Environmental Biology of Fishes **64:** 175–181, 2002.

Seasonal timing and diel activity of lacustrine brook charr, *Salvelinus fontinalis*, spawning in a lake outlet

Michel Baril[a,b] & Pierre Magnan[a,b,c]
[a]*Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, Québec G9A 5H7, Canada*
[b]*Brook Trout Foundation, Centre for Research and Education, 850 avenue du Hibou, Stoneham, Québec G0A 4P0, Canada*
[c]*Corresponding author (e-mail: pierre_magnan@uqtr.ca)*

Received 30 October 2000 Accepted 6 December 2001

Key words: spawning migrations, reproduction, homing, fish, salmonid

Synopsis

The objectives of this study were to determine (1) the seasonal timing and diel activity patterns of lacustrine brook charr when migrating to a lake outlet for spawning, and (2) the homing of reproducing individuals. In 1995, 745 individuals were captured while migrating to the spawning ground compared to 1148 in 1996. In both years, the sex ratio was not significantly different from 1 : 1 but females were significantly longer than males. The spawning migrations lasted about 48 d and were more nocturnal (between 20:00 and 8:00 h) than diurnal. The migration to the spawning ground began when water temperature decreased to 13°C and peaked when water temperature decreased from 11°C to 7°C. Peaks in migration activity were always preceded by a sudden decrease followed by an increase in temperature. The spawning migration lasted until the third week of October, when water temperature varied between 3°C and 8°C. Males, especially larger ones, arrived on the spawning ground before females in both years. The length of males migrating to the spawning ground decreased during the spawning season while the females' length showed no pattern. Only 9.7% of the 745 fin-clipped individuals from 1995 returned to the lake outlet to spawn in 1996. The results of this study indicate that lacustrine brook charr show similarities to other anadromous and lake-spawning salmonid populations when migrating to spawning grounds.

Introduction

Lacustrine brook charr, *Salvelinus fontinalis*, are reported to spawn either in the littoral zone or in both inlets and outlets of Canadian Shield lakes (Scott & Crossman 1974, Power 1980). Two factors are important in redd site selection and hatching success and have been well described for both lake- and stream-spawning stocks: the need of groundwater seepage (Webster & Eiriksdottir 1976, Fraser 1982, 1985, Snucins et al. 1992, Curry et al. 1994, 1995, Curry & Noakes 1995, Curry & Devito 1996, Blanchfield & Ridgway 1997, Bernier-Bourgault & Magnan 2002) and specific substrate characteristics (Fraser 1982, 1985, Witzel & MacCrimmon 1983a,b, Chapman 1988, Young et al. 1989, Bernier-Bourgault & Magnan 2002). In streams, brook charr reproduce from August to December, depending on the geographical area (Scott & Crossman 1974, Power 1980). More recently, Blanchfield & Ridgway (1997) described the reproductive timing, diel activity, and use of redd sites by a lake-spawning population. However, little is known on seasonal timing and diel activity of lacustrine brook charr when migrating to lake inlets or outlets for spawning. Spawning migrations have been described for anadromous populations (White 1940, Smith & Saunders 1958, Castonguay et al. 1982) and for a small number of lacustrine brook charr spawning in three inlets of a Canadian Shield lake, using telemetry (Bourke et al. 1997). Vladykov (1942) and O'Connor &

Power (1973) studied homing of lacustrine brook charr to spawning areas; Vladykov reported low percentages of fin-clipped individuals returning to their natal stream while O'Connor & Power reported high percentages.

The main objectives of this study were to determine (1) seasonal timing and diel activity patterns of a lacustrine brook charr stock when migrating to a lake outlet for spawning and (2) homing of reproducing individuals.

Materials and methods

Study site

The study was done from 1995 to 1997 in the outlet of Lake St-Michel, Charlevoix (Québec) Canada (47°10′N, 71°02′W), at 840 m of altitude. Lake St-Michel has a surface area of 220 ha. The outlet had been enhanced from 1987 to 1989 to increase the availability of spawning ground for brook charr. The length of the managed section is 150 m, its width varies from 4 to 9 m, and its depth from 0.20 to 1.5 m in summer. The substrate is composed of a layer of particles 15–30 mm in diameter over a sand and silt bottom. Brook charr and pearl dace, *Margariscus margarita*, are the only known fish species in Lake St-Michel. Intensive brook charr stocking (fingerlings) was stopped in 1986 and sport fishing is carefully controlled by the resort managing this territory (Gesti-Faune Inc.). Lake St-Michel has supported a sport fishing exploitation of 3000 brook charr per year since 1992 without any stocking.

Fish sampling

A bidirectional counting fence allowed us to catch all individuals migrating to the spawning ground in 1995 and 1996. This fence was located at the mouth of the lake outlet and its wings were stretched from one bank to the other in both the up- and downstream directions. The trap was made with multifilament net (stretched mesh of 15.9 mm) in 1995 and a metal grid in 1996. The trap was covered with a metal grid in 1996 because minks, *Mustela vison*, and muskrats, *Ondatra zibethicus*, damaged the net on two occasions in 1995. Although the holes made by these aquatic mammals allowed charr to pass through the counting fence, repairs were made within 24 h. The trap was divided into two sections, thus allowing us to capture brook charr migrating to and from the spawning ground (lake outlet). The fence was visited once or twice a day, depending on spawning activity, between 15 September and 25 October 1995 and between 7 September and 25 October 1996. The fence was not checked on 21, 22, 26, and 27 September and 17, 21, and 23 October 1995 due to logistical constraints. All fish were measured (±1 mm; total length, TL), weighed (±1.0 g), sexed, fin-clipped, and then released in the direction of their movement, either downstream (moving toward the spawning ground) or upstream (moving toward the lake). The adipose fin was clipped the first time a fish crossed the counting fence. After having entered the spawning ground, some of the fish were recaptured while moving upstream or downstream. For each subsequent crossings (downstream or upstream), another fin was clipped in the following order: half right pelvic, half left pelvic, entire right pelvic, and entire left pelvic. At the end of the spawning period, each fish returning to the lake was also measured (±1 mm; TL), weighed (±1.0 g), sexed, and the occurrence of fin clip was noted.

In 1996, fish were sampled at the counting fence every 4 h (4:00, 8:00, 12:00, 16:00, 20:00, and 24:00 h) on 20–21 September, 30 September–1 October, 4–5 October, and 9–10 October to determine the diel activity patterns of fish when migrating from the lake to the outlet for spawning. Each fish was measured, weighed, and fin-clipped as above. The fence was disassembled on 25 October 1995 and 1996 because few or no individuals were migrating to the spawning ground in the preceding days.

Statistical analyses

We used chi-square tests to determine if the sex ratio of individuals migrating to the spawning ground was significantly different from 1 : 1 and if migration movements to the spawning grounds were randomly distributed throughout the day. We used a t-test to determine if the mean lengths of males and females migrating to the spawning ground were significantly different in 1995 and 1996.

Results and discussion

Spawning migration and characteristics of the spawning population

In 1995, 745 individuals were captured while migrating to the spawning ground compared to 1148 in 1996

Table 1. Movements of lacustrine brook charr migrating to and from the spawning ground (lake outlet) of Lake St-Michel (Québec, Canada) in the fall of 1995 and 1996.

	Year	No. males	No. females	Total
Individuals migrating to the spawning ground	1995	373	372	745
	1996	592	556	1148
Individuals returning to the lake	1995	73	113	186
	1996	423	419	842
Multiple crossing at the counting fence	1995	188	55	243
	1996	106	38	144
Individuals marked in 1995 and recaptured in 1996	1996	43	39	72

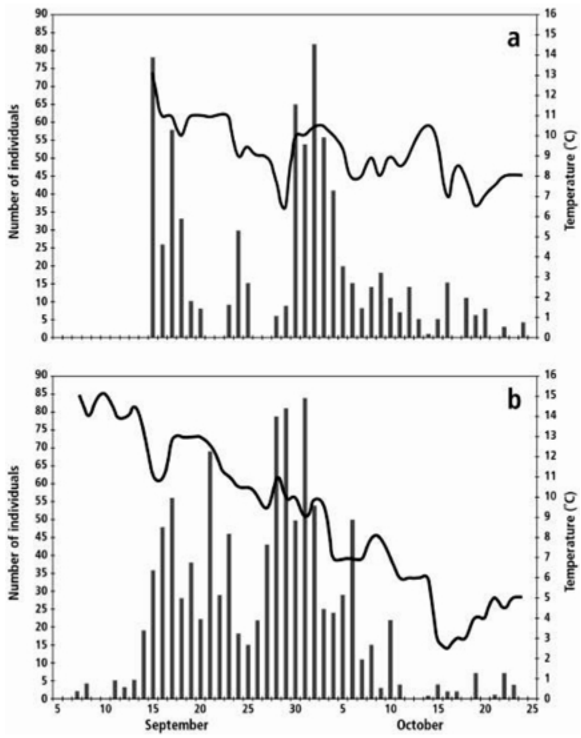

Figure 1. Number of lacustrine brook charr migrating to the spawning ground in the lake outlet (vertical bars) in relation to time and water temperature (curve). a – fall 1995; b – fall 1996. The fence was not checked on 21, 22, 26, and 27 September nor 17, 21 and 23 October 1995 due to logistical constraints.

(Table 1). The lower number of reproducing individuals captured in 1995 may be due to the fact that we missed the beginning of the spawning migration (see below and Figure 1) and that the net of the counting fences was occasionally damaged that year. In addition, abundant rains raised the water level over the counting fence for 3–4 days during the second half of the 1995 spawning period; fish may have passed over the counting fence to reach the spawning ground during this period. The differences in the number of reproducing individuals reaching this spawning ground between 1995 and 1996 may also be due to annual variability in brook charr abundance and in the use of this specific spawning ground. Brook charr also spawn in two inlets of the lake as well as in many sites of the littoral zone (M. Baril personal communication). Fishing cannot account for this difference because the exploitation was comparable in both years (3040 and 2981 brook charr captured in 1995 and 1996 respectively). For both years, fewer fin-clipped fish were captured while returning from than while migrating to the spawning ground (Table 1). Although some fish may have passed over the counting fence when the water level rose in 1995, we observed that 75% (1995) and 27% (1996) of the fish were still in the lake outlet when we disassembled the counting fence. Winter sampling done for another study revealed that adult fish leave the lake outlet before the beginning of winter (Bernier-Bourgault & Magnan 2002). A total of 17.9% (1995) and 21.1% (1996) of fish returning to the lake were not fin-clipped. In 1995, some of these fish had probably reached the spawning ground before we set up the counting fence. However, in both years, most of these fish were small and probably represented the proportion of young-of-the-year individuals that had stayed in the stream for their first year of life.

Males migrating to the spawning ground were 181 ± 39 mm (TL) in 1995 and 179 ± 34 mm (TL) in 1996 ($t = 0.545$, $p > 0.05$). In contrast, females migrating to the spawning ground were 197 ± 32 mm (TL) in 1995 and 203 ± 32 mm (TL) in 1996 ($t = 3.218$, $p < 0.001$). In both years, females were significantly longer than males (1995: $t = 6.125$, $p < 0.0001$; 1996: $t = 12.275$, $p < 0.0001$).

The sex ratio of spawning individuals was not significantly different from 1 : 1 in 1995 and 1996 (1995: $\chi^2 = 0.001$, df $= 1$, $p > 0.05$; 1996: $\chi^2 = 0.504$, df $= 1$, $p > 0.05$; Table 1). Scott & Crossman (1974) reported that males are often more abundant than females on spawning grounds while Fraser (1985) observed a sex ratio of 1 : 1 in an Ontario lake (Canada). Blanchfield & Ridgway (1997) found that males were more abundant than females on the spawning grounds of a lake-spawning population (in Ontario), except at the very end of the reproductive season.

Multiple crossings at the counting fence were more frequent in males than in females for both years

(1995: $\chi^2 = 38.17$, df $= 1$, $p < 0.001$; 1996: $\chi^2 = 16.02$, df $= 1$, $p < 0.001$; Table 1). For both males and females, a proportion of these multiple crossings resulted from individuals reproducing near the counting fence: some redds were located directly upstream or downstream of the counting fence. The higher proportion of males crossing the fence more than once may reflect that they are more active than females during the reproductive season (e.g., searching for a territory, interactions with other males). The higher number of fish remaining on the spawning grounds in 1995 compared to 1996, when the sampling was ended, may have affected the estimates of multiple crossing.

Chronology of the spawning migrations to the lake outlet

The spawning migration lasted 40 days in 1995 and 48 days in 1996 (Figure 1). The results suggest that we missed the beginning of the 1995 spawning migration. Blanchfield & Ridgway (1997), who studied the spawning chronology in a lake-spawning population in Ontario over two consecutive years, reported that individuals were observed on or near the spawning grounds over 61–64 day-periods, but that spawning occurred over periods of about 50 days.

The migration to the spawning ground began when the water temperature decreased to 13°C, which occurred on 15 September in 1995 and on 14 September in 1996 (Figure 1). Most of the migration activity was concentrated between 14 September and 10 October in 1996 while it was more spread out in 1995. The shortened migration activity in 1996 could be due to the more rapid drop in temperature. Similarly, Blanchfield & Ridgway (1997) observed a shortened spawning period with greater rate of temperature lost. Peaks in migrating activity were preceded by a sudden decrease followed by an increase in temperature.

The spawning migration lasted until the third week of October, when the water temperature varied between 3°C and 8°C. In this lake, water temperature falls rapidly and ice cover settles in November. In both years, we observed that peaks in the spawning migrations (between 7°C and 11°C) occurred at the same time as peaks in the spawning activity (highest fish abundance on selected spawning sites and territorial behaviours; personal observations). Blanchfield & Ridgway (1997) observed that the temperature of spawning area varied between 5.9°C and 11.3°C during peak spawning activity in a lake-spawning population. These temperatures are below the upper lethal temperature (11.7°C; Scott & Crossman 1974) and the 50% lethal temperature (TL_{50}; 12.7°C; Power 1980) that have been reported for egg development. Hokanson et al. (1973) also suggested that temperatures below 11°C prior to spawning enhance egg viability in brook charr.

Variations in river discharge is the factor most frequently cited as controlling the rate of upstream migration in anadromous salmonids, even though temperature and other abiotic factors, such as turbidity and lunar cycles, can modify that effect (reviewed in Trépanier et al. 1996; see also Castonguay et al. 1982). After analyzing 12 years of data on spawning migrations of landlocked Atlantic salmon (ouananiche, *Salmo salar*), Trépanier et al. (1996) also suggested that fluctuations in surface water velocity influenced the upstream migrations of a lacustrine population and that temperature had little effect. In these examples, fluctuations in water discharge were usually much more important than variations in temperature, and individuals often responded to decreases in water velocity following a freshet. Because brook charr migrate downstream to reach the spawning ground in Lake St-Michel, fluctuations in water velocity are less likely to stimulate spawning migrations. Also, because fluctuations in water discharge are less predictable in the fall, it is possible that the spawning migrations of populations inhabiting small, post-glacial lakes have evolved in response to temperature variations, which are more predictable at this period of the year.

In both years, males, especially larger ones, arrived on the spawning ground before females (Figure 2). In fact, 44.8% (1995) and 57.0% (1996) of males were present on the spawning ground before the peak of spawning (i.e., 28 September to 4 October) compared to 27.5% (1995) and 36.0% (1996) for females (1995: $\chi^2 = 12.63$, df $= 1$, $p < 0.001$; 1996: $\chi^2 = 49.97$, df $= 1$, $p < 0.001$). Blanchfield & Ridgway (1997) observed that males arrived on the spawning ground before females in a lake-spawning population: 90% of all spawning males were present within 14 days following the first day of spawning while only 60% of the spawning females were present at that time. Power (1980) and Scott & Crossman (1974) also reported that males arrive on the spawning grounds before females.

In both years, the length of males migrating to the spawning ground decreased during the spawning season while the females' length showed no pattern (Figure 2). Castonguay et al. (1982) and Trépanier et al. (1996) also observed that larger anadromous brook charr and landlocked Atlantic salmon migrate

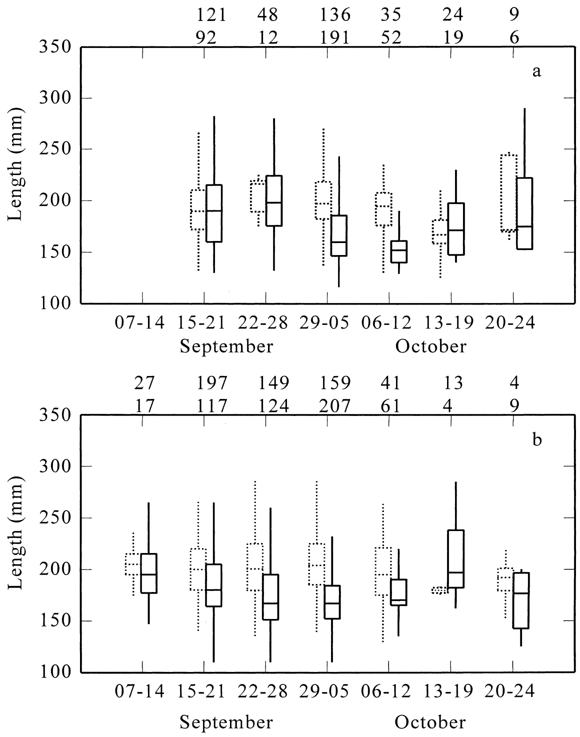

Figure 2. Box-and-whiskers plots of length (TL; mm) for females (dotted line) and males (solid line) migrating to the spawning ground in the lake outlet. a – fall 1995; b – fall 1996. Numbers on top of figures correspond to sample sizes for males (top line) and females (bottom line).

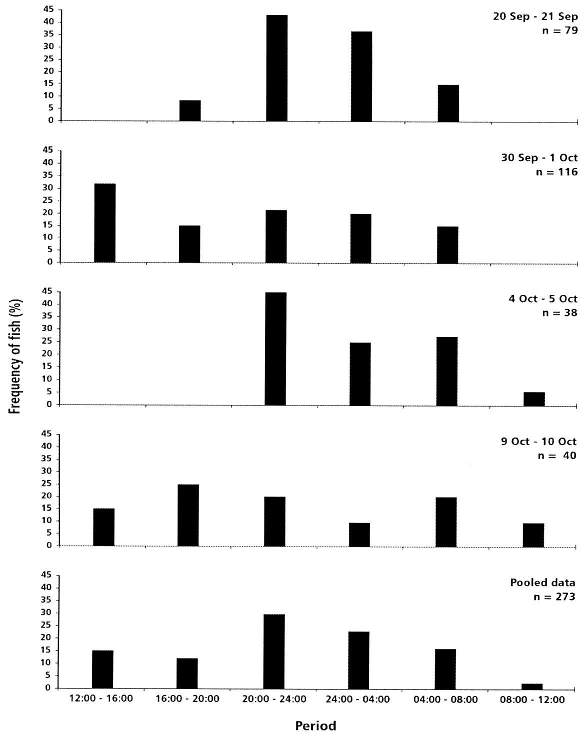

Figure 3. Frequency (%) of lacustrine brook charr migrating to the spawning ground (lake outlet) in relation to the time of day (hours), fall 1996.

upstream earlier than smaller individuals, but they did not consider males and females separately in their analyses. This phenomenon could be related to an earlier migration of maturing fish, which are recruited among the larger individuals of the population (Dutil & Power 1980, Castonguay et al. 1982). In a study on Atlantic salmon, Hawkins & Smith (1986) also suggested that fish that arrive early reserve holding positions, which provide shelter and favourable water velocities.

Diel activity pattern of migrating individuals

Brook charr exhibited a nocturnal activity pattern when migrating to the spawning ground ($\chi^2 = 44.09$, df $=$ 5, $p < 0.001$; Figure 3), with individuals being most active between 20:00 and 8:00 h. Elson (1938), Smith & Saunders (1958), and Castonguay et al. (1982) also observed nocturnal activity peaks of anadromous brook charr migrating to their spawning grounds. Although movements to a spawning area is not a surrogate measure of reproductive activity, we observed no spawning activity during the day in either sampling season (M. Baril personal communication), suggesting that spawning activity also mostly occurred at night. In lake-spawning populations, Curry & Noakes (1995) reported that no actual spawning was observed during the day, suggesting that spawning occurs at night, while Blanchfield & Ridgway (1997) observed peaks in spawning activity around midday (13:00 to 14:00 h). However, no nocturnal observations were made in these studies. Hazzard (1932) reported nocturnal as well as diurnal spawning.

Homing

Only 9.7% of the 745 fin-clipped individuals in 1995 returned to the lake outlet to spawn in 1996 (Table 1). This relatively low homing to spawning area is comparable to the return rates <1.0% to 8.0% observed by Vladykov (1942) in Lake Épaule (Québec) but contrasts with the values between 17% and 43% observed by O'Connor & Power (1973) in two inlets of Lake Matamek (Québec). It is possible that some reproducing individuals were not marked in 1995 because they passed over the counting fence during the flood or when the fence had been damaged on the two occasions reported above. However, these short events cannot account for such a low return rate. Although some fish may have spawned in other locations (inlets and littoral zone) or died from natural causes, sport fishing could be the major cause of these low returns of mature individuals to the lake outlet. As mentioned above, a mean of 3000 brook charr per year have been caught in Lake St-Michel since 1992. Age determinations done in 1996 revealed that the oldest individuals were four years old (4+) (S. Labrie personal communication). This short life cycle is characteristic of exploited brook charr populations (Power 1980, Magnan & FitzGerald 1983) and implies a quick renewal of reproducing individuals.

Conclusion

The results of this study indicate that lacustrine brook charr behave like anadromous populations (Castonguay et al. 1982) and other salmonid species like Atlantic salmon (landlocked and anadromous populations) and brown trout, *Salmo trutta* (reviewed in Trépanier et al. 1996), when migrating to spawning grounds in a stream. Spawning migrations are synchronized over the reproductive season and within diel cycles, and are controlled by environmental factors (water temperature in this study). In addition, the length of individuals migrating to the spawning ground decreases during the spawning season. There are also similarities with lake-spawning populations regarding the temperature at which peaks of spawning activity occur and the early arrival of males on spawning grounds. The rate of homing to spawning grounds observed in this study was low in comparison to other studies. It is possible that these characteristics are population-specific or related to local conditions such as mortality due to sport fishing exploitation.

Acknowledgements

We thank Steve Beauvillier, Claude Baril, Marco Bellavance, Isabel Bernier-Bourgault, Dave Boulet, Martin Chevalier, Vincent Corriveau, Daniel Dessureault, Patrice Gagné, Andrée Giroux, Isabelle Gosselin, Marc-André Juneau, Simon Labrie, André Lapointe, Patrick Laurin, Vincent Préfontaine, François Robert, Manon Robidoux, and Jacques Tremblay for their invaluable field and laboratory assistance. We are also grateful to David Craig, who was particularly helpful with the logistics related to this project. Paul Blanchfield and one anonymous referee gave helpful comments on an earlier version of this paper. This study was primarily supported by the Brook Trout Foundation, Centre for Research and Education. Additional funds were provided by the Natural Sciences and Engineering Research Council of Canada to P. Magnan.

References cited

Bernier-Bourgault, I. & P. Magnan. 2002. Factors affecting small-scale redd site selection and hatching and emergence success of brook charr, *Salvelinus fontinalis*, in streams. Env. Biol. Fish. (this volume).

Blanchfield, P.J. & M.S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 54: 747–756.

Bourke, P., P. Magnan & M.A. Rodriguez. 1997. Individual variations in habitat use and morphology in brook charr. J. Fish Biol. 51: 783–794.

Castonguay, M., G.J. FitzGerald & Y. Côté. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Québec. Can. J. Zool. 60: 3084–3091.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Trans. Amer. Fish. Soc. 117: 1–21.

Curry, R.A., J. Gehrels, D.L.G. Noakes & R. Swainson. 1994. Effects of river flow fluctuations on groundwater discharge through brook trout, *Salvelinus fontinalis*, spawning and incubation habitats. Hydrobiologia 277: 121–134.

Curry, R.A. & D.L.G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 52: 1733–1740.

Curry, R.A., D.L.G. Noakes & G.E. Morgan. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 52: 1741–1749.

Curry, R.A. & K.J. Devito. 1996. Hydrogeology of brook trout (*Salvelinus fontinalis*) spawning and incubation habitats: implication for forestry and land use development. Can. J. For. Res. 26: 767–772.

Dutil, J.D. & G. Power. 1980. Coastal population of brook trout, *Salvelinus fontinalis*, in Lac Guillaume-Delisle (Richemond Gulf) Québec. Can. J. Zool. 58: 1828–1835.

Elson, P.F. 1938. The effect of control of temperature and current on the migration of brook trout. Fish. Res. Board Can. Rep. Biol. St. 132: 1–32.

Fraser, J.M. 1982. An atypical brook charr (*Salvelinus fontinalis*) spawning area. Env. Biol. Fish. 7: 385–388.

Fraser, J.M. 1985. Shoal spawning of brook trout, *Salvelinus fontinalis*, in a precambrian shield lake. Nat. Can. 112: 163–174.

Hawkins, A.D. & G.W. Smith. 1986. Radio-tracking observations on Atlantic salmon ascending the Aberdeenshire Dee. Scottish Fish. Res. Rep. 36: 1–24.

Hazzard, A.S. 1932. Some phases of the life history of the eastern brook trout, *Salvelinus fontinalis* (Mitchill). Trans. Amer. Fish. Soc. 62: 344–350.

Hokanson, K.E.F., J.H. McCormick, B.R. Jones & J.H. Tucker. 1973. Thermal requirements for maturation, spawning and embryo survival of brook trout, *Salvelinus fontinalis*. J. Fish. Res. Board Can. 30: 975–984.

Magnan, P. & G.J. FitzGerald. 1983. Âge scalaire et otolithique de l'omble de fontaine (*Salvelinus fontinalis*): comparaison et interprétation des faux annuli. Nat. Can. 110: 149–154.

O'Connor, J.F. & G. Power. 1973. Homing of brook trout (*Salvelinus fontinalis*) in Matamek Lake, Québec. J. Fish. Res. Board Can. 30: 1012–1014.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. pp. 141–203. *In*: E.K. Balon (ed.) Charrs: Salmonid Fishes of the Genus *Salvelinus*, Dr W. Junk Publishers, The Hague.

Scott, W.B. & E.J. Crossman. 1974. Poissons d'eau douce du Canada. Office des recherches sur les pêcheries du Canada, Ministère de l'environnement, Service des pêches et des sciences de la mer, Bulletin 184, Ottawa. 1026 pp.

Smith, M.W. & J.W. Saunders. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and saltwater. J. Fish. Res. Board Can. 15: 1403–1449.

Snucins, E.J., R.A. Curry & J.M. Gunn. 1992. Brook trout (*Salvelinus fontinalis*) embryo habitat and timing of alevin emergence in a lake and stream. Can. J. Zool. 70: 423–427.

Trépanier, S., M.A. Rodriguez & P. Magnan. 1996. Spawning migrations in landlocked Atlantic salmon: time series modelling of river discharge and water temperature effects. J. Fish Biol. 48: 925–936.

Vladykov, V.D. 1942. Precision with which speckled trout (*Salvelinus fontinalis*) return to the same spawning grounds. Canadian Field Naturalist 56: 143–136.

Webster, D.A. & G. Eiriksdottir. 1976. Upwelling water as a factor influencing choice of spawning sites by brook trout (*Salvelinus fontinalis*). Trans. Amer. Fish. Soc. 105: 416–421.

White, H.C. 1940. Life history of sea-running brook trout (*Salvelinus fontinalis*) of Moser River, N.S. J. Fish. Res. Board Can. 5: 176–186.

Witzel, L.D. & H.R. MacCrimmon. 1983a. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Trans. Amer. Fish. Soc. 112: 760–771.

Witzel, L.D. & H.R. MacCrimmon. 1983b. Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. Can. J. Zool. 61: 1783–1792.

Young, M.K., W.A. Hubert & T.A. Wesche. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. Trans. Amer. Fish. Soc. 118: 379–385.