

Acidic Groundwater Discharge and in Situ Egg Survival in Redds of Lake-Spawning Brook Trout

DANA R. WARREN*

Department of Natural Resources, Cornell University, Ithaca, New York 14853, USA

STEPHEN D. SEBESTYEN¹

*Forest and Natural Resources Management, College of Environmental Science and Forestry,
State University of New York, Syracuse, New York 13210, USA*

DANIEL C. JOSEPHSON, JESSE M. LEPAK, AND CLIFFORD E. KRAFT

Department of Natural Resources, Cornell University, Ithaca, New York 14853, USA

Abstract.—Spawning of brook trout *Salvelinus fontinalis* in lakes occurs over areas of groundwater discharge. The rate and chemistry of groundwater discharge influence brook trout egg survival and reproductive success. While most studies have reported that groundwater discharge in brook trout redds is buffered relative to the surrounding lake water, we documented brook trout spawning over an area of acidic groundwater discharge (pH as low as 4.7) in a lake with circumneutral surface waters (pH > 6.1). A follow-up experiment that assessed in situ egg survival indicated 0% survival in redds with either low-pH groundwater or adequate groundwater pH but low groundwater discharge. More than 80% of eggs survived in a reference lake with well-buffered groundwater and adequate discharge rates. These results suggest that both low pH and low groundwater flow rates may contribute to brook trout egg mortality. Low-pH groundwater may be a factor to consider in brook trout restoration efforts, especially in lakes where whole-lake liming has been unsuccessful in reestablishing wild brook trout populations.

Several studies highlight the importance of spawning habitat for maintaining reproduction of wild brook trout *Salvelinus fontinalis* in lakes (Webster 1962; Carline 1980; Blanchfield and Ridgway 1997). Groundwater discharge is widely considered the characteristic of primary importance in spawning site selection for brook trout (Webster and Eiriksdottir 1976; Blanchfield and Ridgway 1997; Ridgway and Blanchfield 1998). Additionally, groundwater must also have chemical characteristics capable of sustaining eggs and alevins through the winter and early spring (Fiss

and Carline 1993; Lachance et al. 2000; Curry and MacNeill 2004). In this paper, we assess groundwater discharge and groundwater pH in the redds of lake-spawning brook trout in the Adirondack region of New York.

In addition to groundwater discharge, water chemistry may substantially influence brook trout egg survival. Respiration by eggs and alevins may completely consume dissolved oxygen in brook trout redds, thereby leading to anoxia and poor survival. However, continuous groundwater discharge is generally thought to maintain adequate dissolved oxygen levels in brook trout redds (Fraser 1985; Curry et al. 1995). Studies investigating the influence of low pH and high cation concentrations on brook trout eggs indicate low egg survival under acidic conditions but minimal impacts associated with heavy metals (Ingersoll et al. 1990; Fiss and Carline 1993; Lachance et al. 2000). To date, studies of the influence of pH on brook trout egg survival have occurred under laboratory conditions or have focused on stream ecosystems where eggs are more likely to be exposed to episodic acidity through the rapid exchange of surface and groundwater in the hyporheic zone (Ingersoll et al. 1990; Fiss and Carline 1993; Lachance et al. 2000).

In lakes, the impacts of acidic groundwater within redds are rarely addressed because groundwater chemistry at spawning shoals is generally considered to be well buffered relative to surface water (Kenoyer and Anderson 1989; Curry and Noakes 1995; Essington et al. 1998). This characterization is supported by previous studies examining lake-spawning brook trout redds in which groundwater pH was comparable to or greater than surface water pH (Snucins et al. 1992; Curry and Noakes 1995; Quinn 1995). However, acidic

* Corresponding author: drw23@cornell.edu.

¹ Present address: Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720-3114, USA.

Received October 11, 2004; accepted March 26, 2005
Published online August 10, 2005

groundwater discharge in lakes and chronically acidified streams provides evidence of the perennial discharge of acidic groundwater in a variety of landscapes (Hultberg and Johansson 1981; Schafran and Driscoll 1993; Runkel and Kimball 2002). In areas that receive chronic inputs of acidic deposition, such as the Adirondack region, groundwater buffering capacity is influenced by till depths that can vary among watersheds as well as along lakeshores (Schofield et al. 1985; Newton et al. 1987; Peters and Driscoll 1987). Impermeable bedrock in Adirondack watersheds restricts groundwater to shallow flowpaths through poorly to moderately buffered glacial tills (Schofield et al. 1985; Peters and Driscoll 1987; Staubitz and Zarriello 1989). If acidic atmospheric deposition is not neutralized along groundwater flowpaths, the discharging waters remain acidic (Schnoor and Stumm 1985; Schofield et al. 1985; Newton et al. 1987).

In the Adirondack region, surface water pH and adequate groundwater discharge have generally been the habitat features of concern for managers assessing potential wild brook trout reproduction in lakes (Schofield 1993). When initiating this study, we hypothesized that limited wild brook trout reproduction in one of our study lakes resulted from low groundwater discharge. After a survey of redds in this lake, we discovered acidic groundwater discharging along the spawning shoal. We then hypothesized that the acidic groundwater may limit viable reproduction despite the presence of adequate discharge rates. To assess this hypothesis, we initiated a preliminary study evaluating *in situ* brook trout egg survival relative to groundwater discharge and pH.

Study Site

Groundwater flow and pH were initially measured in 10 brook trout redds from Lower Sylvan Pond in 2000. Lower Sylvan Pond, a small lake (5.9 ha) located in the western Adirondacks, does not thermally stratify in the summer. Brook trout populations in Lower Sylvan Pond are supplemented primarily through stocking, but young wild fish can enter the lake from a single inlet stream and from the lake outlet. Stocked populations thrive during cool summers, and in 2000 the largest female brook trout captured in trap-net surveys was 424 mm in total length (1,056 g). Brook trout were observed spawning in Lower Sylvan Pond in November 1998, 1999, and 2000 (28, 11, and 36 redds, respectively, counted on the main spawning shoal). Warm temperatures in 2001 and 2002

caused a summer die-off, after which almost no brook trout spawning has been observed (one redd in 2002 and one in 2004).

In 2003, we reevaluated water chemistry characteristics in redds at Lower Sylvan Pond and in brook trout redds of nearby Panther Lake (17 ha). Panther Lake sustains a population of lake-spawned wild brook trout that has also been supplemented with stocking. Brook trout spawn annually in Panther Lake, and redds are easily distinguished as circular depressions that are cleared of detritus. In 2003, former redd locations in Lower Sylvan Pond were still discernable as circular depressions where coarse sand was exposed along the spawning shoal.

Lower Sylvan Pond and Panther Lake, which are typical of Adirondack lakes without shoreline development, are oligotrophic and possess "chemically dilute" surface water characterized by low concentrations of base cations and low acid-neutralizing capacity (Schofield et al. 1985; Sebestyen and Schneider 2004). These lakes episodically acidify during snowmelt but are circumneutral throughout the rest of the year (Schofield et al. 1985; Sebestyen and Schneider 2004). Fourteen tons of lime were applied to Lower Sylvan Pond in 1971. Circumneutral tributary inputs and groundwater discharge along extensive sections of the Lower Sylvan Pond shoreline maintain current neutral surface water pH despite the inflow of acidic groundwater at the spawning shoals (Sebestyen and Schneider 2004). At Panther Lake, deep tills around the entire lake shoreline buffer groundwater from acidification (Peters and Murdoch 1985; Schofield et al. 1985).

Methods

In Lower Sylvan Pond, spawning activity in the form of redd construction began in late October 2000, and activity over the spawning shoals continued through mid-November. On October 29, we placed piezometers (2-cm diameter) at the centers of 10 recently excavated redds along the main spawning shoal of Lower Sylvan Pond to collect water samples and measure groundwater discharge (upwelling) or recharge (downwelling) through redds (Freeze and Cherry 1979). Piezometers are commonly used to measure groundwater flow in hydrologic research and have previously been used to quantify groundwater flow through brook trout redds (Freeze and Cherry 1979; Curry and Noakes 1995). Hydraulic head and hydraulic conductivity were measured to calculate the magnitude of groundwater flow, which was considered to be rep-

TABLE 1.—Brook trout redd characteristics measured by means of piezometers in Lower Sylvan Pond, New York, during November 2000. Lake surface samples were used for comparison with redd samples.

Redd characteristic	Date	Redd number										Lake surface
		1	2	3	4	5	6	7	8	9	10	
pH	3 Nov	4.81		6.42	4.92	4.74	4.80	4.89	5.34	6.25	5.16	7.32
	7 Nov	4.82	5.29	5.40	4.76	4.69	4.72	4.73	4.83	6.06	4.82	7.26
Discharge (cm/h)	3 Nov		0.05	13.04	0.06	0.63	0.53	0.14	0.19	0.87		
	7 Nov	819.02	0.02		0.09	3.71	0.59	0.08	0.41	0.34	19.26	
	9 Nov	206.15	0.03	7.49	0.18	0.44	0.42	0.06	0.39	0.45	10.43	

representative of flow conditions within the individual redds where piezometers were placed. Piezometers were inserted 25 cm into the substrate of each redd (numbered 1–10; Table 1) to provide a point measurement of groundwater discharge. The bottom 5 cm of each open-bottomed piezometer were screened to prevent clogging and to allow the free flow of water from the area surrounding the piezometer. Hydrologic conductivity was measured on November 9, 2000. Lake surface and piezometer water levels were subsequently measured on November 3, 7, and 9 to calculate discharge rates in the 10 redds.

The pH was measured in lake surface and piezometer water samples collected on November 3 and 7. Water samples from the piezometers were withdrawn through tubes inserted to the bottom of the piezometers and were collected by means of a 60-mL syringe after initially triple rinsing the syringe and bottle with sample water. All water samples were collected in high-density polyethylene bottles with no head space, and pH was measured on the unfiltered water samples within 24 h at a nearby field laboratory. Sample pH was measured at room temperature by use of an Orion Model 370 pH meter. After all hydrologic measurements were completed, substrate samples were collected with a 50-mm-diameter polyvinyl chloride pipe (corer) inserted 10 cm from the piezometer. Sieves were used to separate substrate proportions according to the Wentworth scale (Bain et al. 1985). The samples were air dried and weighed, and the percent composition by substrate category was calculated as a proportion of all substrate types.

On November 5, 2003, piezometers were placed in redds along each of the spawning shoals in Panther Lake (four piezometers) and Lower Sylvan Pond (four piezometers). Because no active redds were observed in Lower Sylvan Pond during 2003, piezometers were placed in the cleared redd depressions that were still clearly visible from previous spawning. Redds sampled in 2003 are referred to by letter rather than number to avoid

confusion with the Lower Sylvan Pond redds surveyed in 2000. Piezometers were inserted to a depth of 15 cm in 2003 based on observation by Snucins et al. (1992) that eggs in the redds of lake-spawning brook trout were found at depths between 7 and 19 cm. Surface water and piezometer water levels were measured with automatic water level recorders (TruTrack, Inc., Christchurch, New Zealand) every 15 min during November 6–24 to detail groundwater flow dynamics throughout the period of observation, which ended when surface ice formed. Wider piezometers (2.5-cm diameter) were used in 2003 to accommodate the insertion of water level recorders. The automated water level data measurements were verified with manual measurements on November 11, 18, 20, and 24, and water samples were subsequently collected from each piezometer and from the lake surface. The 2003 water sampling techniques and pH measurements were identical to those used during 2000.

Egg survival–groundwater interaction.—On November 8, 2003, two in situ brook trout egg incubators were placed adjacent to three of the four piezometers in each lake (total of six incubators per lake). Egg incubators were 20-cm × 7.5-cm × 1.3-cm Plexiglas sheets with 50 evenly spaced, 1.3-cm holes (Schofield and Keleher 1996; Baird 2000). Nylon mesh was placed on either side of the Plexiglas and was held in place by two 0.5-cm-thick Plexiglas sheets with 1.3-cm holes corresponding to those in the main sheet that held the eggs. Eggs were stripped from multiple fish captured in Green Lake, a nearby lake with a brook trout population used as a broodstock for the fish hatchery at Cornell University's Little Moose Field Station. One egg was placed in each hole of an incubator within the time period shortly after fertilization when eggs could be safely transported. Within 48 h of fertilization, all incubators were buried adjacent to a piezometer and were covered with approximately 3–5 cm of substrate. At Lower Sylvan Pond, we removed silt (when present) from

areas around the piezometer while burying incubators. Incubators were buried to a depth of 3–5 cm in both lakes; once in place, incubators were covered with sand. In Panther Lake, we chose to bury incubators at this shallow depth to reduce disturbance to eggs buried deeper in the redds during natural spawning. For consistency, we maintained the same incubator burial depth in both lakes, but shallower burial was also preferred in Lower Sylvan Pond to reduce potential egg suffocation. Two additional incubators were placed in an incubator tray at the nearby Little Moose Field Station to evaluate fertilization rates and mortality in a controlled environment through which neutral-pH water was circulated. Incubators were collected from each lake at ice-out (April 21, 2004), at which time the numbers of swim-up fry, sac fry, eyed eggs, and uneyed eggs in each incubator were counted.

Analysis.—For statistical analysis, the pH was converted to hydrogen ion concentration and groundwater discharge was log transformed to achieve normality. We used a regression analysis (SPSS 1998) to test two linear models: (1) the relationship between mean groundwater pH and the mean discharge in each redd and (2) the proportion of fine material in each redd relative to groundwater discharge. For 2003 data, a single-factor repeated-measures analysis of variance (ANOVA) was used to evaluate differences in groundwater hydrogen ion concentrations between redds (eight redds over four sampling dates).

Results

In 2000, surface water pH at Lower Sylvan Pond was 7.32 on November 3 and 7.26 on November 7 (Table 1). In contrast, the pH of discharging groundwater in redds ranged from 4.72 to 6.42 (Table 1). On November 3, 2000, five redds had groundwater with pH less than 5, and one of those had a pH below 4.8 (Table 1). On November 7, seven of the 10 redds had groundwater with pH below 5.0, and four of those seven exhibited pH values below 4.8 (Table 1). Specific discharge at the 10 Lower Sylvan Pond redds varied by more than five orders of magnitude, ranging from less than 0.02 to 819.02 cm/h (median across all dates = 0.42 cm/h; Table 1). The redds in Lower Sylvan Pond were dominated by sandy material less than 2 mm in size (range = 57–90%, mean = 81%), and the proportion of gravel (2–16 mm) in the redds ranged from 7% to 42% (mean = 16%).

In 2000, no significant relationship was found between groundwater discharge rate and hydrogen

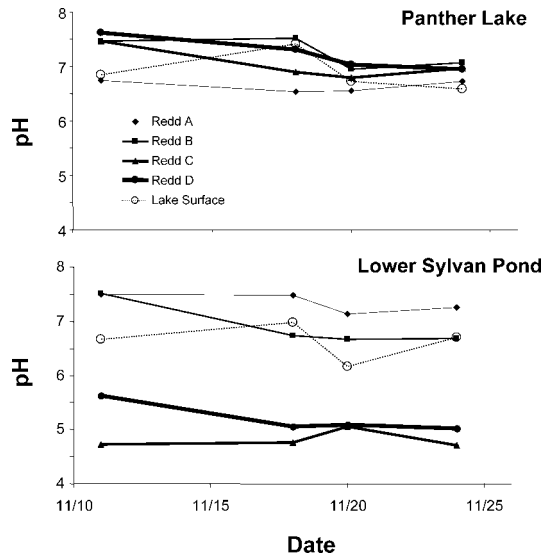


FIGURE 1.—Groundwater pH in brook trout redds of Lower Sylvan Pond and Panther Lake, New York, over four dates in November 2003. Hydrogen ion concentrations were significantly different among redds (repeated-measures ANOVA; $P < 0.05$). Panther Lake redds A, B, and D had 83%, 89%, and 93% brook trout egg survival, respectively. No eggs survived in redds A, C, and D of Lower Sylvan Pond. Lower Sylvan Pond redd B and Panther Lake redd C did not have associated incubators.

ion concentration ($P = 0.83$, $n = 10$). Redd 1 in the 2000 survey of Lower Sylvan Pond exhibited discharge rates much greater than any other site. Groundwater discharge was significantly related to the proportion of fines when this high value was included in the analysis ($P = 0.04$, $n = 10$), but when this point was removed no relationship was found between discharge rate and proportion of fines ($P = 0.85$, $n = 9$).

In 2003, surface water pH in Lower Sylvan Pond ranged from 6.17 to 6.97. In the four Lower Sylvan Pond redds, the pH across all dates ranged from a minimum of 4.71 to a maximum of 7.51. Acidic groundwater was found in two redds (C and D), and two redds were circumneutral. The pH declined through the month of November in two of the Lower Sylvan Pond redds (Figure 1). The repeated-measures ANOVA indicated significant differences in hydrogen ion concentration among redds ($P = 0.001$, $t = -4.5$; $n = 8$ sites, 4 sampling dates). Variable discharge rates were also found in the Lower Sylvan Pond in 2003. Redd A's discharge was four orders of magnitude less than that of the other three redds and exhibited virtually no fluctuation over time because of the uniquely low

hydraulic conductivity (Figure 2). In contrast, redd B showed a more dynamic flow pattern that shifted between discharge and recharge, indicating a more pronounced circulation of surface water and recharge into the sediments for a short period of time (Figure 2). Throughout the 3-week evaluation, redds C and D generally discharged groundwater but exhibited some groundwater recharge in early November. These shifts to recharge at all three redds occurred in response to changing hydraulic head conditions brought about by rapid changes in surface water levels from waves and increased water levels after rainfall (Figure 2).

Surface water pH in Panther Lake ranged from 6.58 to 7.42, and the lowest pH observed in a Panther Lake redd was 6.53 (Figure 1). Discharge in these redds was also spatially variable (Figure 2). Panther Lake redds B and C generally exhibited groundwater discharge and brief shifts to recharge (Figure 2). The discharge rates observed in Panther Lake redd A were similar in magnitude to those of redds C and D at Lower Sylvan Pond, where groundwater also occasionally recharged for brief time periods. In contrast, Panther Lake redd B had continuous discharge that was at least an order of magnitude greater than the discharge in all other redds in either lake. The pH also declined through November in three of the four Panther Lake redds but remained well above the acidic pH values of Lower Sylvan Pond redds C and D. The pH in the hatchery water where control eggs were incubated ranged between 6 and 7 throughout the winter.

In situ egg survival was dramatically different between Panther Lake and Lower Sylvan Pond. Egg survival was 83–93% within the Panther Lake redds. Of the unhatched eggs, none were eyed. In Lower Sylvan Pond, 100% mortality was observed in all six incubators. Only 6 of 100 eggs developed to the eyed stage in Lower Sylvan Pond redd A, where pH was circumneutral and discharge was negligible. In Lower Sylvan Pond redds C and D, 25% and 12% of the eggs, respectively, developed to the eyed stage. In the two hatchery incubators, 90% and 88% of eggs survived the winter.

Discussion

This study documents low-pH groundwater in brook trout redds of a small Adirondack lake and demonstrates a strong linkage between groundwater and brook trout egg survival. Groundwater seepage occurs along most lakeshores (Lee 1977; Sebestyen and Schneider 2001); in small mountain lakes, areas of in-lake groundwater discharge provide particularly important spawning habitat for

brook trout (Webster 1962; Fraser 1985; Quinn 1995; Ridgway and Blanchfield 1998). Although no other studies have specifically documented acidic groundwater in brook trout redds, similar geomorphic conditions (small, poorly buffered watersheds with thin soils, bedrock outcroppings, and shallow water flowpaths) occur elsewhere in the Adirondacks. Additionally, acidic groundwater with pH as low as 4.6 has been measured along other lakeshores in this region (Schafran and Driscoll 1993). Brook trout in lakes with similar geomorphic and depositional conditions may encounter similar low-pH groundwater conditions along spawning shoals and therefore experience a subsequent decrease in reproductive success.

Other factors considered when evaluating brook trout redd characteristics include dissolved oxygen levels, monomeric aluminum concentrations, and substrate composition. The discharge measurements in Lower Sylvan Pond redds C and D suggest that these redds remained well oxygenated. A previous study in Lower Sylvan Pond found oxic sediments in other locations around the shoreline when groundwater discharge was greater than 0.01 cm/h or when recharge was less than -0.01 cm/h (Sebestyen and Schneider 2004). Redd D in Lower Sylvan Pond had groundwater discharge that remained well above this 0.01 cm/h threshold. In Lower Sylvan Pond redd C, groundwater discharge was usually greater than 0.01 cm/h but switched between discharge and recharge toward the end of the monitoring period. The switch to recharge is unlikely to have impacted egg survival here because of its rapid fluctuation and the continuous movement of water. Redd A at Panther Lake regularly switched between discharge and recharge during the early part of our study, and the in situ egg survival in this redd was over 90%. The overall suitable groundwater discharge suggests that low dissolved oxygen was unlikely to cause high egg mortality in redds C and D at Lower Sylvan Pond. The results from Lower Sylvan Pond redd A support the general consensus regarding the importance of adequate groundwater discharge to egg survival. The low discharge rates in redd A at Lower Sylvan Pond probably did result in low dissolved oxygen levels, thereby producing high egg mortality despite suitable pH. The hydraulic head at this site was relatively high, but the extremely low hydrologic conductivity made groundwater movement within this redd negligible. Egg mortality may have resulted from respiration of the limited oxygen available within flowing groundwater at this site, in which discharge was only

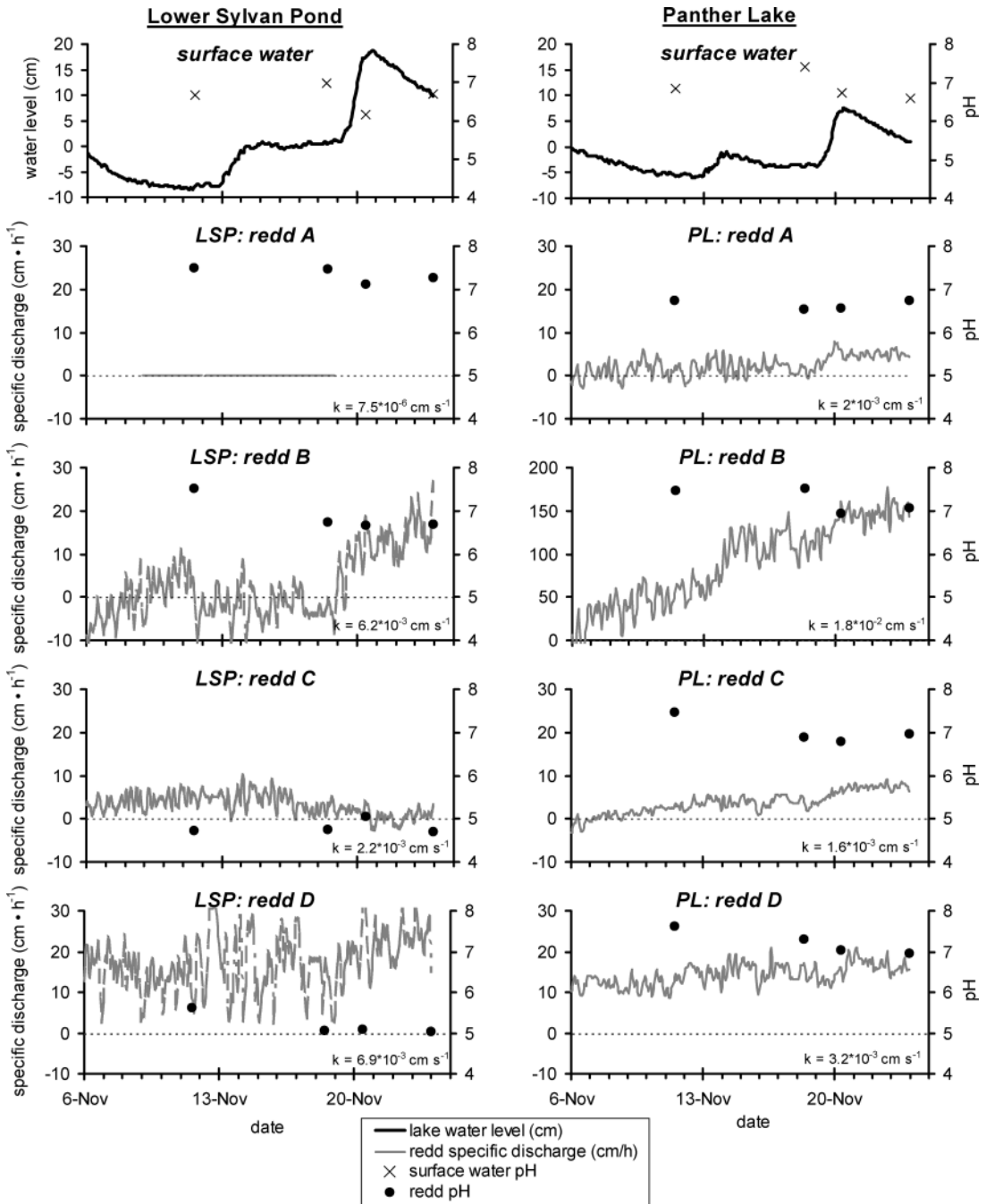


FIGURE 2.—Lake water level (cm), surface water pH, brook trout redd pH, and redd groundwater discharge (cm/h) in Lower Sylvan Pond and Panther Lake, New York, during November 5–24, 2003. The dotted line indicates zero discharge or recharge. Values above zero indicate discharge from groundwater to the lake, whereas values below zero show short-term recharge pulses in response to rapidly fluctuating hydraulic heads caused by surface water level fluctuations. The hydraulic conductivity (k) values for each redd are listed in each panel. Note the different specific discharge scale (0–200 cm/h) for Panther Lake redd B.

slightly above the 0.01-cm/h threshold for oxygenated groundwater in this system. Although aluminum is particularly toxic to fish and sac fry, monomeric aluminum is generally recognized as having little impact on brook trout eggs (Driscoll et al. 1980; Baker 1982; Ingersoll et al. 1990). Given that no eggs survived to the sac fry stage in any of the four incubators at redds C or D in Lower Sylvan Pond, monomeric aluminum was probably not a factor in the observed egg mortality (Ingersoll et al. 1990). Blanchfield and Ridgway (1997) indicated that the presence of groundwater discharge is more important than substrate type for brook trout redd site selection in lakes in Ontario, Canada. The Lower Sylvan Pond redds in 2000 contained, on average, a relatively high proportion of fine material (Carline [1980] reported up to 76% fines; Curry and MacNeill [2004] reported up to 67% fines). However, with the exception of the site with extremely high discharge, the groundwater discharge rates in Lower Sylvan Pond redds in 2000 were unrelated to substrate composition. The continuous water level data from Lower Sylvan Pond also indicated that groundwater could move through substrates in redds B, C, and D.

Johnson and Webster (1977) found that female brook trout clearly avoided spawning over groundwater with a pH of 4.0 or 4.5. No preference was observed, however, when groundwater pH was greater than 5.0. Data from 2003 in Lower Sylvan Pond demonstrates a clear decline in groundwater pH from mid- to late November in at least two redds. Groundwater pH was above 4.5 and close to 5.0 in mid-November. Under these conditions, brook trout would not have avoided these potentially lethal redd sites based on pH in discharging groundwater. Between November 3 and 7, 2000, the groundwater pH also declined in eight of the nine sites.

Acidification of surface water and groundwater is related to acidic deposition, geology, and hydrologic factors (Schnoor and Stumm 1985; Schofield et al. 1985; Newton et al. 1987; Driscoll et al. 2001). Sebestyen and Schneider (2001) hypothesized that spatial and temporal patterns of seepage along Lower Sylvan Pond were related to deep tills along one section of shoreline and shallow tills along another section of shoreline. In addition to controlling groundwater fluxes, the deep tills would promote acid neutralization (Schofield et al. 1985; Newton et al. 1987; Peters and Driscoll 1987); groundwater was circumneutral along this section of the Lower Sylvan Pond shoreline (pH

= 5.5–6.8, $n = 76$; Sebestyen and Schneider 2004). Alternatively, the shallow tills are immediately inshore of the redds and probably represent discharge from a shallow flowpath along which acidic deposition inputs are not completely neutralized before entering the lake as groundwater. Groundwater characteristics are highly variable around Lower Sylvan Pond; however, the observation of acidic groundwater in multiple redds over several weeks in 2000 and again in 2003 suggests that groundwater is chronically acidic along brook trout spawning shoals in Lower Sylvan Pond and falls below a critical threshold for egg survival. In contrast, the Panther Lake watershed has deeper tills around the entire margin of the lake (Peters and Murdoch 1985; Schofield et al. 1985).

Variations in groundwater conditions over space and time have substantial implications for fisheries management, particularly for brook trout lakes within the Adirondack region. Even lakes with “good” surface water chemistry can have low brook trout reproductive success due to chemical, not just physical, limitations in spawning habitat quality. Lake liming and subsequent stocking have successfully restored fisheries in a number of acid-stressed aquatic systems. However, in some areas, continued stocking is needed to sustain populations of native fish such as brook trout (Driscoll et al. 1989; Gloss et al. 1989; Schofield et al. 1989; Schofield 1993). For example, Woods Lake in the Adirondack Mountains exhibited reasonable survival of stocked fish after lake liming, yet continued to have low brook trout spawning success (Schofield et al. 1991). In Woods Lake, the lack of successful spawning was attributed to poor physical habitat characteristics along the in-lake spawning shoals and poor chemical conditions in the chronically acidified tributary streams, although groundwater chemistry in redds was not specifically assessed in this study (Schofield and Keleher 1996). Brook trout reproductive success did not improve within Woods Lake until tributary watersheds were limed, which indicated that in-lake pH restoration alone was insufficient to restore a self-sustaining brook trout population (Driscoll et al. 1996; Schofield and Keleher 1996). The Woods Lake study also emphasizes the importance of coupled hydrological and geochemical processes in the delivery of acidic or neutral water to a lake. We present preliminary evidence indicating that in some systems where lake liming has been unsuccessful in restoring wild brook trout populations, acidic groundwater discharge rather

than just poor substrate characteristics may be responsible for low reproductive success.

Schofield (1993) found that headwater Adirondacks lakes with thin soils and small watersheds had limited groundwater inputs, low lake pH, and few wild brook trout. The ability of various small Adirondacks lakes to sustain wild brook trout populations was attributed to lake pH and to the absence of adequate groundwater inputs. We suggest that in some of these lakes, the interaction between groundwater chemistry and hydrology controls the ability of managers to successfully re-establish naturally reproducing populations. Other ecosystems are influenced by acidic groundwater: for example, streams receiving acid mine drainage, chronically acidified streams, and the lakes into which such streams drain. These ecosystems represent cases in which acidic groundwater discharge may reduce brook trout populations and, as such, require systemwide restoration efforts to re-establish viable fish populations.

Acknowledgments

We thank Jason Robinson, Les Resseguie, and Travis Andrews for help with fieldwork and data collection. Andrew Millward, Rich Phillips, Geoff Steinhart, Brian Weidel, Fred Utter, and three anonymous reviewers provided valuable feedback on this manuscript. Cornell University's Biogeochemistry and Biocomplexity National Science Foundation Integrative Graduate Education and Research Traineeship small grant program funded this work (NSF DGE-0221658). We thank James M. Hassett (College of Environmental Science and Forestry, State University of New York) for use of TruTrack water level recorders. We thank the Adirondack League Club for access to study lakes and support facilities.

References

- Bain, M. B., J. T. Finn, and H. E. Booke. 1985. Quantifying stream substrate for habitat analysis studies. *North American Journal of Fisheries Management* 5:499–506.
- Baird, O. E. 2000. Distribution and abundance of fish in relation to pH and temperature in an Adirondack river system: potential for fish community restoration. Master's thesis. Cornell University, Ithaca, New York.
- Baker, J. P. 1982. Effects on fish of metals associated with acidification. Pages 165–176 in R. E. Johnson, editor. *Acid rain/fisheries: symposium on acidic precipitation and fishery impacts in northeastern North America*. American Fisheries Society, Bethesda, Maryland.
- Blanchfield, P. J., and M. S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:747–756.
- Carline, R. F. 1980. Features of successful spawning site development for brook trout in Wisconsin ponds. *Transactions of the American Fisheries Society* 109:453–457.
- Curry, R. A., and D. L. G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1733–1740.
- Curry, R. A., D. L. G. Noakes, and G. E. Morgan. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1741–1749.
- Curry, R. A., and W. S. MacNeill. 2004. Population-level responses to sediment during early life in brook trout. *Journal of the North American Benthological Society* 23:140–150.
- Driscoll, C. T., W. A. Ayling, G. F. Fordham, and L. M. Oliver. 1989. Chemical response of lakes treated with calcium carbonate to reacidification. *Canadian Journal of Fisheries and Aquatic Sciences* 46:258–267.
- Driscoll, C. T., J. P. Baker, J. J. Bisogni, and C. L. Schofield. 1980. Effect of aluminium speciation on fish in dilute acidified waters. *Nature (London)* 284:161–164.
- Driscoll, C. T., C. P. Cirimo, T. J. Fahey, V. L. Blette, P. A. Bukaveckas, D. A. Burns, C. P. Gubala, D. J. Leopold, R. M. Newton, D. J. Raynal, C. L. Schofield, J. B. Yavitt, and D. B. Porcella. 1996. The experimental watershed liming study: comparison of lake and watershed neutralization strategies. *Biogeochemistry* 32:143–174.
- Driscoll, C. T., G. B. Lawrence, A. J. Bulger, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystems effects, and management strategies. *BioScience* 51:180–198.
- Essington, T. E., P. W. Sorensen, and D. G. Paron. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2310–2316.
- Fiss, F. C., and R. F. Carline. 1993. Survival of brook trout embryos in three episodically acidified streams. *Transactions of the American Fisheries Society* 122:268–278.
- Freeze, R. A., and J. A. Cherry. 1979. *Groundwater*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Fraser, J. M. 1985. Shoal spawning of brook trout *Salvelinus fontinalis* in a pre-Cambrian shield lake. *Naturaliste Canadien* 112:163–174.
- Gloss, S. P., C. L. Schofield, R. L. Spateholts, and B. A. Plonski. 1989. Survival, growth, reproduction, and diet of brook trout (*Salvelinus fontinalis*) stocked into lakes after liming to mitigate acidity. *Canadian Journal of Fisheries and Aquatic Sciences* 46:277–286.

- Hultberg, H., and S. Johansson. 1981. Acid ground-water. *Nordic Hydrology* 12:51–64.
- Ingersoll, C. G., D. R. Mount, D. D. Gulley, T. W. La Point, and H. L. Bergman. 1990. Effects of pH, aluminum, and calcium on survival and growth of eggs and fry of brook trout *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1580–1592.
- Johnson, D. W., and D. A. Webster. 1977. Avoidance of low pH in selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Journal of the Fisheries Research Board of Canada* 34:2215–2218.
- Kenoyer, G. J., and M. P. Anderson. 1989. Groundwater's dynamic role in regulating acidity and chemistry in a precipitation-dominated lake. *Journal of Hydrology* 109:287–306.
- Lachance, S., P. Bérubé, and M. Lemieux. 2000. In situ survival and growth of three brook trout (*Salvelinus fontinalis*) strains subjected to acid conditions of anthropogenic origin at the egg and fingerling stages. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1562–1573.
- Lee, D. R. 1977. A device for measuring seepage flux in lakes and estuaries. *Limnology and Oceanography* 22:140–147.
- Newton, R. M., J. Weintraub, and R. April. 1987. The relationship between surface water chemistry and geology in the north branch of the Moose River. *Biogeochemistry* 3:21–35.
- Peters, N. E., and C. T. Driscoll. 1987. Hydrogeologic controls of surface water chemistry in the Adirondack region of New York State. *Biogeochemistry* 3:163–180.
- Peters, N. E., and P. S. Murdoch. 1985. Hydrogeologic comparison of an acidic-lake basin with a neutral-lake basin in the west-central Adirondack Mountains, New York. *Water, Air, and Soil Pollution* 26:387–402.
- Quinn, N. W. S. 1995. General features of brook trout, *Salvelinus fontinalis*, spawning in sites in lakes in Algonquin Provincial Park, Ontario. *Canadian Field Naturalist* 109:205–209.
- Ridgway, M. S., and P. J. Blanchfield. 1998. Brook trout spawning areas in lakes. *Ecology of Freshwater Fish* 7:140–145.
- Runkel, R. L., and B. A. Kimball. 2002. Evaluating remedial alternatives for an acid mine drainage stream: application of a reactive transport model. *Environmental Science and Technology* 36:1093–1101.
- Schafran, G. C., and C. T. Driscoll. 1993. Flow path–composition relationships for groundwater entering an acidic lake. *Water Resources Research* 29:145–154.
- Schnoor, J. L., and W. Stumm. 1985. Acidification of aquatic and terrestrial systems. Pages 311–338 in W. Stumm and J. L. Schnoor, editors. *Chemical processes in lakes*. Wiley, New York.
- Schofield, C. L., and C. Keleher. 1996. Comparison of brook trout reproductive success and recruitment in an acidic Adirondack lake following whole-lake liming and watershed liming. *Biogeochemistry* 32:323–337.
- Schofield, C. L., C. Keleher, and H. K. Van Offelen. 1991. Population dynamics of brook trout (*Salvelinus fontinalis*) during maintenance liming of an acidic lake. *Water, Air, and Soil Pollution* 59:41–53.
- Schofield, C. L., S. P. Gloss, B. Plonski, and R. Spateholts. 1989. Production and growth efficiency of brook trout (*Salvelinus fontinalis*) in two Adirondack Mountain, New York, lakes following liming. *Canadian Journal of Fisheries and Aquatic Sciences* 46:333–341.
- Schofield, C. L., J. N. Galloway, and G. R. Hendry. 1985. Surface water chemistry in the ILWAS basins. *Water, Air, and Soil Pollution* 26:403–423.
- Schofield, C. L. 1993. Habitat suitability for brook trout (*Salvelinus fontinalis*) reproduction in Adirondack lakes. *Water Resources Research* 29:875–879.
- Sebestyen, S. D., and R. L. Schneider. 2001. Dynamic temporal patterns of nearshore seepage flux in a headwater Adirondack lake. *Journal of Hydrology* 247:137–150.
- Sebestyen, S. D., and R. L. Schneider. 2004. Seepage patterns, pore water, and aquatic plants: hydrological and biogeochemical relationships in lakes. *Biogeochemistry* 68:383–409.
- Snucins, E. J., R. A. Curry, and J. M. Gunn. 1992. Brook trout (*Salvelinus fontinalis*) embryo habitat and timing of alevin emergence in a lake and a stream. *Canadian Journal of Zoology* 70:423–427.
- SPSS. 1998. SYSTAT, version 8.0. SPSS, Chicago.
- Staubitz, W. W., and P. J. Zarriello. 1989. Hydrology of two headwater lakes in the Adirondack Mountains of New York. *Canadian Journal of Fisheries and Aquatic Sciences* 46:268–276.
- Webster, D. A., and G. Eiriksdottir. 1976. Upwelling water as a factor influencing choice of spawning sites by brook trout (*Salvelinus fontinalis*). *Transactions of the American Fisheries Society* 105:416–421.
- Webster, D. A. 1962. Artificial spawning facilities for brook trout, *Salvelinus fontinalis*. *Transactions of the American Fisheries Society* 91:168–174.