

## Staying Cool: Behavioral Thermoregulation during Summer by Young-of-Year Brook Trout in a Lake

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**Abstract.**—Thermal habitat selection and behavior by young-of-year brook trout *Salvelinus fontinalis* was studied in a lake in central Ontario, Canada. In May, trout foraged actively within 2 m of shore in the warmest water available (~15°C). In early June, trout foraged near the bottom within 4 m of shore, where bottom water temperatures were near, or at, the upper thermal tolerance, for trout, of 20°C. In July, when ambient water temperatures ranged from 23°C to 27°C, trout lay on the bottom in the coldest water available (18–20°C) in discrete areas 3–8 m from shore. Flow rate of cold groundwater accounted for 87% of the variance in trout density in these areas, and the data suggest that a minimum flow rate of 125 mL·m<sup>-2</sup>·min<sup>-1</sup> is required for trout to take up station. When trout were displaced from holding positions, sites with greater groundwater flow were more quickly reoccupied by trout than sites with lower flow. Experimentally created trough-like depressions at these sites attracted higher densities of trout than the same sites with their natural topography and restricted trout distribution to within each depression. Preliminary behavioral observations suggest that trout lie on the bottom and defend cool microhabitats at the expense of daytime feeding. These results suggest that areas with cold groundwater may be a limiting resource for young-of-year brook trout in the littoral zone during summer, and resource managers should consider protecting such areas from lakeshore development and logging.

The coldwater requirements of salmonine fishes (trout and salmon; Behnke 1992) limit their distribution and abundance to more northern latitudes and high altitudes where summer temperatures do not exceed the thermal tolerance of the fish (Scott and Crossman 1973; MacCrimmon and Campbell 1969; Fausch 1989; Flebbe 1994). In marginal (suboptimal) habitats at the extremes of their range, salmonines often adapt behaviorally by adjusting activity rates and changing habitats when temperatures exceed their coldwater requirements (Thorpe 1994).

Salmonines commonly migrate to cooler up-stream reaches in streams (Fausch 1989; Meisner 1990a) or to deeper water in lakes (Kennedy 1941; Martin and Olver 1980; Olsen et al. 1988) when water temperatures rise beyond those preferred by the fish or reach their lethal limit. Where such migration is not possible, such as within a marginal stream habitat, individuals often aggregate in areas where temperatures are lower, such as deep pools that are thermally stratified (Matthews et al. 1994; Nielsen et al. 1994) or small shallow areas with cool water (Elson 1942; Fry 1951; Gibson 1966).

If thermal refuges are limited, then fish may

compete for access to this potentially consumable resource much the same as fish compete for food or mates (Magnuson et al. 1979). Inferior competitors may be excluded from high quality areas and potentially suffer increased metabolic stress and mortality when thermal resources are limited. If so, then population size following periods of thermal stress may be proportional to the abundance of refuge areas. Indeed, sources of cold groundwater may allow persistence of salmonine populations in marginal stream habitats (e.g., Barton et al. 1985; Meisner et al. 1988; Meisner 1990a, 1990b), but the importance of groundwater as a thermal refuge for young salmonines in lakes is poorly understood.

Young-of-year brook trout *Salvelinus fontinalis* inhabit shallow nearshore areas of lakes during spring (Biro and Ridgway 1995; Biro 1996). During summer, however, young-of-year brook trout respond to high littoral water temperatures by (1) seeking areas with cold water, presumably groundwater-derived (Griswold 1967; Wurtsbaugh et al. 1975), (2) entering cool inlet streams (Curry et al. 1997; P.A.B., personal observation), or (3) migrating to deeper benthic habitats (Venne and Magan 1995).

Water temperatures in the littoral zone of brook trout lakes in Algonquin Provincial Park, Ontario, commonly exceed 20°C in summer and frequently

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reach 25–28°C (P.A.B., unpublished data). These values exceed upper tolerance (20°C) and lethal limits (25°C) for juvenile brook trout in the laboratory (Fry et al. 1946; McCormick et al. 1972). Preliminary observations in one particular lake indicated that some portion of the young-of-year brook trout cohort remained in the littoral zone in summer but were restricted to discrete areas with cool bottom water temperatures within a well-known brook trout spawning area with abundant groundwater seepage (Ridgway and Blanchfield, in press). Qualitative observations indicated that the brook trout lay on the bottom in these areas, did not actively feed, and aggressively defended areas about their location from conspecifics.

Previous studies have noted the use of coldwater areas by salmonines in summer, but there is a clear paucity of information that demonstrates (1) selection (not simply use) of such areas, (2) a quantitative link to groundwater flow, or (3) whether such areas may be a limiting resource. The lake described above provides an ideal situation to study fine-scale thermal habitat selection, its link to groundwater flow, and the thermoregulatory behavior of a salmonine species under thermal stress. The aim of this field study is to investigate the relative importance of groundwater refuges and to speculate about the longer-term consequences of observed behavioral patterns to year-class strength.

The following predictions were tested: (1) young-of-year brook trout select habitats close to their thermal preference (~18°C; Coutant 1977) from spring through summer; (2) thermal habitat selection occurs at a microhabitat scale; (3) areas with high groundwater flow and cool water are inhabited by more trout than low-flow areas with warmer water; (4) sites with higher groundwater flow are more quickly reoccupied by fish after being displaced than sites with lower flow; and (5) fish defend cool microhabitats at the expense of daytime feeding, which may suggest that groundwater is a limiting resource.

### Methods

*Study site.*—Charles Lake is a small headwater lake with good visibility for behavioral observations (surface area = 12.3 ha, maximum depth = 8.2 m, Secchi depth = 6.4 m) located in Algonquin Provincial Park, Ontario, Canada (45°54'N, 78°43'W). The nearshore littoral zone is virtually devoid of woody debris and inundated shoreline vegetation; substrates comprise cobble, gravel, and sand with little organic matter and no aquatic macrophytes, in contrast with other lakes in the

area (P.A.B., unpublished data). Charles Lake supports a naturally reproducing population of brook trout which, despite previous stocking, closely resembles (genetically) indigenous brook trout populations in the area (Danzmann and Ihssen 1995).

Observations previous to this study, in 1993 and 1994, indicated that substantial numbers of young-of-year brook trout inhabited discrete shallow areas in the littoral zone of the lake during summer but were absent elsewhere in the littoral zone. Consequently, the study site was centered over these areas and extended to include adjacent areas inhabited by trout in spring (P.A.B., unpublished data). The study site encompassed a 120-m<sup>2</sup> area parallel to the shoreline which was overlaid with a 1 × 1 m grid of lead-core rope placed on the substrate (Figure 1).

*Thermal habitat selection.*—To describe the seasonal changes in spatial distribution and thermal habitat selection of brook trout, the presence of brook trout in each cell on the grid was recorded between 1100 and 1500 hours on May 6, 12, and 30 (spring samples), June 6 (early summer), and July 18 and 28 (summer), 1995. It was not possible to obtain reliable density estimates for the entire area because neither snorkeling nor shoreline observations would allow an approach close enough to estimate density without causing fleeing behavior and a redistribution of brook trout on the grid. Brook trout distribution (presence) during May and June was noted by a snorkeler at a distance of approximately 4 m from shore because the distribution of fish was generally restricted to within 2 m of the shoreline (see Results). Fish foraged actively in the water column during these months, as did fish observed in other lakes in the park (Biro and Ridgway 1995; Biro et al. 1997). In July, however, fish were observed farther from shore (>2 m), but only within the confines of the grid which allowed overhead observations to be made while slowly wading the perimeter of the grid and by walking the shoreline. Only brook trout that lay on the bottom were recorded as present within a cell so that data would not reflect moving fish in search of a site in which to settle. After these observations, the surface water temperature was measured ( $\pm 0.1^\circ\text{C}$ ) with a calibrated electronic thermometer. Next, bottom water temperature was measured only once within one centimeter of the substrate at the center of each cell on the grid by a snorkeler floating at the surface.

*Thermal microhabitat selection.*—To test the prediction that brook trout thermal habitat selection takes place at spatial scales smaller than the

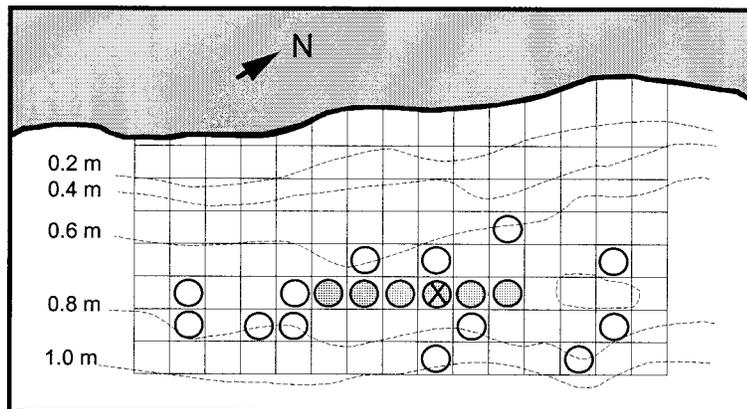


FIGURE 1.—The littoral study site in relation to the shoreline of Charles Lake, Ontario, showing depth contours; each cell represents 1 m<sup>2</sup>. Circles represent locations where groundwater flow was measured, shading indicates locations used in “latency to reoccupy” experiments, and the ‘X’ indicates the location of the reference seepage meter.

resolution of the study grid (1 m<sup>2</sup>), bottom temperatures where individual fish lay and at five adjacent locations within the same grid cell were recorded in six grid cells that were inhabited by fish on July 30.

*Trout abundance and groundwater seepage.*—To test the prediction that the abundance of brook trout is associated with cold groundwater seepage, the number of fish within a subset of grid cells was counted, and then bottom temperature and groundwater flow rate were measured in each cell. On July 31, a small stepladder was placed near an area with densities of fish previously estimated to vary from zero to as many as 15 fish/m<sup>2</sup>. One hour later, the observer carefully approached and sat on the ladder, waited 30 min, then counted the number of brook trout in all the cells within view. Immediately afterwards, bottom water temperatures were measured in each cell as previously described.

Groundwater flow rate (seepage) was measured with the same seepage meters and methods as described by Blanchfield and Ridgway (1996). Seepage meters are the ends of barrels that are pushed into and over the substrate and to which plastic bags are attached for collecting groundwater; they provide a direct measure of the upward flux of water at the substrate–water interface (Lee 1977). Seven seepage meters, 57 cm in diameter and 15 cm in height, were pushed into the substrate in the center of each cell to a depth of 7–10 cm on August 1 and were left overnight to equilibrate before samples were taken the following day. It was not possible to place seepage meters in all cells for which

there were density data due to the substrate in some cells preventing proper placement of the meters (i.e., poor seal). Seven samples were obtained on August 2 and six samples were obtained during each of the next 2 d; one seepage meter remained in place to check for daily variations in flow (Figure 1). All measurements were taken between 1200 and 1500 hours. The volume of water ( $\pm 1$  mL, graduated cylinder) collected in the bag after 30 min was used to calculate seepage flow rate (mL·m<sup>-2</sup>·min<sup>-1</sup>) by using the equation in Blanchfield and Ridgway (1996). Half-hour trials were appropriate given the high flow rates (Blanchfield and Ridgway 1996). The mean rate from three consecutive trials taken at each cell was used in analyses. Flow rates within cells and across days varied little with a coefficient of variation of only 6% within cells and 3% at the reference cell.

*Latency to reoccupy sites with manipulated topography.*—To investigate whether sites with greater groundwater seepage are more quickly reoccupied than sites with lower seepage (suggesting they are sought after), six cells with brook trout densities ranging from low to high were disturbed, and the latency for fish to reoccupy the sites (or occupy for the first time) was measured. The largely sand substrate in the six chosen sites (Figure 1) was flattened so that any differences among the sites should be due to differences in groundwater flow rate and not to topographic depressions which might hold pockets of cool water resistant to mixing with ambient lake water. Observations were made on July 31 from the same ladder and location as described above so that the

seepage flow estimates (all six sites measured August 2) could also be used for this experiment (Figure 1). Flattening the sites took 7 min to complete and insured that all fish had been excluded from these sites. Observations began immediately after the disturbance, and the number of fish within each cell was noted at 2-min intervals (scan sample) for the first 10 min and every 5 min for another 30 min (40 min, total observation).

To assess whether depressions accumulated cold water and influenced the distribution of brook trout within cells, as suggested from preliminary observations, a single trough-like depression ( $55 \times 9 \times 5$  cm) was excavated in the center of each cell and perpendicular to the shore immediately after the initial 40-min trial outlined above. This process took approximately 30 min to ensure uniformity among the troughs and was followed immediately by another 40 min of observations.

*Trout behavior.*—Brook trout were videotaped from above the water to assess whether the fish were defending cool microhabitats at the expense of feeding. A Sony<sup>TM</sup> Hi-8 video camera mounted on a tripod was used to videotape eight grid cells inhabited by fish on July 28–30. Trout fled upon approach by the video operator to set up the camera, but they did not go far and returned to their prior locations usually within 1 min. Behavior was quantified from the videotape following an initial 15-min period of taping. Videotapes were analyzed to obtain the proportion of time fish spent moving, the total time they spent in agonistic interactions, and the frequency of agonistic interactions and feeding attempts (Biro and Ridgway 1995; Biro et al. 1997). Time intervals that did not include agonistic or feeding behavior were used to calculate the proportion of search time spent moving, which included time spent searching for prey and scanning for potential competitors (McLaughlin et al. 1992; Biro and Ridgway 1995). Agonistic behavior was recorded when the focal fish either chased or was chased by a conspecific. Chases and nips were also observed during chases but were included with chases when recording data. More subtle agonistic displays, such as lateral displays, may have occurred, but it was not possible to detect them from the videotapes (Keenleyside and Yamamoto 1962). Feeding attempts were any sudden movement to intercept potential prey items (e.g., Grant 1990). It was not possible to distinguish on the videotape whether captured items were ingested or rejected, so feeding rate estimates may overestimate individual fish ingestion rates (Biro et al. 1996).

*Statistical analyses.*—Kolmogorov–Smirnov two-sample tests were used to determine if the frequency distributions of bottom temperatures used by brook trout were significantly different from those which were available. This test was used because the data were highly skewed, and this procedure is sensitive to the shape of the distribution and not highly influenced by location (Sokal and Rohlf 1981). Bottom temperatures were used in analyses throughout for consistency even though brook trout foraged in the water column during spring. This should not strongly affect the results because depths inhabited by trout in spring were generally less than 20 cm (see Figures 1, 2) and because surface and bottom temperatures in those areas were similar (see Results). Water levels rose in June, and consequently the sample size of available bottom temperatures was higher in summer than in spring. Linear regression was used to determine the influence of groundwater flow rate on bottom temperature and brook trout density. Trout density was  $\log_{10}(x + 1)$  transformed, and bottom temperatures were  $\log_{10}$  transformed to meet assumptions of normality for regression analyses; groundwater flow rate did not require transformation.

## Results

### *Thermal Habitat Selection*

Young-of-year brook trout were restricted in their distribution to areas within 2 m of shore throughout May (Figure 2A, B). Surface water temperatures in these areas averaged 13.0°C (SD = 0.10,  $N = 15$ ) on May 6, 15.5°C (SD = 0.17,  $N = 15$ ) on May 12, and 18.5°C (SD = 0.37,  $N = 22$ ) on May 30. On May 12, fish selected areas with the warmest of the available bottom temperatures ( $D_{\max} = -0.51$ ,  $P < 0.01$ ;  $N_{\text{used}} = 16$ ,  $N_{\text{avail}} = 112$ ) which were closest to their preferred temperature of 18°C (Figure 3A). Throughout May, fish foraged actively in the middle portion of the water column while closely following the shoreline, a behavior qualitatively similar to that observed in other Algonquin Park lakes in spring (Biro and Ridgway 1995; Biro et al. 1997).

On June 6, brook trout were observed as far as 4 m from shore although most sightings of trout were still within 2 m of shore (Figure 2C). At this time, surface water temperatures in areas within 1 m of shore ranged from 21.5°C to 23.5°C (mean temperature = 22.4°C,  $N = 15$ ). Fish again selected the warmest of the available bottom temperatures ( $D_{\max} = -0.41$ ,  $P < 0.001$ ;  $N_{\text{used}} = 35$ ,

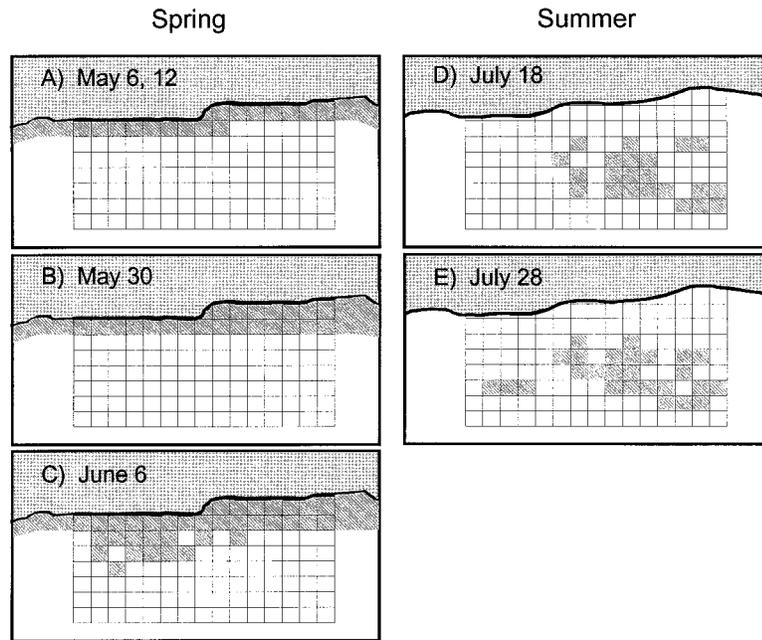


FIGURE 2.—Spatial distribution of young-of-year brook trout in the littoral zone of Charles Lake during (A, B) spring, (C) early summer, and (D, E) summer. Shaded areas indicate presence of trout; trout were also present outside the study site along the shoreline in spring. The study site is larger in summer due to higher water levels.

$N_{\text{avail}} = 112$ ) which were warmer than usually preferred even though temperatures closer to their preference were available nearby (Figure 3B). Those fish which were 3–4 m from shore were sedentary on or very near the bottom, whereas fish closer to shore were more active and moved about just above the bottom.

In July, brook trout were patchily distributed and lay on the bottom in discrete areas located 3–7 m from shore (Figure 2D, E). The areas used by fish were similar on July 18 and 28 but, in contrast with their spring distribution, no fish were observed within 2 m of shore (Figure 2). Mid-afternoon surface water temperatures across the grid on July 18 and 28 reached 24.5°C and 25°C, respectively. Fish selected the coldest of the available bottom temperatures on July 18 ( $D_{\text{max}} = 0.70$ ,  $P < 0.001$ ;  $N_{\text{used}} = 22$ ,  $N_{\text{avail}} = 120$ ) and on July 28 ( $D_{\text{max}} = 0.63$ ,  $P < 0.001$ ;  $N_{\text{used}} = 26$ ,  $N_{\text{avail}} = 120$ ). Brook trout were not frequently observed in areas where bottom temperatures exceeded 21°C in July, although a few were observed in areas with bottom temperatures as high as 25°C (Figure 3C, D) even though some cooler sites were left unoccupied.

#### Thermal Microhabitat Selection

Bottom temperatures at brook trout locations were significantly lower than at adjacent locations

within grid cells ( $D_{\text{max}} = -0.82$ ,  $P < 0.001$ ; 6 grid cells in total,  $N_{\text{trout}} = 20$ ,  $N_{\text{adjacent}} = 30$ ) and appeared to be associated with depressions in the substrate. Bottom temperatures averaged 18.3°C (SD = 2.14) at fish locations and 23.2°C (SD = 1.68) at adjacent locations on July 30 when the surface water temperature was 26.4°C.

#### Trout Abundance and Groundwater Seepage

Grid cells with greater numbers of fish also had cooler bottom temperatures and higher groundwater flow than areas with fewer trout on July 31. Areas with higher groundwater flow had cooler bottom temperatures than areas with lower groundwater flow ( $r = -0.71$ ,  $P = 0.001$ ,  $N = 19$ ). More importantly, groundwater flow rate explained 87% of the variation in trout density observed in this area ( $P < 0.001$ ,  $N = 19$ ; Figure 4). None of the sampled cells had zero seepage and the data suggest that a groundwater flow threshold of approximately 125 mL·m<sup>-2</sup>·min<sup>-1</sup> is required before trout will take up station (Figure 4).

#### Latency to Reoccupy Sites with Manipulated Topography

Only the site with the highest groundwater flow rate was quickly reoccupied by brook trout (within 2 min), and numbers continued to rise between 10

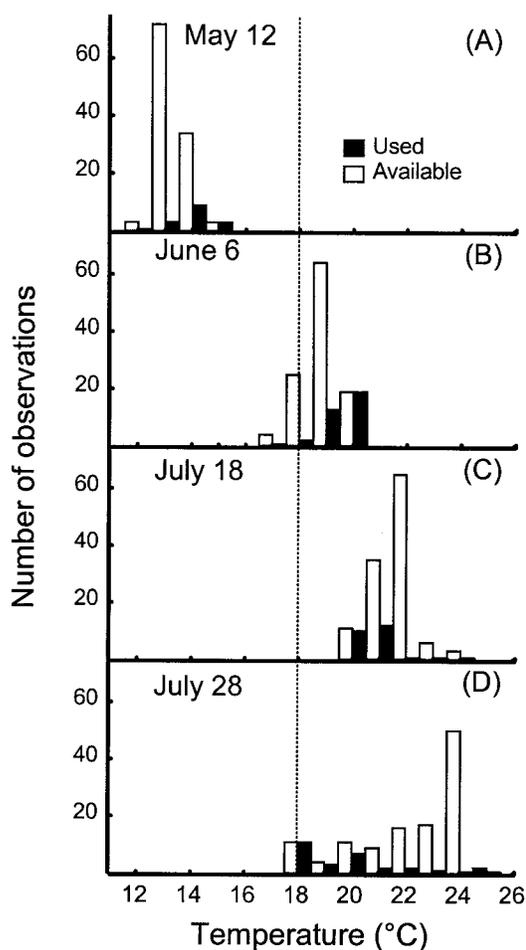


FIGURE 3.—Frequency distributions of bottom temperatures in used (solid bars) and available (open bars) cells in the study site from (A) spring through (B) early summer and (C, D) summer. Dotted line represents the approximate preferred temperature of 18°C for juvenile brook trout (Coutant 1977).

and 40 min following the flattening of the grid cells (Figure 5A). Those cells with lower groundwater flow took much longer to be reoccupied by fish, and sites with the lowest flow were not inhabited by fish, as prior to the manipulation (Figure 5A). Densities of brook trout were consistently lower than premanipulation densities in each site throughout the trial. Numbers of fish in each cell often fluctuated as the result of fish settling to a cell and then moving away shortly after, indicating that site selection is a sampling process (Figure 5A).

The addition of a depression to each cell recruited higher densities of brook trout more quickly, in general, than in the previous trial despite the

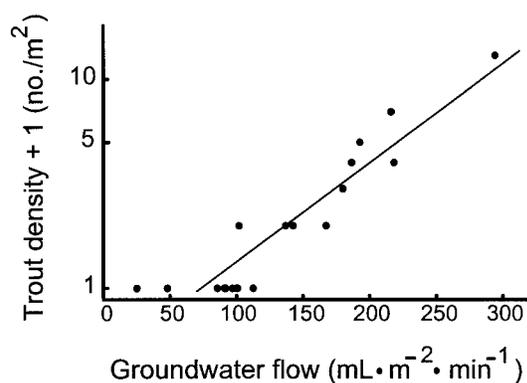


FIGURE 4.—Brook trout density versus groundwater flow rate on July 31. Solid line represents the least-squares regression,  $\log_{10}(\text{density} + 1) = 0.00485(\text{flow}) - 0.368$ .

30 min of disturbance required to setup this second trial (Figure 5B). Further, those cells with higher groundwater flow recruited more fish faster than those with lower flow; final densities of brook trout were higher in three of the four cells which had trout in them prior to manipulations (Figure 5B). The two cells with lowest groundwater flow did not recruit trout to them (Figure 5B).

#### Trout Behavior

Behavioral observations made at eight grid cells on July 28–30 indicated that brook trout were generally sedentary and lay at the bottom with the caudal and pectoral fins, and sometimes the abdomen, touching the substrate. Fish spent a low proportion of time moving (mean proportion = 0.25), and only three individuals spent more than half of the time moving (Figure 6). Active individuals often entered the field of view, remained sedentary for a short while, and then left voluntarily or were expelled by an aggressive conspecific already present. Fish were observed for periods ranging from 0.2 min for the most active trout to 11 min for sedentary fish (mean observation duration = 2.74 min, SD = 2.7,  $N = 26$ ). Agonistic interactions were common and occurred in almost 70% of observations (18/26). Overall, trout spent about 8% of the time (6 of 71 min total observation time) engaged in agonistic interactions with conspecifics. Aggressive fish typically defended from a central place (returned to the same place on the substrate) which was often a small depression. Use of groundwater seepage areas by trout appeared to be at the expense of daytime feeding because only two individuals attempted to capture prey and ex-

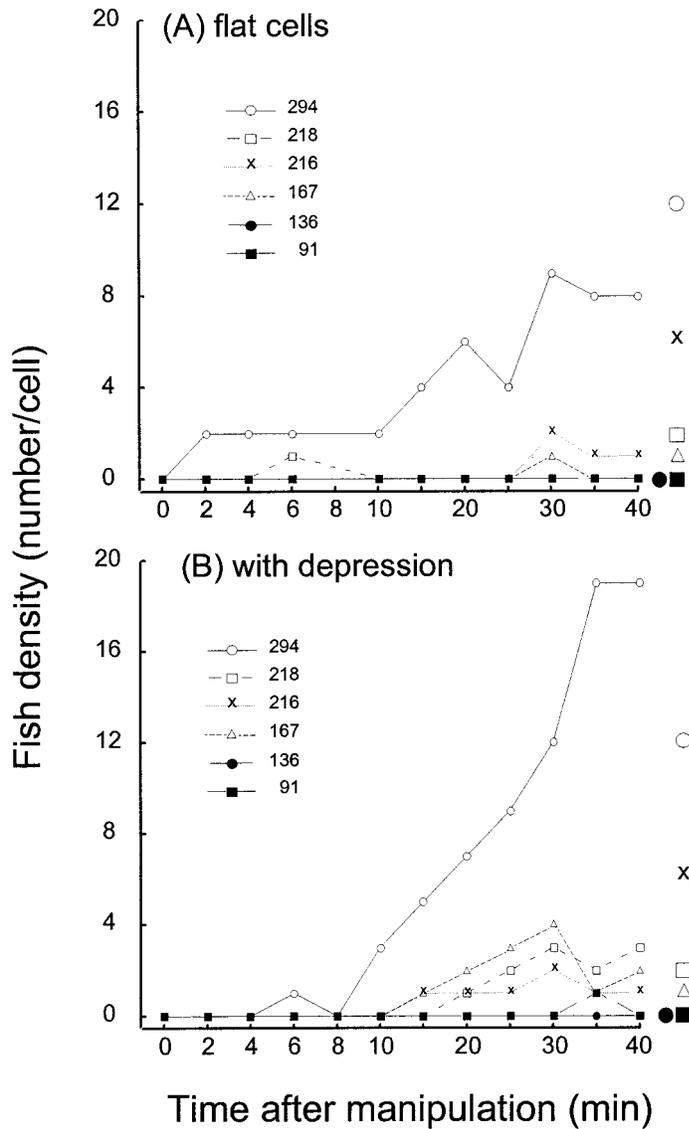


FIGURE 5.—Density of brook trout as a function of time on July 31 for six sites (grid cells) following disturbance by (A) flattening substrate to remove effects of topography and (B) introduction of a single elongate depression in each. Symbols with corresponding numeric values indicate groundwater flow rate measured at each cell. Enlarged symbols in the right-hand margin of each plot represent the trout densities in each site prior to any manipulations.

perienced low foraging attempt rates (<1 attempt/5 min).

**Discussion**

Young-of-year brook trout in Charles Lake moved from areas adjacent to shore in May and early June to discrete areas with cool bottom water (several meters from shore) when ambient water temperatures neared their lethal limit in July. In these areas, brook trout selected cool microhabitats

within a given square-meter area. Areas with greater groundwater flow were associated with cooler bottom temperatures and significantly higher densities of brook trout. In addition, areas with greater groundwater seepage were reoccupied by brook trout sooner and in greater numbers than areas with low groundwater seepage. Behavioral evidence suggests that microhabitats with cool groundwater may be aggressively defended at the expense of daytime feeding, indicating that groundwater in-

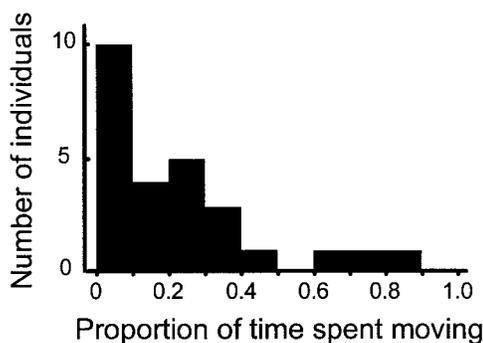


FIGURE 6.—Frequency distribution of the proportion of time spent moving by young-of-year brook trout ( $N = 26$ ) in Charles Lake.

puts may be a limiting resource at the scale of this study.

Brook trout did not consistently select areas with bottom temperatures near their preferred temperature of  $\sim 18^{\circ}\text{C}$  (Coutant 1977). From May to early June, trout used areas immediately adjacent to the shoreline and thereby selected the warmest of the available water temperatures even when bottom temperatures were at their upper thermal tolerance of  $20^{\circ}\text{C}$  (Fry et al. 1946; McCormick et al. 1972). In July, trout selected the coldest of the available bottom temperatures in discrete areas located 3–8 m from shore at a time when shoreline bottom, and ambient surface, water temperatures exceeded  $25^{\circ}\text{C}$ . These results are consistent with previous studies that have shown young-of-year brook trout to aggregate in discrete coldwater areas when ambient water temperatures rise above  $20^{\circ}\text{C}$  in lakes (Griswold 1967; Wurtsbaugh et al. 1975) and in streams (Elson 1942; Fry 1951; Gibson 1966).

Predation risk may have restricted young-of-year brook trout to warm nearshore areas in early summer (e.g., Tabor and Wurtsbaugh 1991). It is not uncommon to observe adult brook trout attempting to cannibalize their young in spring in this lake (P.A.B., personal observation), and cannibalism by brook trout in small lakes has been confirmed (Griswold 1967). Later, warm water temperatures may drive adult brook trout from the shallows, reducing predation risk, and allow young-of-year brook trout to move farther from shore to areas with groundwater seepage (this study) or to migrate to deeper habitats (Venne and Magnan 1995).

At the spatial resolution within the study grid, it is apparent that young brook trout select cold seepage areas at a relatively fine spatial scale.

However, not all of the coldest cells were used by trout in July, whereas some cells with bottom temperatures as high as  $25^{\circ}\text{C}$  were used. This anomaly, of course, is a reflection that bottom temperatures were measured at the center of each grid cell even though, in some instances, trout lay in peripheral areas which were cooler within a cell. Indeed, bottom temperatures were significantly cooler where trout lay on the bottom than in locations without trout; this observation illustrates the need to carefully consider the spatial resolution of measurements in future field studies of behavioral thermoregulation by young salmonines.

Coldwater areas used by brook trout were clearly linked to groundwater seepage. Areas with greater groundwater flow had cooler bottom water temperatures. Most importantly, however, groundwater flow rate accounted for 87% of the variance in trout density for a subset of cells within the littoral study site. Previous studies have noted the use of coldwater areas by salmonines in summer and some have made qualitative links to groundwater inflow (e.g., Griswold 1967; Wurtsbaugh et al. 1975; Nielsen et al. 1994; Snucins and Gunn 1995; Matthews and Berg 1997), but this study has established a quantitative link between groundwater flow and the distribution and abundance of a salmonine species under stressful thermal conditions. This link is crucial because it provides a solid basis for management recommendations to ensure that such areas are not affected by logging or development in situations where they are shown to be (or strongly suspected) important to overall young-of-year salmonine survival. Unfortunately, this study does not have data to draw any conclusions about the importance of this area to the overall survival of young-of-year brook trout in this lake. However, it is possible that this area, and another tiny area nearby (see below), provide refuge for a substantial portion of the cohort that survive to summer. This additional littoral refuge, where a small spring flows very slowly into a small shoreline indentation, has consistently (1993–1995) been inhabited by 100–200 young-of-year brook trout holding station on bottom in an area of only 2 to 3  $\text{m}^2$  (Figure 7). Bottom water temperatures range from  $13^{\circ}\text{C}$  to  $17^{\circ}\text{C}$  within the inlet, while surface water temperatures just 3–8 cm above the backs of the fish were  $23$ – $25^{\circ}\text{C}$  on July 27; few, if any, trout were present outside this tiny cool area. This is an extreme example of a thermal refuge and illustrates that small and easily overlooked groundwater inputs may provide refuge for substantial numbers of fish.



FIGURE 7.—Photograph taken at a spring inlet near the study site in Charles Lake on July 29. Shown are 80 fish holding station in an area less than  $1 \text{ m}^2$  in a very slight current on bottom (determined by releasing a few silt particles into the water column). Bottom and surface water temperatures were  $15^\circ\text{C}$  and  $23.5^\circ\text{C}$ , respectively; depth of water column was 7 cm.

Brook trout quickly reoccupied areas with high groundwater flow, suggesting that such areas are a preferred resource. After controlling for topography among the sites (flattening), brook trout densities were consistently lower within each site than prior to flattening. The addition of a depression to each cell resulted in brook trout densities that were higher than in their natural state, and those with greater seepage were most quickly reoccupied and reached higher final densities than sites with lower seepage. In addition, fish were restricted in their distribution to within the depression in each cell. These results suggest that depressions either act to slow the mixing rate of groundwater with lake water, locally enhance groundwater flow into them due to reduced resistance to flow, or provide some concealment from predators. Numbers of fish in each cell fluctuated in both trials, indicating that fish either were moving back and forth, perhaps sampling various locations for cool water, or were displaced from a previous location due to crowding or aggression.

Many brook trout were sedentary on the bottom and aggressively defended sites from a central place but did not feed during the day (only two individuals made a single foraging attempt each). This observation contrasts dramatically with the

spring foraging behavior of young-of-year brook trout in Charles Lake (personal observation) and other Algonquin Park lakes, where fish tend not to be aggressive, are highly active, range widely while foraging, and make frequent foraging attempts (Biro 1996; Biro and Ridgway 1995; Biro et al. 1997). This seasonal difference suggests that trout may be defending very small areas (often small depressions, see above) of cold groundwater, rather than food resources, from conspecifics. Clearly, the data supporting these conclusions are limited and further study would be needed to confirm them. However, this study does appear to present some of the first field data to support the notion that temperature is a consumable and competitively guarded resource (Magnuson et al. 1979). For instance, Beitinger and Magnuson (1975) and Beitinger et al. (1975) found that larger dominant fish tended to occupy areas of their preferred temperature and exclude smaller individuals to less preferred temperatures in laboratory experiments. Perhaps the small number of active fish in my sample had been aggressively excluded from areas with cold water by trout with prior short-term residence. Active fish would often swim to a location and settle to the bottom for a moment before mov-

ing on to another location, suggesting that they were searching for cool sites in which to settle.

How these young brook trout trade off lost foraging opportunities with thermoregulation will require further study. It is certainly possible, if not likely, that feeding takes place at night when water temperatures are lower, or perhaps the few active fish observed in the littoral site were making short ventures away from seepage areas to feed. Investigation into the effects of groundwater flow variability on the aggressiveness and densities of fish under more controlled conditions would be extremely informative. Finally, future studies should attempt to ascertain the importance of coolwater refuges to the bioenergetics, growth, and ultimately survival and year-class strength of coldwater fishes in temperate lakes.

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