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Brook trout spawning areas in lakes

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Abstract – Nine lakes containing self-sustaining populations of brook trout (*Salvelinus fontinalis*) were surveyed to provide quantitative information on the abundance and distribution of redd sites. We measured rates of groundwater flow at redds in four of these lakes, and in one of these lakes we also compared the frequency of site use over four years from spawning observations. The number of redd sites in each lake ranged from 1 to 53 (mean=30) with most found relatively close to shore (≈1 m deep). Spawning areas per lake (16.9–829.4 m^2) were not related to lake size and were often not continuous areas of littoral zone habitat. Rates of groundwater flow in lakes, averaged across redd sites in each lake, ranged from 20.0 to 107.9 $ml \cdot m^{-2} \cdot min^{-1}$. The intensive survey of redd site use in one lake demonstrated that only 11% of sites (10 of 92) were used in all four years of observation. The mean rates of groundwater flow at sites used in all four years were significantly greater than at sites used intermittently. Data from this and other studies point to the conservation of subcatchments associated with groundwater discharge areas used by spawning brook trout as a means of maintaining self-sustaining populations.

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Introduction

A general feature of brook trout (*Salvelinus fontinalis* Mitchell) spawning habitat is the requirement for groundwater upwelling at redd sites (Curry & Noakes 1995; Curry & DeVito 1996; Blanchfield & Ridgway 1996, 1997). Two approaches at detecting these areas are represented in published accounts on the reproductive ecology of this species. First, some field studies have taken a broad perspective in delineating spawning areas by relying on detection of above-ambient water temperatures in the fall and winter (White 1930; Benson 1953) or the presence of nearby riparian seepage areas (Hazzard 1932; Witzel & MacCrimmon 1983). Following visual identification of spawning areas, a second approach has taken a detailed perspective and focused on groundwater flow at a few redds ($n \leq 5$ redds) within a spawning area for one or a few populations (Snucins et al. 1992; Curry & Noakes 1995; Curry et al. 1995). Neither perspective has so far provided information on the distribution and abundance of redd sites within spawning areas of self-sustaining brook trout populations.

The only previous field work to examine an entire spawning area of a self-sustaining brook trout population estimated a large population of adults (approximately 1,300 fish) using a large area that remained relatively unchanged in both location and area over many years (Fraser 1985). A second study in another lake found an order of magnitude fewer adults based on direct observations of the spawning area (Blanchfield & Ridgway 1997). In contrast, a recent survey of brook trout spawning areas in a number of lakes found relatively few redds per lake (mean, 6.7 redds/lake) (Quinn 1995). The differences in these approaches stem from site-intensive observations at one lake (Fraser 1985; Blanchfield & Ridgway 1997), compared to a survey of sites in different lakes using observers positioned in a boat (Quinn 1995). Estimates of adult populations using spawning areas in lakes therefore range from very large adult populations to populations sustained by very few fish. The common element in all studies focusing on the reproductive ecology of brook trout has been the limitation of groundwater seepage areas in lake or stream systems. Evidence for site limitation comes from observations of repeated use of sites during a breeding season and rapid replacement of spawning females taken from their redds in removal experiments (Blanchfield & Ridgway 1997).

The objective of this field study was to determine the abundance and distribution of all redd sites in a set of nine lakes in Algonquin Park, Ontario. This study provides the first complete census of the sites in which brook trout construct redds within spawning areas of lakes. In four of the nine lakes, groundwater seepage estimates were made to provide a quantitative survey of this critical resource. In one of these lakes, the use of sites over a period of four years was also determined and compared with groundwater seepage rates.

Material and methods

Nine lakes in south-central Ontario with self-sustaining brook trout populations were surveyed in 1994 and 1995 for spawning areas in the nearshore zone of each lake. Observations of redd locations and adult distribution were made from underwater using dry suits, masks and snorkels. Fish concentrated on spawning activity and did not appear to respond to the presence of observers who could remain near fish at close distance (approximately 1 m). The general location of some spawning areas was known from previous field work (Fraser 1985; Quinn 1995), while other lakes were surveyed to locate the spawning areas. This information was used to concentrate our activity in mapping redd distribution and determining the boundaries of the spawning area.

In each lake, redds were mapped with one observer located in the water above a redd site and a second person triangulating the position of the observer in the water using a surveyor's transit. Redds were located based on the digging, guarding or covering activity of females or, in the absence of fish, the presence of recently cleared substrate with a small mound indicating a recently covered redd. The distance of each redd from shore and the depth of each redd were determined (to the nearest cm) with a tape measure. The limits of each spawning area were determined by swimming along shore for 200 m in either direction from the observed extent of visible redds in lakes with known spawning areas. In lakes with unknown spawning areas, observers in a boat cruised the shoreline to initially locate spawning areas. This process was followed by the underwater mapping techniques described above. Once all redds were mapped in a spawning area, the minimum convex polygon method was used to determine the total spawning area in each lake (White & Garrott 1990). Outer redds were used to delimit the convex polygon to provide a total area encompassed by the redd distribution. In some lakes, spawning areas were separated by more than 20 m. In these cases, the minimum convex polygon method was used for each separate area, and the results were then summed to arrive at a total spawning area. The spawning area in Scott Lake was determined using redd locations from all years of observation (1993–1996).

In three of the eight lakes, groundwater seepage rates were determined for nine redds using the seepage meter method (Shaw & Prepas 1989; Blanchfield & Ridgway 1996). Three seepage estimates, each separated by two hours, were made at each redd. The three seepage estimates per redd were used to calculate a mean groundwater seepage rate for each redd. The mean seepage rates for each of the nine redds were combined to determine an overall seepage rate for redds in each of the lakes.

In one lake (Scott Lake), the distribution of redd sites was mapped each year for four years (1993–1996; Blanchfield & Ridgway 1997). The marking of individual redds and the use of permanent shoreline markers from which to take measurements allowed us to determine whether redds were constructed in the same sites in one, two, three or four out of four years. Seepage meter estimates of groundwater flux were taken from redds in three of four years (1994–1996) by the method described in Blanchfield & Ridgway (1996). In 1996, additional measures were made at redd sites using smaller seepage meters (25 cm diameter) where the regular meters (57 cm diameter) would not fit. We corrected for any biases in groundwater flow due to the size of the meter with triplicate measures of flow at redd sites using both the large and small meters. The ratio of flow into large versus small meters at the same site provided an unbiased estimate of groundwater flow as opposed to using only the difference in area covered by the meters based on the size of the meters. The rates of groundwater flow were pooled for all years at each site and related to use in each of the year classes. Means ($\pm$SD) are presented unless otherwise stated.

Results

The abundance of redd sites in each lake ranged from 1 to 53, with most found between 3 and 13 m from shore (Table 1). Spawning areas were often not continuous areas of littoral zone habitat but were sometimes divided into two, and in one lake six, areas separated by at least 20 m of littoral zone area without spawning activity (Fig. 1). Most redds were found in water approximately 1 m deep (lake mean depths; 60–260 cm), with Westward Lake having the deepest redds of the lakes surveyed (Table 1).

The total spawning area per lake ranged from 16.9 m^2 to 829.4 m^2 (Table 1). The density of redds

Table 1. Characteristics of brook trout redd sites from nine Canadian Shield lakes

Lake	Latitude	Lc ι	Surface area (ha)	Number of redd sites	Distance to shore (m)[d]	Depth (cm)[d]	Spawning area (m^2)[e]	Redd site density (100 m^{-2})	Number of spawning areas
Charles	45°54′	78°23′	12	39	4.5 (2.2)	79 (39)	340	11.5	2
Dickson	45°48′	78°12′	986	34[b]	13.8 (6.8)	61 (19)	497	6.8	1
Gull	46°02′	78°33′	26	21	3.1 (1.2)	86 (32)	49	42.5	2
Guskewau	45°29′	78°49′	12	10	4.8 (1.9)	107 (14)	42	23.9	1
Mykiss	45°41′	78°13′	24	53	11.7 (4.8)	152 (42)	515	10.3	1
Scott[a]	45°29′	78°43′	28	47	6.8 (4.7)	110 (42)	829	5.7	6
Shallnot	45°39′	78°03′	10	1[c]	5.7	100	17	88.8	1
Stringer	45°26′	78°30′	35	48	10.5 (6.6)	138 (58)	631	7.6	2
Westward	45°29′	78°47′	63	13	10.0 (3.8)	261 (165)	83	15.7	2

[a] Data from 1995 only
[b] 24 individual redds plus 10 additional redds within one large seepage area
[c] 15 redds within one large seepage area
[d] Mean (±1 SD) reported
[e] Determined by minimum convex polygon method

(number of redds · 100 m^{-2}) within spawning areas appeared to separate into two groups. Lakes with low redd density had relatively large spawning areas (Dickson, Mykiss, Scott, and Stringer Lakes), while high redd density lakes had small total spawning areas (Gull, Guskewau, Shallnot Lakes), with two lakes falling between these two groupings (Charles and Westward Lakes).

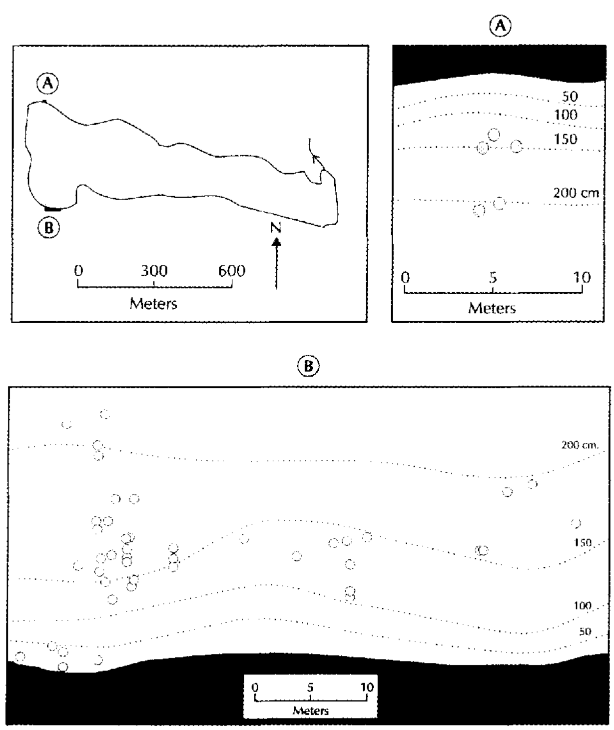

Fig. 1. An example of the distribution of brook trout spawning areas in one Canadian Shield lake (Stringer Lake). Circles represent redds and dotted lines represent depth contours.

Average seepage rates in Stringer Lake (35.3 ml · m^{-2} · min^{-1}; 95% confidence interval (CI)= ±25.1 ml · m^{-2} · min^{-1}) and Dickson Lake (107.9 ml · m^{-2} · min^{-1}; 95% CI=±63.1 ml · m^{-2} · min^{-1}) were generally higher than the sites used each year at Scott Lake (Fig. 2). Seepage rates at redd sites in Mykiss Lake (20.0 ml · m^{-2} · min^{-1}; 95% CI=±5.8 ml · m^{-2} · min^{-1}) tended to be lower than observed among sites used each year in Scott Lake (Fig. 2).

Redds were constructed in a total of 92 separate sites over a four-year period at Scott Lake (Fig. 2, 3). However, not all sites were used in each year. Redds were constructed at only 10 sites in each of the four years, with an additional 11 sites used in three of the four years (Fig. 2). Therefore less than a quarter of all redd sites used in a four-year period were used each year or in all but one year. The remaining spawning sites (77%) were used during only one or two years of the four-year observation period. The redd sites used each year had higher average seepage rates compared with sites not used in each year (Mann-Whitney: U=23.0, P=0.0007; Fig. 2). The spatial distribution of redds in Scott Lake in each year of the four-year observation period did not indicate clumping at

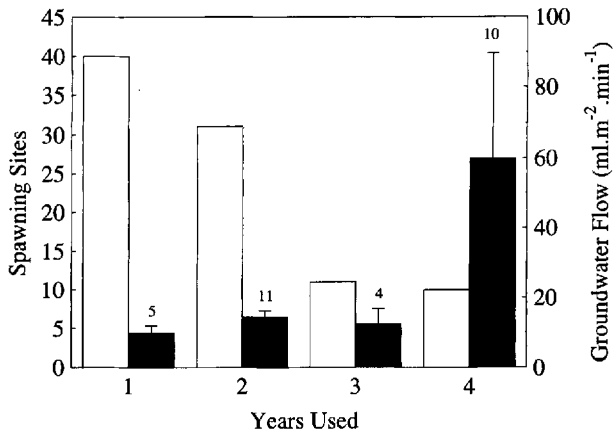

Fig. 2. The frequency of spawning site use (open bars) and mean groundwater seepage rates (+ SE; solid bars) of spawning sites used in varying numbers of years at Scott Lake. The number of redd sites in which groundwater estimates were made is presented.

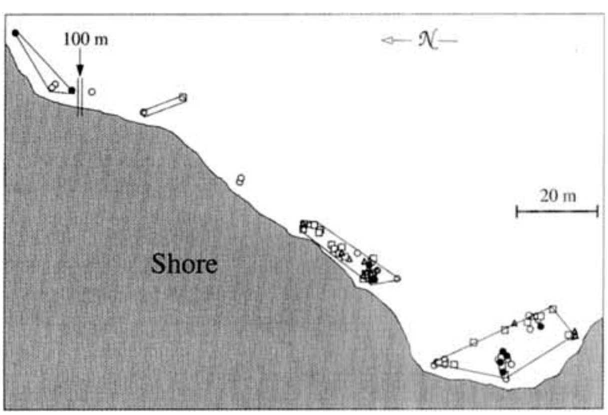

Fig. 3. Map of part of the Scott Lake shoreline indicating redd site locations recorded from 1993–1996 and the spawning area determined by way of the minimum convex polygon method (see text for details). Symbols represent if redds were constructed at the same site in one (○), two (□), three (△) or four (●) years.

any one location (Fig. 3). Instead, smaller groups of redds tended to clump into small aggregations along the shore, often around a site in which a redd was constructed in each year.

Discussion

The range in the number of redds per lake was greater in this survey than in a previously published account of brook trout spawning in lakes (Quinn 1995). The fundamental difference between this study and other field surveys was the use of underwater observations to determine the distribution and abundance of redds. Although spawning areas tended to be well defined based on redd distribution, five of the nine lakes surveyed had spawning areas that were not contiguous. In almost all cases, it was possible to distinguish a main spawning area with the majority of redds from a secondary spawning area with relatively few redds. This observation indicates that the lenses of coarse overburden material that serve to focus groundwater seepage for brook trout spawning areas in the nearshore zone may be larger or more numerous in some lakes than previously recorded (<17 m wide; Curry & DeVito 1996). Indeed, in five lakes (Charles, Gull, Mykiss, Scott and Stringer) the length of the spawning areas exceeds 40 m along the shoreline.

In Scott Lake, redds were constructed at 47 sites in 1995, with 60 to 90 adults observed daily at the peak of the spawning season (Blanchfield & Ridgway 1997). In total, 92 sites were used over a period of four years (1993–1996), but not all sites were used in any single year. Only 10 of the 92 sites were used in each of the four years. This observation suggests that annual differences in rainfall and subsequent run-off may be important in year-to-year variation in use of specific sites (Blanchfield & Ridgway 1997). As well, the number of sites used in a given year tends to increase with the number of breeding females (P. J. Blanchfield, unpublished data). The sites used each year had the highest levels of groundwater seepage, whereas sites used less frequently had lower seepage rates. Unfortunately, we have no information on whether this observation of shifting redd site use is common to other brook trout populations. In Dickson Lake, the location and dimensions of the spawning area have not changed significantly over decades (Fraser 1985), although the location of specific redds may have shifted within this spawning area.

In addition to the relationship between the annual use of redd sites and groundwater seepage rates in Scott Lake (Fig. 2), other observations at this lake indicate that groundwater flow influences the choice of redd sites by female brook trout. Seepage rates at redds are significantly higher than at sites chosen randomly within the spawning area or at other littoral zone sites in the lake (Blanchfield & Ridgway 1997). Half of all observed spawnings in Scott Lake occurred in just 11 redd sites out of a total of 60 sites used over a two-year period (1994–1995; Blanchfield & Ridgway 1997). These observations stand in clear contrast to an earlier conclusion that groundwater seepage did not influence the selection of individual redd sites within discharge areas (Curry & Noakes 1995). Our reliance on underwater observations to detect actual spawning activity and map redd sites, the use of seepage meters and greater sample sizes may account for the disparity between our results and earlier work.

There was a large gradient in the density of redd sites among the lakes surveyed (Table 1). In Shallnot Lake, only one redd site was found in a small area (Fraser 1982), whereas in Scott Lake 47 redd sites distributed along 340 m of shoreline were used in 1995. The resulting differences in site quality, abundance and distribution have strong implications for site choice by females and mate searching strategies by males in the brook trout mating system. In brook trout, males move frequently among females that have selected a redd site (Blanchfield & Ridgway in press). The observed differences in redd density among our study lakes suggests that limited movements among males competing for females are likely in lakes with high redd densities, with the possibility of more extensive movements in lakes with low redd densities.

Brook trout in lakes use spawning areas that are stable in location over decades and probably much longer (Fraser 1985), select sites based on relatively high seepage rates (this study; Blanchfield & Ridgway 1997) and rely on groundwater seepage for successful embryonic development (Curry et al. 1995). It also appears that populations are sustained by relatively few redd sites within any lake (this study; Blanchfield & Ridgway 1997). However, not all lakes have spawning areas in the shallow littoral zone (Quinn 1995). In some lakes, spawning areas appear to be deeper and may not be based simply on groundwater discharge from surface runoff. In these cases, deeper groundwater sources may contribute to redd site selection. Whatever the origin of groundwater discharge, we believe the evidence from this and other studies (such as Curry & DeVito 1996) is sufficient to call attention to the protection of forested subcatchments associated with discharge areas as a conservation strategy to protect self-sustaining brook trout populations in lakes. As previously shown (Curry & DeVito 1996), standard buffer strips used in forestry operations afford little protection to these particular subcatchments as a whole. Since forestry practices can significantly alter water yield in subcatchments (Hibbert 1967), it is premature to suggest that forestry practices have not altered the reproductive ecology of brook trout in lakes (Quinn 1995). Whether protecting subcatchments associated with groundwater discharge areas is sufficient to also protect young-of-year habitat in the shallow littoral zone (Curry et al. 1993; Biro et al. 1997) remains to be determined.

Resumen

1. En nueve lagos con poblaciones auto-suficientes de *Salvelinus fontinalis* estudiamos la abundancia y distribución de frezaderos. En cuatro de estos lagos, medimos las tasas de corriente de agua subterránea de los frezaderos. Además, en uno de ellos comparamos la frecuencia de utilización del frezaderos durante cuatro años seguidos. El número de frezaderos de cada lago varió entre 1 y 53 ($\bar{x}=30$), y la mayoría se localizaron próximas a la costa (≈ 1 m de profundidad).

2. Las áreas de desove por lago (16.9–829.4 m^2) no estuvieron relacionadas con el tamaño del lago ni estuvieron en zonas continuas de litoral. Las tasas de agua subterránea en cada lago variaron entre 20.0 y 107.9 $ml \cdot m^{-2} \cdot min^{-1}$.

3. El muestreo sistematizado del uso de frezaderos en uno de los lago demostró que sólo el 11% de las localidades (10 de 92) fueron utilizadas durante los cuatro años de observación. Las tasas medias de agua subterránea en las localidades utilizadas durante estos cuatro años fueron significativamente mayores que en las localidades utilizadas de forma intermitente.

4. Los datos obtenidos en éste y en otros estudios apuntan hacia la necesidad de conservar las subcuencas asociadas a zonas de descarga subterránea de agua utilizadas para la freza por *S. fontinalis*, como medio para mantener poblaciones autosuficientes.

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