Survival, Distribution, and Ion Composition in Two Strains of Brook Trout (*Salvelinus fontinalis*) Fry after Exposure to Episodic pH Depressions in an Adirondack Lake

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Brook trout (*Salvelinus fontinalis*) fry are susceptible to high mortality in acidified waters because of their low tolerance to acidic conditions and the potential occurrence of this life stage with episodic acidification associated with snowmelt. Prior to snowmelt, equal numbers of Assinica and Temiscamie strain fry were placed into enclosures. Twelve days after stocking, no consistent differences between strains were observed in survival, distribution, or ion composition. No fry of either strain survived in enclosures placed in shallow water (pH 4.8; 0.7 m depth). Fifty to 100% of fry of both strains survived in enclosures placed in deep water (pH 6.3; >2.0 m depth). Fry survival in long enclosures that extended from shallow to deep water was 80–99%. Within long enclosures, both strains were recovered in higher densities from middle and deep sections of the enclosures than from shallow sections. High fry survival and nonrandom distributions in the long enclosures indicated that both strains were able to avoid lethal, nearshore waters during spring snowmelt by moving to deeper water.

La mortalité peut être élevée lorsque les alevins de l'omble de fontaine (*Salvelinus fontinalis*) se trouvent en eaux acides car ils tolèrent mal l'acidité. Or, il est possible que ce stade de vie coïncide avec l'acidification épisodique des plans d'eau associée à la fonte des neiges. Avant celle-ci, des alevins des souches Assinica et Temiscamie ont été introduits en nombre égal dans des parcs. Douze jours après l'ensemencement, il n'y avait pas de différence établie entre les souches sur les plans de la survie, de la distribution ou de la composition ionique. Peu importe les souches, aucun alevin n'a survécu dans les parcs placés en eau peu profonde (pH 4,8; 0,7 m de profondeur). Cinquante à 100 % des alevins des deux souches ont survécu dans les parcs placés en eau profonde (pH 6,3; plus de 2,0 m de profondeur). La survie des alevins dans les longs parcs qui s'étiraient des eaux peu profondes aux eaux profondes, a été de 80 à 99 %. Dans ce dernier cas, les alevins des deux souches ont été récupérés en plus grande densité dans la section centrale et la section profonde des parcs, plutôt que dans la section peu profonde. Le taux élevé de survie des alevins et les distributions non aléatoires dans les grands parcs indiquent que les deux souches sont capables d'éviter les eaux peu profondes et létales durant la fonte des neiges en allant en profondeur.

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Acidification of lakes and streams has had adverse effects on fish populations throughout northeastern North America (Haines 1981; Schofield 1982; Kelso et al. 1986). Changes in fish population structure and abundance, indicative of recruitment failure, have been observed in these acidified lakes (Beamish and Harvey 1972; Harvey 1982; Frenette and Dodson 1984; Schofield and Driscoll 1987) and in whole-lake acidification experiments (Mills et al. 1987).

Extensive laboratory investigations with brook trout (*Salvelinus fontinalis*) have demonstrated that exposure of fertilized eggs, alevins, and fry to natural acidic conditions (low pH, high total Al, low Ca) can result in high mortality. For example, brook trout emergent fry suffered mortalities of 94, 82, and 100% when exposed to waters with pH 4.2, 4.6, and 5.2 and elevated Al levels, respectively (Baker and Schofield 1982). Fertilized eggs and embryos exposed to similar conditions suffered significantly less mortality than alevins and fry. Lethality of acidic conditions to brook trout has been shown to depend not only on pH and the life stage exposed but also on the concentrations of Al and Ca present in the water (e.g., Wood et al. 1988). Sensitivity to pH typically decreases with age whereas sensitivity to Al exposure increases with age, while increasing Ca concentrations tend to reduce sensitivity of all life stages to acid and Al (e.g., Ingersoll et al. 1990b).

In addition to being physiologically sensitive to acidic conditions, early life stages of brook trout occur simultaneously with acidification associated with snowmelt. Runoff from melted snow may inundate nearshore areas of lakes with water of lethal low pH and high Al concentrations (Cronan and Schofield 1979; Jeffries et al. 1979; Gunn and Keller 1984; Galloway et al. 1987). Brook trout spawn in the fall often in groundwater seepage areas where pH levels may be higher than those of surface waters (Webster and

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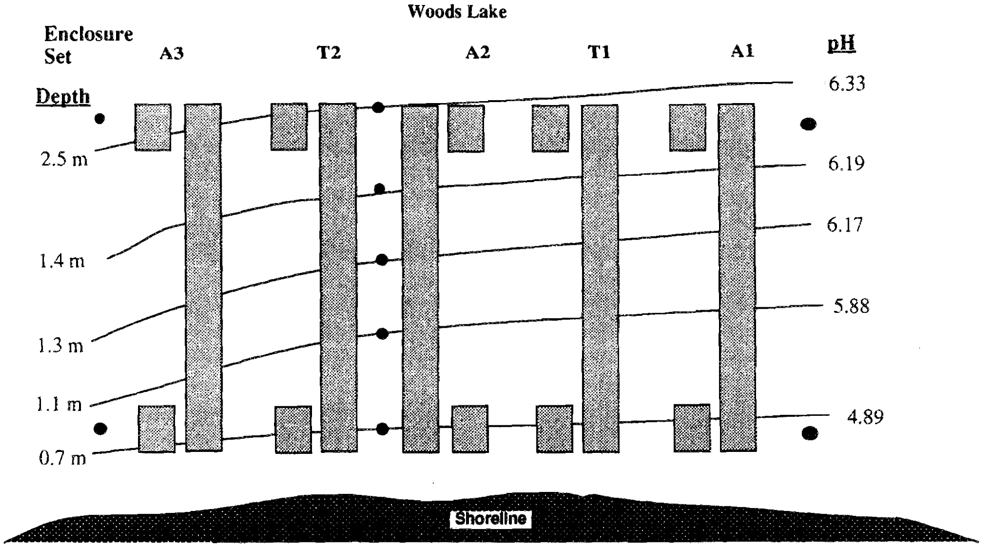

FIG. 1. Position of horizontal enclosures on the bottom of Woods Lake. Three sets of enclosures (each set is one long and two short enclosures) were stocked with Assinica strain (A1–A3) brook trout and two sets were stocked with Temiscamie strain (T1 and T2) brook trout. Depths and pH levels represent conditions at the end of the study. Circles indicate the locations where water was sampled.

Eiriksdottir 1976; Johnson and Webster 1977). Eggs located in these seepage areas would probably be protected if surface waters became acidic; however, alevin development and fry emergence from substrates often coincide with snowmelt events. In turn, mortality of young brook trout in acidified waters may be expected to depend on the intensity and duration of episodic acidification, the quantity and quality of groundwater seepage in the spawning redds, the mixing of acidic surface water with deeper layers, and the behavioral response of young fish to acidified water (see Gunn 1986).

Laboratory investigations have provided evidence that brook trout alevins and juveniles actively avoid low-pH waters, particularly when the water contains high concentrations of Al. Brook trout alevins were observed to actively avoid pH less than 5.0 and this response increased when test waters contained Al (33–500 μg/L; Gunn and Noakes 1986). In another study, brook trout juveniles similarly avoided test waters with pH <5.5 (Pedder and Maly 1986). Other sublethal responses to acidified water include changes in whole-body ion composition. Whole-body ions (Ca, Na, K) are expected to decline after sublethal exposure to acidic conditions (low pH, elevated Al; Wood et al. 1990). Sublethal reductions in these ions have contributed to reduced fitness in lake trout alevins exposed to acidic conditions (Gunn and Noakes 1987).

Direct extrapolation of these laboratory observations to natural systems may not be valid because changes that occur in nearshore areas during episodic pH depressions are difficult to simulate. During natural pH depressions, lake level, ice thickness, and light penetration, water temperature, dissolved oxygen, and other related chemical conditions stochastically change and interact. These variables are potential stimuli to early life stages of brook trout and may affect their net response to acidified nearshore waters. No field investigations have been available to compare laboratory results and to provide direct observations on the effects of episodic pH depressions associated with snowmelt on brook trout fry.

The objective of this study was to describe and compare the effects of natural episodic pH depressions on the survival, depth distribution, and whole-body ion content of two strains of brook trout fry in an Adirondack lake.

Study Site

This study was conducted in March 1990 over a 12-d period before ice-out in Woods Lake (43°52′N, 71°58′W), a 23-ha headwater lake located in the west-central region of the Adirondack Mountains, New York. The physical and hydrological characteristics of Woods Lake and its lake basin have been described by Staubitz and Zarriello (1989). The lake has been included in the Lake Acidification Mitigation Project (LAMP) since 1984 (see Porcella 1989). Circumneutral conditions have been maintained through applications of calcium carbonate directly to the lake in May 1985, September 1986, and October 1988. Catchments of the two perennial tributaries to Woods Lake were limed during October 1989 as part of the Experimental Watershed Liming Study (Porcella 1991). Despite these mitigative liming treatments, episodic pH depressions have been documented annually during spring snowmelt in shallow nearshore areas of the lake (Gubala and Driscoll 1991). Complete mortality of caged brook trout fry was observed during these episodes, in shallow (<1 m) water, where acidic meltwater depressed pH levels to 4.2–4.8. However, captive fry experienced little or no mortality at greater depth (2 m), where pH levels generally remained above 6.0 (LAMP, unpublished data).

The experiments in this study were conducted in the eastern nearshore zone of Woods Lake, which received intermittent tributary drainage from an unlimed area of the watershed. The substrate in the study area consisted of organic sediments greater than 0.5 m in depth.

Methods

Enclosure Construction and Placement

Five sets of three cylindrical enclosures were placed in Woods Lake in March 1990 before ice-out (Fig. 1). Long

TABLE 1. Mean dry weights of Assinica (A) and Temiscamie (T) strain brook trout fry from the hatchery and enclosures during the study ($N = 20$). Two standard errors of each estimate are given in parentheses. No live fry were recovered from the short–shallow enclosures. *Statistically different from fry at the start ($P < 0.05$).

Location	Date	Strain	Mean weight (mg)	% change from start
Hatchery	March 16, 1990	A	25.1 (3.2)	—
		T	16.7 (1.6)	—
Hatchery	March 27, 1990	A	20.3 (3.4)	−19
		T	24.5 (3.4)	48*
Short–deep enclosure	March 28, 1990	A	19.7 (2.7)	−22*
		T	16.3 (1.0)	−2
Long enclosure, deeper sections	March 28, 1990	A	24.8 (2.8)	−1
		T	15.0 (1.4)	−10
Long enclosure, shallow section	March 28, 1990	A	23.4 (2.4)	−7
		T	16.2 (1.6)	−3

enclosures (15.0 m in length) and short enclosures (2.0 m in length) were constructed of fiberglass mesh, sewn into cylinders approximately 25.0 cm in diameter.

Each set of enclosures was composed of one long enclosure and two short enclosures (Fig. 1). Long enclosures extended 15 m perpendicular from shore from a depth of approximately 0.7 m to approximately 2.5 m. Short enclosures were placed on the lake bottom parallel to the long enclosures. One short enclosure in each set extended from the shallow end of the long enclosure offshore (hereafter referred to as the short–shallow enclosure). The other short enclosure in each set extended from the deep end of the long enclosure inshore (hereafter referred to as the short–deep enclosure). Two short enclosures were also suspended vertically from the ice surface near the shallowest end of the enclosure sets. These short vertical enclosures permitted periodic assessments of mortality during the 12-d study.

Enclosures were placed in the lake 1 d prior to stocking. To place enclosures on the lake bottom, nearshore and offshore rectangular holes were cut into the ice. Five polypropylene lines were run under the ice between the holes. The enclosures were then placed on the ice surface near the offshore hole. Concrete-filled 3.81-cm plastic (PVC) pipes were then fitted through loops sewn in the ends of the enclosures to provide a secure fastening point for the lines. The lines under the ice were then connected to each set of enclosures and the enclosures were slowly pulled into the lake. After placement, the ends of enclosures were aligned in the nearshore hole and anchored with concrete blocks. Concrete blocks were also connected to the lines at the deep end. Lines to the surface remained attached to the anchors to permit stocking and removal. Prior to stocking, divers inspected the enclosures to ensure they were properly positioned on the lake bottom.

Enclosure Stocking

Assinica and Temiscamie strain brook trout were stocked into the enclosures. These strains originated from two adjacent river systems in northern Quebec (see Flick 1977; Cone and Krueger 1988; Van Offelen et al. 1993) and have been reported to be genetically different (Perkins et al. 1993). Fry were reared at the Brandon Park Hatchery in the northern Adirondacks in separate circular fiberglass tanks. Gametes for both strains were collected from brood stocks maintained in natural ponds in the Adirondack region. Fertilized eggs were incubated in hatchery water (pH > 7.0, Ca > 9.5 mg/L). At stocking, the Assinica strain fry ranged in age from approximately 71 to 81 d post-hatch, while the Temiscamie strain fry were from 58 to 68 d old. Exogenous feeding by Assinica and Temiscamie fry had begun 28 and 17 d before stocking, respectively. Because of their different stage of development, Assinica fry either did not change weight or lost weight during the experiment, while Temiscamie fry either did not change weight or gained weight (Table 1). Fry were not fed 24 h before stocking. Prior to stocking, a sample of 20 fish of each strain was collected from rearing tanks for whole-body ion analysis. Fry destined for each enclosure were counted and placed in oxygenated plastic bags for transport to the study site.

One day after the enclosures were placed into the lake (March 16), fry were stocked at a density of 20 fish/m enclosure length (40 fish per short enclosure, 300 fish per long enclosure). Three sets of enclosures were stocked with Assinica strain fry. Two sets were stocked with Temiscamie strain fry. The fish were stocked into the nearshore ends of both the long and short–shallow enclosures. The short–deep enclosures were stocked at their offshore end. Two short enclosures placed vertically under the ice to monitor mortality were stocked separately with 20 Assinica and 20 Temiscamie fry.

Enclosure Removal

Eleven days after stocking (March 27), divers working from the deep ends to the shallow ends divided each long enclosure into three sections by tying them off. The first section was the first 1–3 m meters of each long enclosure, from its deep end (approximately 2.5 m) to where the water was approximately 1.4 m deep. The second section extended from the end of the first section for 6–10 m to a depth of approximately 1.1 m, the shallowest point under the ice that a diver could reach. The third section was the remaining 4–8 m of the enclosure to the shallow end (approximately 0.7 m deep).

The experiment was concluded approximately 24 h after the long enclosures were divided (March 28). All enclosures were removed from the lake through the offshore trench. As the long enclosures were withdrawn from the

TABLE 2. Chemical characteristics of hatchery and Woods Lake water sampled during pH depressions caused by snowmelt in 1990. When mean chemical values for a location are presented, the range is given in parentheses. Brook trout fry were placed into enclosures March 17. The study was concluded on March 28.

Date/location	pH	Ca (mg/L)	Total Al (mg/L)
March 16			
Hatchery	7.05	9.96	0.09
0.9 m	5.58	—	—
2.5 m	6.59	—	—
March 18			
0.9 m	4.91 (4.73, 5.03)	2.27 (1.73, 2.81)	1.02 (0.88, 1.16)
2.5 m	6.29 (6.24, 6.34)	6.76 (6.51, 7.01)	0.48 (0.44, 0.52)
March 23			
0.9 m	5.11 (4.81, 5.29)	2.01 (1.97, 2.05)	1.38 (1.16, 1.60)
1.0 m	4.80	1.88	1.01
1.5 m	6.06	4.71	0.86
2.0 m	5.75	4.19	0.89
2.5 m	6.26 (6.25, 6.27)	6.60 (6.20, 6.99)	0.46 (0.44, 0.49)
March 28			
0.7 m	4.89	2.52	1.26
1.1 m	5.88	4.33	0.49
1.3 m	6.17	5.14	0.52
1.4 m	6.19	5.48	0.43
2.3 m	6.33	6.04	0.49

lake, each section was cut open consecutively and the fish were removed. Live and dead fish recovered from the shallow, middle, and deep sections of the enclosures were counted and placed in separate containers. Twenty live fry of each strain were collected from short–deep enclosures and shallow sections of the long enclosures to determine dry weights and ion content. In addition, fry of each strain collected from the middle and deep sections of the long enclosures were pooled and a sample of 20 fry of each strain was collected to determine dry weights and ion content.

Water Chemistry Collection and Analysis

To determine the timing and magnitude of pH depressions, water was sampled from the study area at the time of stocking, two times during the study, and at the conclusion of the study. Water samples were collected from a point approximately 5.0 to 10 cm above the lake bottom. These samples were taken through the ice at the corners of the study area and at four sites that bisected the sampling area (see Fig. 1 for locations). The first 500 mL of water pumped through the samplers was discarded to ensure that only water from the lake bottom was sampled. pH was measured with a pH meter within 4 h of sample collection. Total Al and related Ca concentrations were determined with inductively coupled argon plasma spectroscopy (ICP) analysis.

Dissolved oxygen (DO) levels and water temperature were monitored throughout the study with an oxygen/temperature meter. Discharge of the two main lake tributaries and lake level were monitored at United States Geological Survey gaging stations.

Whole-Body Ion Analysis

To determine the effects of acidic conditions on the whole-body ion content of exposed fry, 20 fry of each strain were collected from the hatchery before stocking, from the hatchery at the end of the study, from the short–deep enclosures, from shallow sections of the long enclosures, and from deeper sections (pooled from middle and deep sections) of the long enclosures. Fish were rinsed with deionized water, placed in individual plastic sampling tubes, and immediately frozen in liquid nitrogen. Individual fish were ashed for 6 h at 450°C and weighed (dry ash weight). The ashed sample was then combined with 2.0 mL of redistilled HNO_3 and 0.25 mL of ultrapure $HClO_4$ and heated for 1 h at 100°C and further digested at 180–200°C for approximately 2 h until clear. The digested samples were then ICP processed.

Statistical Procedures

The distributions of the fry between the shallow and deep sections of each long enclosure were compared with chi-square tests. A two-way contingency test was used to detect differences in the distributions of the strains between the enclosures. Analysis of variance (ANOVA) and t-tests were used to compare dry weights of fry. Linear regression analysis was used to evaluate the relationship between dry weights of fry and Ca concentrations. Significant differences were recognized at the 0.05 level ($P \leq 0.05$). Upper and lower 95% confidence interval limits are reported in the results section as ± values.

Results

Nearshore Acidification

Snowmelt events throughout the study period created a gradient of conditions from lethal low pH and high total Al in the shallows to nonlethal water conditions of moderate pH and low total Al in the deeper areas (Table 2; Fig. 1).

The disappearance of snowpack resulted in a 40-cm decrease between March 18 and 29 in lake level and large fluctuations in discharges in a tributary on the opposite shore from the study site (Fig. 2). The pH at the shallowest water samplers (<0.75 m) ranged from 4.73 to 5.29 during the study. Total Al concentrations at the shallow stations

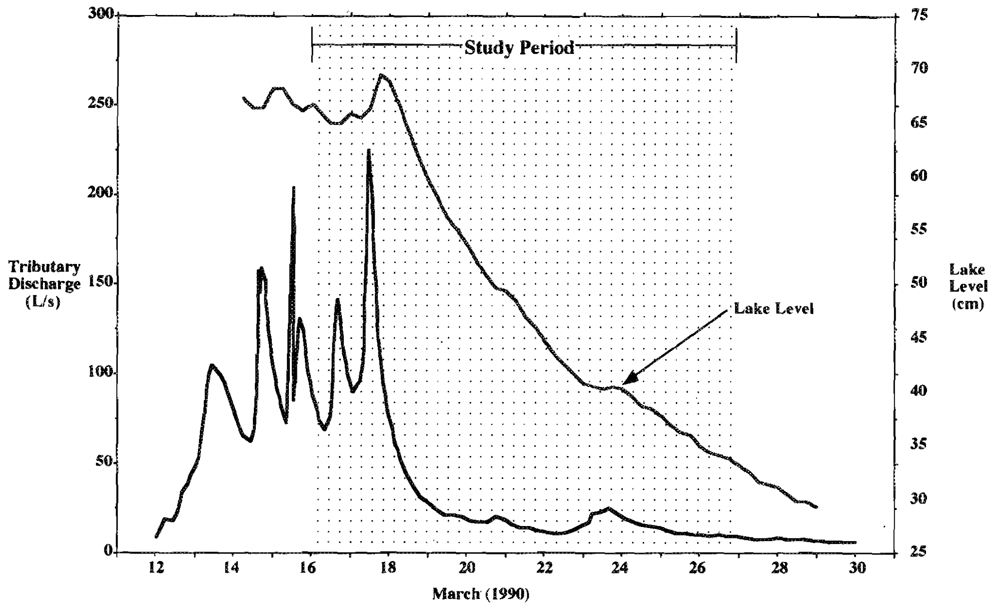

FIG. 2. Lake level and tributary discharge from one of two primary tributaries to Woods Lake measured at U.S. Geological Survey gaging stations during March 1990.

TABLE 3. Observed mean survival of Assinica (A) and Temiscamie (T) strain brook trout fry in enclosures after exposure to an episodic pH depression. Two standard errors are given in parentheses. N = the number of enclosures.

Enclosure	Strain	Day after stocking	% survival	N
Short vertical	A	6 d	0	1
	T	6 d	0	1
Short–shallow	A	12 d	0 (0)	3
	T	12 d	0 (0)	2
Short–deep	A	12 d	78 (24)	3
	T	12 d	99 (2)	2
Long	A	12 d	86 (6)	3
	T	12 d	94 (2)	2

were >1 mg/L and toxic monomeric Al species were dominant at these low pH levels (Gubala et al. 1991; see also Driscoll et al. 1980). Although total Al was relatively high at deeper stations, monomeric Al concentrations were probably <0.1 mg/L (Gubala et al. 1991). When the long enclosures were removed, the pH at their shallow end was 4.89. In the deeper, offshore region of the study area (>2.0 m), pH remained above 6.0 during the entire study period. The interface between lethal acidic and nonlethal circumneutral conditions was located probably between 1.0 and 1.5 m at the beginning of the study and between 0.7 and 1.0 m at the conclusion of the study. DO concentrations adjacent to the lake bottom remained near saturation throughout the study period (13.6–14.0 mg/L).

Survival

No fry survived in the short–shallow or short vertical enclosures in contrast with the high survival of both strains in the short–deep and long enclosures (Table 3). All fry were dead in the short vertical enclosures after 6 d of exposure. An average 78 ± 24% of the Assinica and 99 ± 2% of the Temiscamie fry were alive in the short–deep enclosures at the end of the study. Fourteen Assinica fry found dead in the sealed opening of one short–deep enclosure were presumed trapped in the enclosure opening at time of stocking. These fry were not included in the Assinica survival estimates. Survival in the long enclosures ranged from 80 to 96% for both strains.

No differences in survival between strains were observed in the long enclosures ($P > 0.2$; Table 3). An average 86 ± 6% of the Assinica fry survived compared with 94 ± 2% of the Temiscamie fry. Total recovery of fry, dead and alive, ranged from 91 to 98% of the number originally stocked in each enclosure. If fry were distributed evenly (20 fry/m) in long enclosures and the water was lethally acidic to a depth of 1 m, then the number of fry that survived in long enclosures (80–96%) was higher than expected (67–77%) in each enclosure.

Fry Distribution in Long Enclosures

Brook trout fry were not distributed evenly within long enclosures at the end of the study (Fig. 3). Significantly more live fry were found in the middle and deep sections combined (>1.1 m) than in shallow sections ($P < 0.001$). Averages of 29.8 Assinica and 27.3 Temiscamie fry/m were recovered from the combined middle and deep sections of long enclosures compared with only 4.5 Assinica and 3.1 Temiscamie fry recovered/m from shallow sections. More dead fry were recovered from shallow sections than deep sections of long enclosures ($P < 0.001$). Seventy of 76 dead Assinica (92%) and 15 of 23 (65%) dead Temiscamie fry were recovered from shallow sections of long enclosures.

More fish were recovered from middle sections than deep sections of long enclosures ($P < 0.01$; Fig. 3). Averages of 35 Assinica and 29 Temiscamie fry/m were recovered from middle sections of long enclosures, while 21 Assinica and 16 Temiscamie fry/m were recovered from deep sections. Fry distribution within each enclosure was similar among the five enclosures ($P > 0.05$).

Whole-Body Ion Content

At the end of the study, whole body Ca of fry increased,

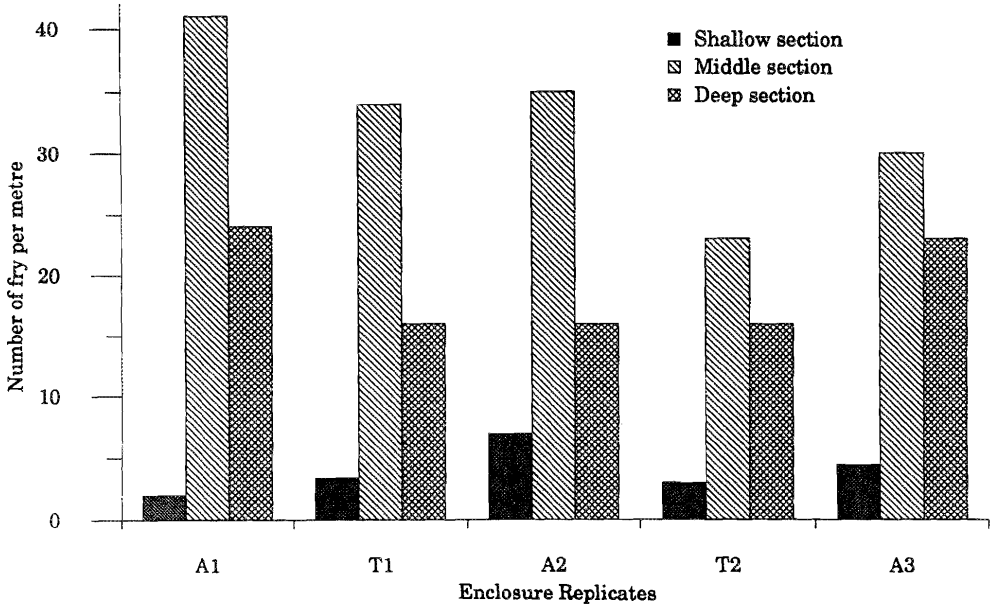

FIG. 3. Number of Assinica (A) and Temiscamie (T) brook trout fry present per metre at the end of the study in the shallow, middle, and deep sections of each long enclosure.

TABLE 4. Whole-body concentrations of Ca, Na, and K based on dry weights of Assinica (A) and Temiscamie (T) fry sampled from the hatchery and enclosures at the beginning and end of the study. Two standard errors of each estimate are given in parentheses. Percent change is expressed for each strain relative to concentrations in hatchery fish at the start of the study. $N = 20$ in all cases.

		Ca		Na		K	
Fry sample	Strain	µg/g	% change	µg/g	% change	µg/g	% change
Hatchery	A	10.92 (0.62)	—	8.27 (0.52)	—	19.80 (0.36)	—
at start	T	9.46 (0.44)	—	8.48 (0.36)	—	20.91 (0.44)	—
Hatchery	A	14.51 (1.38)	33	9.96 (0.66)	20	19.61 (0.72)	−1
at end	T	10.76 (1.02)	14	7.93 (0.48)	−7	18.81 (0.62)	−10
Short–deep	A	14.41 (0.50)	32	9.39 (0.54)	14	19.93 (0.46)	1
enclosure	T	11.82 (0.44)	25	9.10 (0.36)	7	19.57 (0.56)	−6
Long enclosure,	A	12.30 (0.32)	13	7.37 (0.44)	−11	17.71 (0.48)	−11
deeper sections	T	11.14 (0.66)	18	8.20 (0.46)	−3	18.56 (0.54)	−11
Long enclosure,	A	13.23 (0.58)	22	7.94 (0.42)	−4	18.18 (0.54)	−8
shallow section	T	10.84 (0.70)	16	8.30 (0.54)	−2	18.75 (0.38)	−10

while Na and K concentrations either increased or decreased relative to concentrations at the start (Table 4). No strain-specific changes in ion concentration occurred. Ca levels in both strains were significantly greater in fry from the hatchery and enclosures at the end of the study than in fry at the beginning of the study. Ca levels in Assinica fry from both the hatchery and short–deep enclosures at the end of the study were similar and significantly greater than in fry collected from long enclosures. In Temiscamie fry, Ca levels were similar among all fry sampled at the end of the study. Increases in Ca ranged from 13% in Assinica fry from long enclosures to 33% in hatchery Assinica fry at the end of the study. No association between Ca levels and dry weights of fry was identified through regression analysis ($P > 0.05$).

Whole-body Na levels in fry both increased and decreased relative to the concentration at the start of the study (Table 4). Na levels in Assinica fry increased the most in samples from the hatchery at the end of the study (+20%) and from the short–deep enclosures (+14%; Table 4). Na levels decreased slightly in fry sampled from shallow sections of deep enclosures (−2 to −4%). Na levels were lowest in Assinica fry sampled from the deep sections of long enclosures and significantly lower than in those sampled from the hatchery at the start (11% decrease). Temiscamie fry from short–deep enclosures had significantly higher Na levels than those sampled at the beginning of the study (+7%).

K levels in Assinica and Temiscamie fry declined 8–11% in long enclosures and changed little in short–deep enclosures when compared with those in fry at the beginning (Table 4). Assinica fry from the short–deep enclosures exhibited significantly greater K levels than fry from long enclosures, and levels were similar to those in hatchery fry at the start and end of the study period. In Temiscamie fry, K levels were similar among all fry sampled at the end of the study and were significantly lower than in hatchery fry sampled at the start (−6 to −10%).

Discussion

Brook trout fry survived in Woods Lake during episodic pH depressions when given the opportunity to move from shallow acidified waters to deeper circumneutral waters (Table 3). The uneven distributions of fry between shallow and deep sections of long enclosures and the higher survival than expected if the fry had been evenly distributed suggested that most fry remained out of acidified nearshore waters. In laboratory investigations, brook trout alevins and juveniles avoided acidified waters, especially when test waters had high Al concentrations (Gunn and Noakes 1986; Pedder and Maly 1986). A similar avoidance response to low pH and high Al has been shown in the laboratory for lake trout (*Salvelinus namaycush*) alevins (Gunn et al. 1987). No field investigations previously have focused on the response of brook trout fry to acidified waters.

The fry may have been influenced by factors other than acidic conditions. Gradients along the length of long enclosures did occur for water temperature, light intensity, and CO_2. Water temperature ranged from 0 to 4°C and exhibited a 2°C gradient, with the shallow ends of long enclosures colder than the deep ends. The potential effect of the 2°C temperature gradient on fry movement in this investigation could not be evaluated because preferences of brook trout fry over this temperature range are unknown. Light intensity presumably was greatest at the shallow and least at the deep end of the long enclosure. Brook trout alevins typically shift from photonegative to photopositive behavior as they get older (Carey and Noakes 1981; Godin 1982; Nunan and Noakes 1985). Thus, brook trout fry in enclosures should have been attracted to the shallower depths under the ice. This interpretation corresponds with our experience electrofishing in circumneutral lakes which indicates that fry typically remain in shallow waters (0.5 m) into late spring (early June). However, low densities of fry were recovered from the shallowest section of the long enclosures (Fig. 3). High $P\text{CO}_2$ has elicited avoidance responses in Arctic char (*Salvelinus alpinus*) (Jones et al. 1985). However, $P\text{CO}_2$ in Woods Lake generally increased with depth (Gubala and Driscoll 1991) which likely would have favored a shallow distribution of fry, opposite to that observed. Although some of these variables may have contributed to fry distribution in our long enclosures, the most reasonable interpretation was that low pH and high Al concentrations were the variables that triggered an avoidance response and caused fry to seek deeper waters and to survive.

The analysis of the ion content of fry provided evidence that fry in the long enclosures did not suffer any long-term sublethal effects from their limited exposure to the acidic conditions (Table 4). Whole-body ions are expected to decline after sublethal exposure to acidic conditions (Wood et al. 1990). In our investigation, Ca concentrations actually increased among fry in the enclosures at the end of the study over fry from the hatchery at the start (Table 4). Na and K levels decreased by a maximum of only 11% (Assinica fry, long enclosures) when compared with hatchery fry at the start. Interpretation of the ion content data was difficult because of the unknown influence of original rearing conditions, the short exposure time to acidified water, a possible lack of food in the enclosures, changes in weight, and changes in body composition due to development. The small declines in Na and K suggest that fry in the long enclosures may have been negatively affected by acidic conditions; however, the increased Ca levels in the fry and the moderate water Ca levels (see Wood et al. 1990) indicate that permanent injury was unlikely.

No consistent differences between the Assinica and Temiscamie strains were observed in survival, distribution, or ion composition. A genetic component to acid tolerance has been reported in brook and brown trout (*Salmo trutta*) strains (Gjedrem 1976; Robinson et al. 1976; Swarts et al. 1978). However, in a study that compared a hybrid strain (Temiscamie × domestic) against Washington strain brook trout, no substantial differences in survival, weight, and gill histology were reported between 1-yr-old brook trout exposed for 28 d to 14 combinations of pH, Al, and Ca (Ingersoll et al. 1990a). Additional investigations are needed to quantify whether a differential physiological tolerance or avoidance behavior exists between these and other strains to acidic conditions. Differences in behavior among strains in response to acidic conditions could be as important to survival as physiological tolerance. For example, a strain physiologically tolerant to low pH could exhibit a weaker avoidance response to acidic conditions in the wild than a strain less physiologically tolerant. In this case, the physiologically less tolerant strain may more rapidly sense and avoid acidic conditions than a more tolerant strain and thus avoid lethal exposure.

This investigation and others help explain why lake trout populations characteristically suffer recruitment failures earlier than do brook trout in lakes susceptible to episodic acidification. Brook trout typically spawn earlier and take less time to hatch than lake trout (Power 1980). Thus, under natural conditions, brook trout occur as free-swimming fry when lake trout are still relatively immobile alevins. In addition, lake trout alevins have been reported to prefer to remain near substrate rather than exhibit an avoidance response to acidic conditions (Gunn et al. 1987). Thus, the temporal relationship between the life stage present and acidified snowmelt combined with different avoidance responses of the species favors survival of brook trout over lake trout in waters that experience episodic acidification. Comparative bioassays with brook trout and lake trout fry in acidic water also have indicated significantly lower mortality rates for brook trout (Grande et al. 1978).

In summary, brook trout fry of two strains were observed to survive in nearshore areas of a lake during episodic pH depressions when they had access to deeper circumneutral waters. The probable mechanism that caused the survival of these fry was an avoidance response to acidic conditions and subsequent movement to deeper waters. Mortality of fry contained in the short–deep and long enclosures was probably higher than would have occurred in fish afforded full freedom of movement; thus, the estimates of survival were likely conservative and lower than in reality. However, the enclosures used in the study provided a practical means to evaluate the behavior of fish exposed to a natural episodic pH depression. Additional investigations with this type of enclosure could be conducted with other life stages of brook trout, other species, and different strains to help determine behavior of fish exposed to natural acidic conditions. Field studies of longer duration are needed to better evaluate and understand the effects of pH depressions on growth, fish behavior, and ion regulation.

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