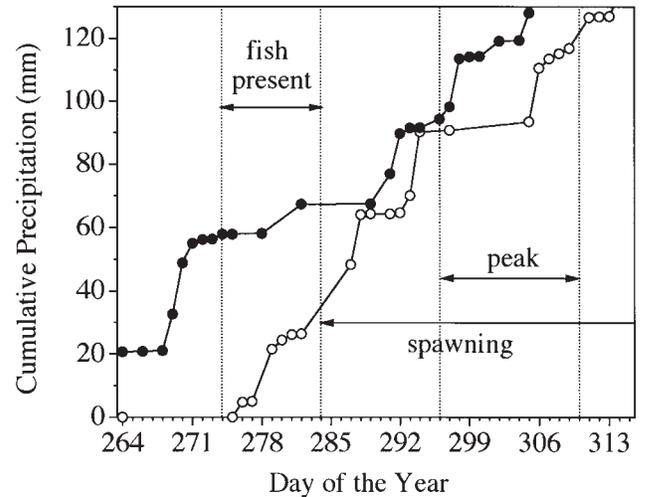


Fig. 6. Cumulative precipitation at Scott Lake as of 1 September 1994 (solid circles) and 1995 (open circles). Peak spawning activity by brook trout was preceded by rainfall events.

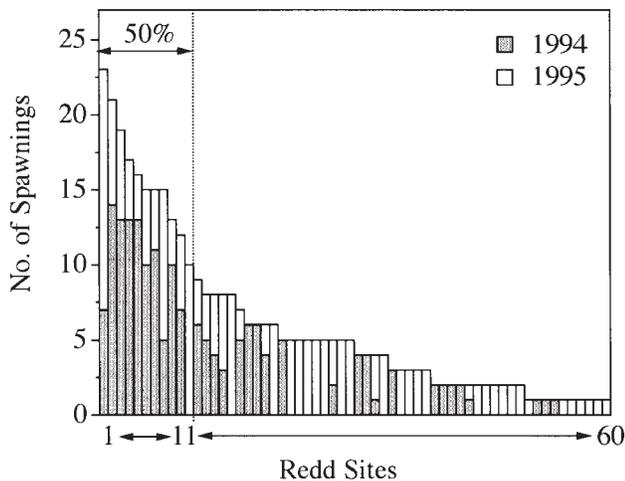


with a continual loss of spent fish, although there was a marked peak in spawning activity. These data, in combination with duration estimates and evidence of ripeness, show males to be sexually active over a much longer period than females. The cumulative distribution of males shows similar trends to

Table 1. Measurements (means and ranges) of groundwater flow and conductivity of brook trout spawning sites and random sites.

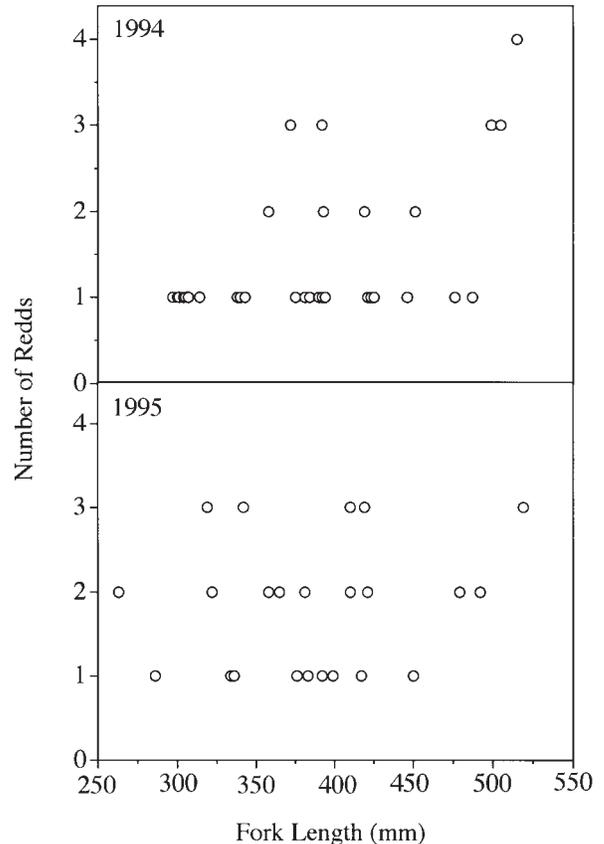
Variable	Year	Spawning sites		Random sites	
		Used sites	Previously used sites	Sites within spawning area	Sites located around lake
<i>n</i>	1994	10	13	13	7
	1995	11	11	11	
Flow rate (mL·m ⁻² ·min ⁻¹)	1994	49.2 (6.2–296.1)	11.1 (3.6–21.8)	3.3* (0–12.2)	2.0* (0.9–5.3)
	1995	45.3 (3.4–238.3)	13.7 (8.1–20.3)	5.4* (1.5–10.5)	
Conductivity (µS·cm ⁻¹ at 25°C)	1994	58.0 (34.5–84.8)	39.1 (30.7–65.5)	31.5* (26.5–55.5)	30.8* (27.1–37.2)
	1995	48.1 (27.8–87.0)	36.5 (28.6–46.6)	31.9* (27.6–41.0)	

Note: *Significantly different ($P < 0.05$) from used spawning sites.

Fig. 7. Number of spawnings that occurred at redd sites in 1994 and 1995. Half of all spawnings occurred at 11 redd sites during the two breeding seasons.

Fraser's (1985) mark–recapture study in that little new recruitment of males occurs after peak spawning and few males leave the spawning grounds.

The number of days male and female brook trout were present on the spawning grounds was dependent on body size during the 1994 season but not in 1995. One reason for a weakening of the body size duration pattern in 1995 was because spawning activity was observed for 11 fewer days than in 1994 and was more synchronous during the 1995 season. For males, this was reflected in the significantly greater mean number of days spent on the spawning grounds in 1994 (31 d) than in 1995 (22 d). There was no difference in amount of time spent on the spawning grounds by females between years, which concurs with our above observations of continual recruitment into the spawning area throughout the breeding season. Another explanation for this difference between years may be due to increased breeding density in 1995 (Fig. 2). Increased breeding density in coho salmon was found to make a significant negative contribution to life span due to increased competition for resources (spawning sites for females; mates for

Fig. 8. Number of redds constructed by spawning brook trout females of different body sizes in 1994 and 1995.

males)(van den Berghe and Gross 1986). Since smaller male brook trout spent less time spawning than larger males (Fig. 3), we attribute the decline in numbers of spawning males that we observed to the disappearance of small males. In such a protracted (some males observed for 64 d) and highly competitive mating system, smaller males may incur higher reproductive costs from physical injury due to mate competition with larger males (Hutchings and Myers 1987; Hutchings 1994). Smaller

males may also incur greater energetic costs relative to large males (Schmidt-Nielsen 1984). Postreproductive energy deficits can be substantial in salmonines (Jonsson et al. 1991) and are known to occur among stream-spawning brook trout (Cunjak et al. 1987; Hutchings 1994). This combination of possible physical injury and energetic demand may be particularly acute for small males in a manner that is similar to Arctic char (*Salvelinus alpinus*) mating systems in lakes (Sigurjónsdóttir and Gunnarsson 1989). In these Arctic char mating systems, as well as the Scott Lake brook trout mating system, satellite males can surround the dominant pair and approach from any depth or direction. This nonlinear arena contributes to continual aggressive satellite–satellite and dominant–satellite interactions, as well as extended assessment and fighting among males, which may be more costly to smaller males.

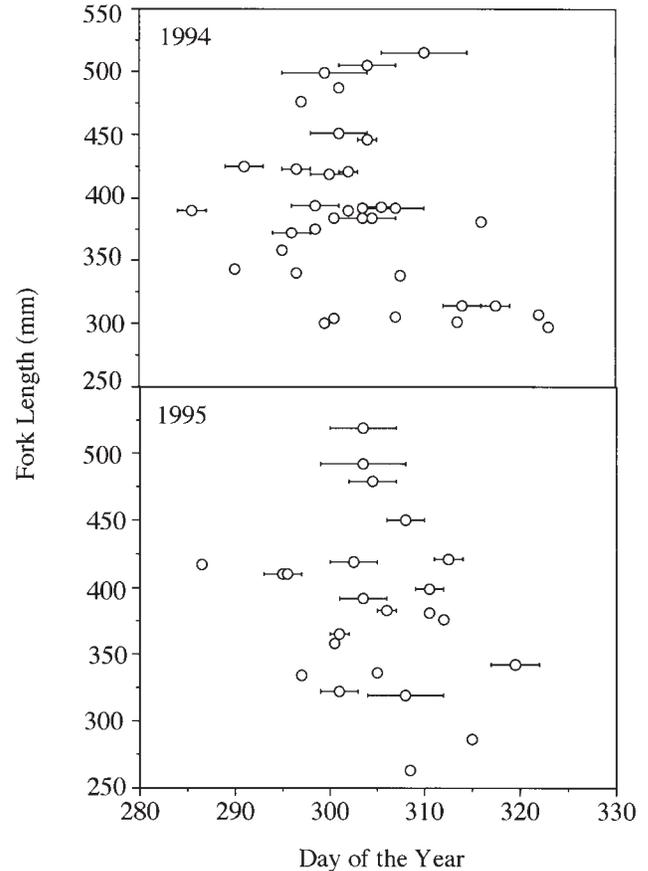
Both male and female brook trout were seen near and around the spawning area prior to the start of spawning. Many of the early-tagged females were not yet ripe. These same females were routinely observed in stationary inactive groups within the spawning area for periods of up to 2 wk or more prior to spawning. Similar behaviour was observed with stream brook trout in which females did not frequent the spawning areas until ready to spawn, although they were often found in nearby pools (White 1930).

Actual spawning by brook trout occurred over 50 d in 1994 and 43 d in 1995, with daily and seasonal peaks in spawning activity observed during these periods. In contrast with a previous field study (Curry and Noakes 1995; Curry et al. 1995), in which no actual spawning was observed, and a laboratory study (Hale and Hilden 1969), in which spawning was observed at night, we observed brook trout spawning primarily during daylight hours, with peak activity occurring around midday (13:00–14:00). Similar peaks in daily activity were found in a spawning population of golden trout (*Oncorhynchus mykiss aquabonita*) (Knapp and Vredenburg 1996).

A distinct seasonal peak in spawning activity occurred over ~15 consecutive days, in which all of the larger females spawned. Peak activity was followed by an extended period of spawning by some of the smallest females. Large females were present on the spawning grounds early and were presumably able to secure a redd site at any given time due to body size. This synchrony in spawning activity suggests that timing of spawning is an important aspect of female reproductive behaviour. Synchronous spawning by large females may also force some of the smaller females to delay breeding, similar to coho salmon (van den Berghe and Gross 1989; Fleming and Gross 1994).

Two hypotheses may account for synchronous spawning by females as a strategy (Knowlton 1979) to increase egg survivorship. First, it is possible that females are choosing to spawn synchronously, thereby lowering the operational sex ratio (OSR) as a strategy to reduce harassment (e.g., Boness et al. 1995) and egg predation by satellite males, since the number of males per active female should be fewer when many females are active (Quinn et al. 1996). Unlike Pacific salmon, which cease feeding prior to spawning, egg cannibalism by satellite males has been observed in this and other lake-spawning populations of brook trout (P.J. Blanchfield, personal observation). Second, females prevent superimposition of their redds, and therefore increase brood survivorship, by spawning when other large females spawn. If nest depth increases with increasing

Fig. 9. Mean spawning date (circles) and the number of days between first and last spawning (lines) by individual females during the 1994 and 1995 breeding seasons.



female size, as in other salmonines (van den Berghe and Gross 1984; Knapp and Vredenburg 1996), then a preferred time to spawn would be with other large females. In this way, larger females compete for preferred redd sites, and smaller females could choose redd sites where large females are not spawning. Superimposition of redds by later-spawning small females may have little consequence for brood survival of larger females. Conversely, smaller females may be choosing to delay spawning as a strategy to decrease redd superimposition by larger females or obtain better mates (Knowlton 1979) if male mate choice is dependent on male size as in other salmonines (Foote 1988b).

The proximate cues for synchronizing a peak in spawning activity may have been a combination of temperature and precipitation. Prior to spawning, daily variations in water temperature below 11°C are thought to enhance egg viability in brook trout (Hokanson et al. 1973). At Scott Lake, spawning started when temperatures fell below 13°C, with most activity occurring as water temperature declined below 11.3 and 10.3°C in 1994 and 1995, respectively. Compelling evidence exists for a significant, positive relationship between mean groundwater discharge rates and mean daily rainfall (Downing and Peterka 1978). In 1994 and 1995, significant rainfall events (~30 mm) occurred just prior to peak spawning activity (Fig. 6). Presumably, groundwater flow increased during this period, and in doing so, greater amounts of water (higher in

conductivity than ambient lake water) would be present at redd sites. We suspect that an increase in groundwater flow in conjunction with a decrease in water temperature below 11°C stimulates brook trout spawning and that these factors are responsible for the dramatic increase in spawning activity observed.

Natural reproduction by female brook trout occurred in areas with groundwater upwelling at a rate of 3.4–296.1 mLm⁻²·min⁻¹. This gradient in flow is consistent with previous quantitative measures of flow rates at brook trout redds in lentic and lotic systems (see Blanchfield and Ridgway 1996). A highly significant difference in flow rates between redd sites and nonspawning sites located within the spawning area indicates that females were actively choosing sites associated with groundwater flow. However, some redd sites were reused, while others were not used in consecutive years (1994–1995). Redd sites that were reused had higher average groundwater seepage rates than those that were not reused in 1995 when compared with 1994. These results indicate that reuse of redd sites may vary according to annual variation in seepage rates at redd sites. It is possible that female brook trout detect upwelling groundwater by its chemical composition (i.e., high conductivity), but later-spawning females may also use visual cues such as cleared areas from previous spawning activity. We observed brook trout spawning over a wide range of gravel substrate sizes as well as on an aggregation of waterlogged sticks and wood chips beside a beaver lodge, as previously observed in another population (Fraser 1982). This variation in spawning substrate suggests that the need for groundwater flow at redds is more important than substrate composition in redd site selection (Witzel and MacCrimmon 1983).

Among the salmonines, brook trout are not unique in their requirement of groundwater upwelling at redds. The use of spring seepage areas by Arctic char (Cunjak et al. 1986), brown trout (*Salmo trutta*) (Hansen 1975), rainbow trout (*Oncorhynchus mykiss*) (Sowden and Power 1985), and sockeye salmon (*Oncorhynchus nerka*) (Lorenz and Eiler 1989) has also been documented. However, these salmonines also spawn in areas without groundwater inflow. Although all redds could not be measured, our data, and those of others (e.g., Curry and Noakes 1995), suggest that lake-dwelling brook trout spawn solely at sites of groundwater upwelling. The relative importance of upwelling groundwater ought to be greater in lake than in stream systems, since there is considerably less movement of water in lakes during the overwinter incubation period as a result of freezing (Curry et al. 1995).

Competition for limited sites available to spawning salmonines can lead to redd reuse and superimposition of redds (e.g., McNeil 1967). The maximum total area used for incubation by the spawning population of brook trout in Scott Lake was 35 m². Our data agree with observations by Carline (1980) and others that lack of suitable sites for redd construction is one likely factor limiting brook trout populations. The fact that active females are readily replaced once removed from their redd indicates that redd sites are a limiting resource and that certain sites are preferred. Such intense reuse of redd sites is most likely a consequence of limited sites (32 and 47 redd sites in total, 1994 and 1995, respectively) and contributes to the construction of multiple redds by females.

It has been suggested that selection of redd sites by female

brook trout is regulated by competition for an opportunity to spawn in a limited area defined by discharging groundwater (Curry and Noakes 1995). We agree that sites are limiting, as shown from redd superimposition data and removal experiments. However, we argue that females do not compete solely for an opportunity to spawn, but instead, females compete for certain sites, and competition is affected by the seasonal timing of spawning. If the selection of sites is determined solely by an opportunity to spawn, then we would expect approximately equal numbers of spawnings among all sites. In contrast, we found preferential use of certain sites during both breeding seasons (Fig. 7). Secondly, we believe that timing of spawning is a significant component regulating female competition for redd sites. The fact that the majority of spawning (up to 84%) occurs over a brief period suggests that the timing is very important.

Similar to other iteroparous salmonine species (e.g., Fukushima 1994), female brook trout tend to deposit eggs in more than one redd. On average, female brook trout at Scott Lake constructed 1.6 redds. Female Atlantic salmon (*Salmo salar*) and brown trout usually spawn in one redd (Crisp and Carling 1989); however, estimates of 8.4 and 5.7 redds per female, respectively, have also been suggested (Barlaup et al. 1994). The large number of redds per female estimated by Barlaup et al. (1994) may be biased, since they sampled only stranded redds and did not observe spawning females in the field. As with stream observations (White 1930), brook trout females generally spawned only once in each egg pit, but multiple spawnings by an individual female can occur in a single egg pit (Greeley 1932; Hazzard 1932; P.J. Blanchfield, personal observation).

Alternative life history strategies are known to occur among some salmonines (Gross 1984). The presence of very small (≤ 140 mm), sexually mature males on the spawning grounds may be evidence of an alternative life history strategy for male brook trout. These smaller fish were always seen hiding among sticks in the proximity of active redds and were never observed at redds that were located in open areas. As well, these fish were never observed as part of the hierarchy formed by males around females, and their behaviour was similar to the sneaking behaviour documented for other salmonines (Gross 1985).

The ability to individually identify and observe a large proportion of a naturally breeding population throughout a reproductive season is rare in research on mating systems in general. However, the implications of such data are that information about aspects of fish reproductive ecology that were previously assumed may now be determined in detail. This is especially true with respect to the reproductive ecology of brook trout in lakes about which few studies exist. Prior research on this subject does not incorporate underwater observations of tagged individuals. The ability to fully observe a spawning population at an individual level allows for detailed measures of spawning behaviour with respect to seasonal timing of breeding, duration on the spawning area, and site choice. The ratio of male to female brook trout present on the spawning grounds at Scott Lake was skewed towards males as a result of differences between males and females in the timing and duration of spawning. Temporal and spatial (i.e., multi-redds tactics appear to be an important part of female spawning behaviour in brook trout. Larger females tend to spawn synchronously and in more redds and over a longer time period

than smaller females. The resulting differences in fitness associated with such behaviour warrant further investigation.

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References

- Barlaup, B.T., Lura, H., Sægrov, H., and Sundt, R.C. 1994. Inter- and intra-specific variability in female salmonid spawning behaviour. *Can. J. Zool.* **72**: 636–642.
- Benson, N.G. 1953. The importance of ground water to trout populations in the Pigeon River, Michigan. *Trans. N. Am. Wildl. Conf.* **18**: 269–281.
- Blanchfield, P.J., and Ridgway, M.S. 1996. Use of seepage meters to measure groundwater flow at brook trout spawning redds. *Trans. Am. Fish. Soc.* **125**: 813–818.
- Boness, D.J., Bowen, W.D., and Iverson, S.J. 1995. Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behav. Ecol. Sociobiol.* **36**: 1–10.
- Carline, R.F. 1980. Features of successful spawning site development for brook trout in Wisconsin ponds. *Trans. Am. Fish. Soc.* **109**: 453–457.
- 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.
- Cole, L. 1962. A closed sequential test design for toleration experiments. *Ecology*, **43**: 749–753.
- 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.* **113**: 383–387.
- Cunjak, R.A., Curry, R.A., and Power, G. 1987. Seasonal energy budget of brook trout in streams: implications of a possible deficit in early winter. *Trans. Am. Fish. Soc.* **116**: 817–828.
- 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.
- Danzmann, R.G., and Ihssen, P.E. 1995. A phylogeographic survey of brook charr (*Salvelinus fontinalis*) in Algonquin Park, Ontario based upon mitochondrial DNA variation. *Mol. Ecol.* **4**: 681–697.
- Downing, J.A., and Peterka, J.J. 1978. Relationship of rainfall and lake groundwater seepage. *Limnol. Oceanogr.* **23**: 821–825.
- 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.
- Footo, C.J. 1988a. Male mate choice in fishes: a review of the evidence in coho salmon. *Anim. Behav.* **36**: 1228–1230.
- Footo, C.J. 1988b. Male mate choice dependent on male size in salmon. *Behaviour*, **106**: 63–80.
- 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.* **112**: 163–174.
- Fukushima, M. 1994. Spawning migration and redd construction of Sakhalin taimen, *Hucho perryi* (Salmonidae) on northern Hokkaido Island, Japan. *J. Fish Biol.* **44**: 877–888.
- Greeley, J.R. 1932. The spawning habits of brook, brown and rainbow trout, and the problem of egg predators. *Trans. Am. Fish. Soc.* **62**: 239–247.
- Gross, M.R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. *In Fish reproduction: strategies and tactics. Edited by R. Wootton and G. Potts. Academic Press, London. pp. 55–75.*
- Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. *Nature (Lond.)*, **313**: 47–48.
- Hale, J.G. 1968. Observations on brook trout, *Salvelinus fontinalis*, spawning in 10-gallon aquaria. *Trans. Am. Fish. Soc.* **97**: 299–300.
- Hale, J.G., and Hilden, D.A. 1969. Spawning and some aspects of early life history of brook trout, *Salvelinus fontinalis* (Mitchell), in the laboratory. *Trans. Am. Fish. Soc.* **98**: 473–477.
- Hansen, E.A. 1975. Some effects of groundwater on brown trout redds. *Trans. Am. Fish. Soc.* **104**: 100–110.
- Hartman, W.L., Merrell, T.R., and Painter, R. 1964. Mass spawning behavior of sockeye salmon in Brooks River, Alaska. *Copeia*, **1964**: 362–368.
- Hazzard, A.S. 1932. Some phases of the life history of the eastern brook trout, *Salvelinus fontinalis*. *Trans. Am. Fish. Soc.* **62**: 344–350.
- Hendry, A.P., Leonetti, F.E., and Quinn, T.P. 1995. Spatial and temporal isolating mechanisms: the formation of discrete breeding aggregations of sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.* **73**: 339–352.
- Hokanson, K.E.F., McCormick, J.H., Jones, B.R., and Tucker J.H. 1973. Thermal requirements for maturation, spawning, and embryo survival of the brook trout, *Salvelinus fontinalis*. *J. Fish. Res. Board Can.* **30**: 975–984.
- Hutchings, J.A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. *Oikos*, **70**: 12–20.
- Hutchings, J.A., and Myers, R.A. 1987. Escalation of an asymmetric contest: mortality resulting from mate competition in Atlantic salmon, *Salmo salar*. *Can. J. Zool.* **65**: 766–768.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1991. Energetic cost of spawning in male and female Atlantic salmon, *Salmo salar*. *J. Fish Biol.* **39**: 739–744.
- Keenlyside, M.H.A., and Dupuis, H.M.C. 1988. Courtship and spawning competition in pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Zool.* **66**: 262–265.
- 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.
- Knowlton, N. 1979. Reproductive synchrony, parental investment, and the evolutionary dynamics of sexual selection. *Anim. Behav.* **27**: 1022–1033.
- Lorenz, J.M., and Eiler, J.H. 1989. Spawning habitat and redd characteristics of sockeye salmon in the glacial Taku River, British Columbia and Alaska. *Trans. Am. Fish. Soc.* **118**: 495–502.
- Martin, N.V. 1957. Reproduction of lake trout in Algonquin Park, Ontario. *Trans. Am. Fish. Soc.* **86**: 231–244.

- McNeil, W.J. 1967. Randomness in distribution of pink salmon redds. *J. Fish. Res. Board Can.* **24**: 1629–1634.
- Needham, P.R. 1961. Observations on the natural spawning of eastern brook trout. *Calif. Fish Game*, **47**: 27–40.
- Quinn, T.P., and Foote, C.J. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. *Anim. Behav.* **48**: 751–761.
- Quinn, T.P., Adkinson, M.D., and Ward, M.D. 1996. Behavioral tactics of male sockeye salmon (*Oncorhynchus nerka*) under varying operational sex ratios. *Ethology*, **102**: 304–322.
- 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*.
- Sargent, R.C., Gross, M.R., and van den Berghe, E.P. 1986. Male mate choice in fishes. *Anim. Behav.* **34**: 545–550.
- Sargent, R.C., Gross, M.R., and van den Berghe, E.P. 1988. Male mate choice in fishes: a reply to Foote. *Anim. Behav.* **36**: 1230–1233.
- Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important?* Cambridge University Press, Cambridge.
- Sigurjónsdóttir, H., and Gunnarsson, K. 1989. Alternative mating tactics of arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Environ. Biol. Fishes*, **26**: 159–176.
- Smith, O.R. 1941. The spawning habits of cutthroat and eastern brook trouts. *J. Wildl. Manage.* **5**: 461–471.
- 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.
- van den Berghe, E.P., and Gross, M.R. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **41**: 204–206.
- van den Berghe, E.P., and Gross, M.R. 1986. Length of breeding life of coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* **64**: 1482–1486.
- 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.
- Webster, D.A., and Eiriksdóttir, G. 1976. Upwelling water as a factor influencing choice of spawning sites by brook trout, *Salvelinus fontinalis*. *Trans. Am. Fish. Soc.* **105**: 416–421.
- White, H.C. 1930. Some observations on the eastern brook trout (*S. fontinalis*) of Prince Edward Island. *Trans. Am. Fish. Soc.* **60**: 101–108.
- Witzel, L.D., and MacCrimmon, H.R. 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. *Trans. Am. Fish. Soc.* **112**: 760–771.
- Young, M.K., Hubert, W.A., and Wesche, T.A. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. *Trans. Am. Fish. Soc.* **118**: 379–385.