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Thermal Characteristics of Wisconsin Headwater Streams Occupied by Beaver: Implications for Brook Trout Habitat

GIL MCRAE[1]

Minnesota Cooperative Fish and Wildlife Research Unit[2]
University of Minnesota Department of Fisheries and Wildlife
1980 Folwell Avenue, St. Paul, Minnesota 55108, USA

CLAYTON J. EDWARDS

U.S. Forest Service, North Central Forest Experiment Station
Post Office Box 898, Rhinelander, Wisconsin 54501, USA

Abstract.—Expansion of populations of beaver *Castor canadensis* in northern Wisconsin has raised concerns over warming of coldwater fish habitats as a result of impoundments created by the mammals. We examined temperature with a network of electronic thermographs that recorded hourly water, air, and soil temperatures on four headwater streams occupied by beaver during summer 1990 and 1991. Stream temperatures followed air temperatures, even near groundwater sources. There was no consistent relationship between size or number of beaver impoundments and the degree of downstream warming. Large impoundments, although often warming downstream temperatures slightly, dampened temperature fluctuations immediately downstream. Local groundwater inflow and vegetative and topographic shading also dampened warming by impoundments. Several beaver impoundments were removed to evaluate ensuing temperature changes. Removal of beaver dams did not generally reduce the difference between upstream and downstream temperatures; in some cases dam removal increased the warming rate. Direct thermal benefits of dam removal in headwater streams may be outweighed by the potentially disruptive effects on the composition of fish and invertebrate communities downstream. It is suggested that management focus on relating topographical and geographical attributes to the potential for substantial groundwater discharge and to suitable summer temperatures for coldwater species such as brook trout *Salvelinus fontinalis.*

Maximum summer water temperature is the single most important factor limiting the geographic distribution of brook trout *Salvelinus fontinalis* (MacCrimmon and Campbell 1969). In Wisconsin, at the southern edge of the brook trout's endemic range, thermal constraints restrict the species to headwater streams, where they rely on groundwater discharges for maintenance of suitable temperatures (Becker 1983; Meisner 1990). Habitat destruction due to logging, agricultural development, and pollution, and the subsequent stocking of more tolerant brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss,* have further restricted the range of brook trout in the state (Brasch et al. 1958; Avery 1983). The proximity and abundance of aspen *Populus tremuloides,* a tree species that rapidly becomes established following the removal of old-growth forests (Barnes and Wagner 1981), provides habitat for beaver *Castor canadensis,* and beaver have responded by colonizing headwater streams in large numbers (Avery 1992). Beaver impoundments provide habitat for other wildlife, particularly waterfowl (Renouf 1972; Brown and Parson 1979).

Warming of downstream reaches by beaver ponds is commonly cited as a detrimental effect of beaver on trout populations (Knudsen 1962; Avery 1992). Stream temperatures were typically not the primary interest in studies of beaver and trout interactions, however, and the literature has established no clear relationship between different sizes or numbers of impoundments and the degree of stream warming. After removal of beaver dams on a headwater stream in northeastern Wisconsin, Avery (1992) observed 0.6°C (after 1 year) and 2.5°C (after 4 years) reductions in the difference between peak summer temperatures at stations in the headwaters and those at the mouth. Evans (1948) measured temperatures at the inlets and outlets of beaver ponds in northeastern Minnesota during July and 1 week in August. Of the 10 ponds included in the study, eight had higher temperatures at the outlet than at the inlet (increases of

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[1] Present address: Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695-7617, USA.

[2] Cooperators: Minnesota Department of Natural Resources, National Biological Survey, University of Minnesota, and the Wildlife Management Institute.

3–14°C), but two ponds had consistently lower temperatures at the outlet than at the inlet; decreases were ascribed to the shading effect of vegetation overhanging the outlet. Rupp (1954) compared water temperatures before and after beaver dam removal in and at two distances downstream from five beaver ponds on Sunkhaze Stream, Maine. He recorded average surface water decreases of 7.2°C at the pond sites, 6.7°C at 46 m downstream from the dams, and 2.8°C at 402 m downstream from the dams. Patterson (1951) collected temperatures in August 1949–1950 at the outlets of nine tributaries to the Peshtigo River, Wisconsin, including two streams (Rock and Halley Creeks) in our study. The streams containing beaver ponds averaged 6.7°C warmer than streams without ponds. The streams without ponds were shorter (mean length, 1.9 km) than those with ponds (mean length, 4.8 km); shorter spring streams are more likely to be influenced by groundwater and less likely to be warmed before reaching the mouth (Ward 1985). Salyer (1935) observed that beaver ponds of 0.2 ha or more in northern Michigan often caused a rise in the temperature of a stream, but that elevated temperatures rarely persisted more than 400 m downstream from the pond.

We conducted a detailed temperature study on four headwater streams in northern Wisconsin occupied by beaver with the following objectives: (1) to examine the relationship between air, soil, and stream temperatures; (2) to evaluate the thermal effects of existing beaver impoundments; and (3) to evaluate the effect of dam removal on stream temperatures. Our analyses focused on within-year comparisons to provide insight regarding thermal habitat suitability for brook trout in terms of the species' lethal temperatures, preferred temperatures and metabolic optima (Fry 1971).

Study Site

Four streams were examined in the Peshtigo River watershed in the Nicolet National Forest in northeastern Wisconsin (Figure 1). Rock Creek is predominantly a sedge meadow (*Carex* sp.) and lowland shrub stream divided into east and west branches, with a total stream length of 11 km. The creek flows through a wide valley (0.25–0.75 km) over much of its length with an average gradient of 2.4 m/km. In June 1991, the average maximum depth in Rock Creek (exclusive of impoundments) was about 0.5 m, and average discharge near the mouth was 0.2 m^3/s. The entire watershed (17 km^2) is forested with a mixture of hardwoods and conifers; aspen is particularly abundant in most areas. Beaver have been reestablished in Rock Creek since the early 1950s (Patterson 1951); in 1990–1991, several large beaver ponds were present on both branches. In 1990, the west branch contained one 9-ha pond and an additional dam which, despite having been recently breached, impounded a small pool. The east branch had four major impoundments. The two uppermost dams impound 3–5 ha each; two large ponds (10–12 ha each) occupied much of the middle portion of the east branch (Figure 1).

Halley Creek flows through a relatively narrow valley (average gradient, 2.5 m/km) and is well shaded over much of its 7.6-km length (Figure 1). In June 1991, maximum depth was about 0.3 m (exclusive of impoundments), and average discharge at the mouth was 0.2 m^3/s. The vegetative cover consists of mixed hardwoods and conifers, and aspens are abundant near the stream. Between study sites H4 and H6, the valley widens considerably and there is little vegetative canopy. Portions of Halley Creek upstream from the uppermost impoundment had no surface water flow after mid-July, although flow was substantial in May and early June. Numerous springs enter Halley Creek, several of which flow intermittently above ground through dense stands of northern white cedar *Thuja occidentalis* before reaching the stream.

No Name Creek 1 (average gradient, 3.3 m/km) flows into the Rat River and was sampled only during 1991 (Figure 1). The creek is 1.6 km long and was dominated by a 12-ha beaver pond immediately upstream of site N1A. Upstream from this pond, the stream is rarely confined to the channel and is extensively braided.

No Name Creek 2 (average gradient, 3.0 m/km) empties into Otter Creek and was also sampled only in 1991. The creek is 3.2 km long and well shaded only in the vicinity of site N2A; there is little vegetative shading over the remainder of the creek due to a sequence of four beaver ponds between sites N2A and N2C (Figure 1).

There were resident brook trout populations in Rock and Halley creeks, according to unpublished electrofishing surveys conducted by the Wisconsin Department of Natural Resources (WDNR) in 1985–1986 and the U.S. Forest Service in 1992–1993. Most brook trout in Rock Creek were found above the uppermost dam on the east branch and near the mouth. Brook trout were found throughout the middle and lower sections of Halley Creek. No other salmonids were found in these surveys

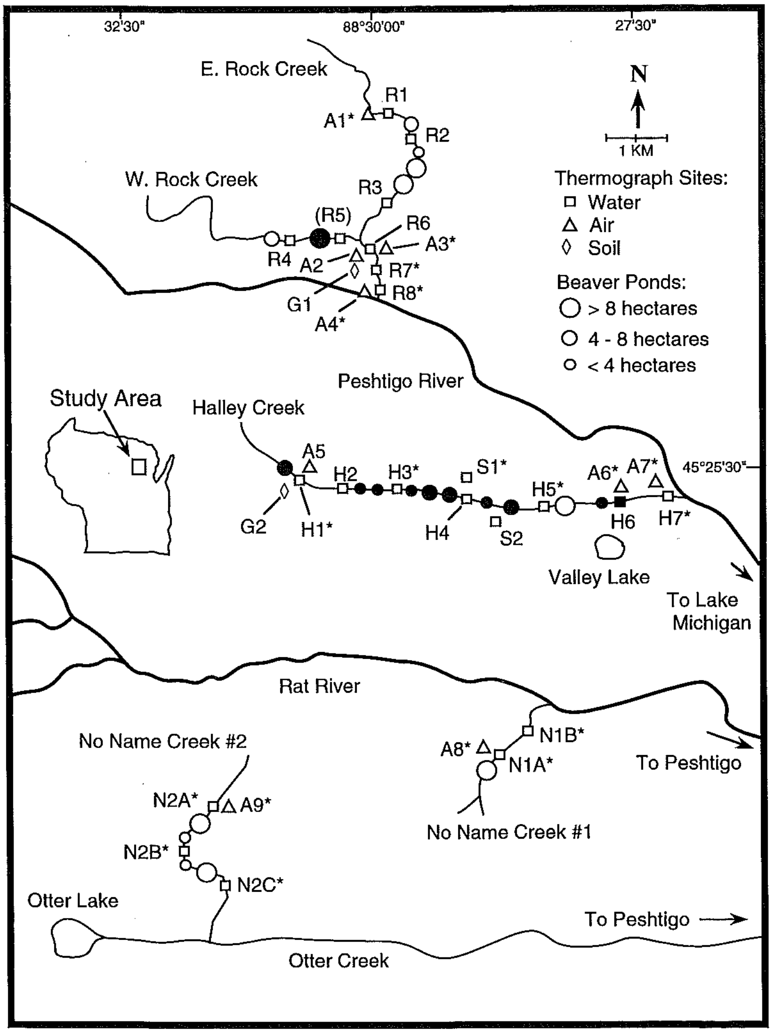

FIGURE 1.—Beaver impoundments and thermograph locations in the Nicolet National Forest, Wisconsin. Sites enclosed in parentheses were sampled only in 1990; those with an asterisk were sampled only in 1991. Blackened impoundments were removed.

and fisheries information was not available for the other two study streams. There is no record of stocking in any of the four streams, but brook trout, brown trout, and rainbow trout have been stocked in the Peshtigo River (WDNR 1980). Fishing pressure has been low on all the study streams due to limited access.

Methods

Data collection and estimation.—Temperatures were collected with chart-type thermographs (Ryan model J-90) and electronic recording thermographs (Ryan model RTM dataloggers) programmed for 1-h sampling intervals. The chart-type thermographs were used on Rock Creek (stations R1–R6) in 1990, whereas the remainder of the data were collected with dataloggers. Both types of thermographs were accurate to 0.3°C, according to laboratory calibrations, and recorded to the nearest 0.1°C.

Thermographs were placed in steel canisters on the stream bottom generally immediately upstream and downstream of beaver impoundments (Figure 1). The lack of a well-defined stream channel often caused us to include areas of braided stream as well as one or more beaver ponds between upstream and downstream thermograph pairs. Soil temperature measurements were taken at two stations during 1990–1991, one at lower Rock Creek and the other at upper Halley Creek (Figure 1); thermistors were inserted 1 m below ground level in a well-shaded area along each stream. Air temperatures were recorded by thermistors attached to the north side of a tree or shrub 1 m above ground level close to the stream monitored.

Combined topographic and vegetative shading (percent) was estimated with the stream segment shade model developed by Bartholow (1989). Based on the output of the shade model, each air and stream site was classified into one of four shade categories: A = 0–24%, B = 25–49%, C = 50–74%, and D = 75–100%. The model uses latitude, stream azimuth, stream width, topographic angle, and several vegetation-related variables (height, crown, offset, density) as input variables. Stream lengths and stream azimuths, which refers to the general orientation of a stream reach with respect to due south (Bartholow 1989), were measured from 7.5-minute topographic maps. Impoundment areas were estimated from a combination of field observations and high-resolution aerial photographs. Meteorological data were obtained from a U.S. Forest Service weather station (monitored daily at 1300 hours) 15 km northwest of the study area. Stream flow was calculated from stream morphology data and velocities measured with a Marsh–McBirney velocity meter by the method of Platts et al. (1983). The remaining input variables were measured or estimated in the field according to methods described by Bartholow (1989).

On August 14–15, 1990, one dam immediately upstream of site R5 on Rock Creek was removed with explosives and 12 smaller dams (generally less than 3 m wide × 0.5 m high) were removed by hand between sites R5 and R6. Between July 15 and July 17, 1991, 36 beaver dams were removed with explosives from Halley Creek, and several smaller dams, many of which had been submerged in the ponds, were removed by hand. The impoundment immediately downstream of site H5 (Figure 1) was the only beaver pond left undisturbed on Halley Creek. Beaver were kept off both Rock and Halley Creeks during the study period by trapping.

Four temperature ranges were defined to assess thermal habitat suitability for brook trout (Raleigh 1982): a lower range (<11°C), an optimal range (11–16°C), an upper range (17–23°C), and a lethal range (≥24°C). The total number of hours in which stream temperatures fell into each of these ranges was calculated for each stream and spring station.

Water–air–soil temperature associations.—The relationship between air, stream, and soil temperatures was examined through multiple-correlation analyses with 1991 data and subsequent testing with an *F*-test. The 1991 data were more suitable for these analyses because air temperatures were available from several sites with varying degrees of shading. Local differences in air temperature were taken into account in the correlation analyses by grouping each water station with an air station of similar characteristics (shade category and elevation).

Water temperature extremes typically lag 1–4 h behind air temperature extremes due to the high specific heat of water relative to that of the atmosphere (Ward 1985). We characterized the delayed response of water temperature to air temperature by calculating coefficients of determination between air temperatures and water temperatures lagged by successive 1-h intervals. The lag corresponding to the maximum coefficient of determination for the water–air relationship (i.e., the magnitude of the phase shift between the two temperature traces) was used as a measure of the responsiveness of the stream to air temperature at a particular site. Smaller phase shifts indicated that water temperature patterns closely mimicked air temperature patterns. The hourly water temperature data were then shifted backwards from 0000 h by the amount of the phase shift, and 24-h means were calculated from the shifted "daily" temperatures. These shifted 24-h-period means were used in the correlation analyses with unlagged daily mean air and daily mean soil temperatures as independent variables. Means from a 24-h period, rather than hourly temperatures or 24-h maxima, were used in the correlation analyses for the following reasons. First, hourly temperature data exhibit a strong systematic effect (a characteristic sinusoidal daily pattern) that can affect the precision of the estimated regression coefficients. Secondly, although daily maximum stream temperatures are more important than daily means in regard to coldwater fish habitat, we considered daily means more appropriate for use in correlation analyses because the relationship between daily maximum stream temperature and air temperature is nonlinear (Theurer et al. 1984).

Temperature patterns and dam removal effects.—Three response variables—daily mean temperature, daily maximum temperature, and the noon rate of heating (°C/h; see definition below)—

were used to examine temperature patterns among water stations on each creek and water temperature changes associated with dam removal. These means were not the phase-shifted means used in the correlation analyses, but those calculated from midnight to midnight. In addition, the differences (downstream minus upstream) in the three response variables associated with station pairs were also used as response variables. Each station pair was formed from thermographs separated by different distances and numbers of impoundments (Table 1). Daily mean and maximum air temperatures were used as response variables to examine differences associated with air temperature stations. To control for day-to-day variation, we used blocked analyses of variance (ANOVA, with days as blocks) to quantify relationships among stream and air temperature sites. Following ANOVA, all pairwise differences were subjected to the Bonferroni significant difference test (BSD; Miller 1981).

Temperature changes associated with dam removal were examined with two sets of two-way factorial ANOVAs. The first assessed the impact of dam removal on the sites along Halley and lower Rock Creeks by fitting separate sets of $n \times 2$ factorial models (n sites $\times$ 2 treatments [before and after dam removal]) for each creek with the three response variables mentioned above. The second assessed the impact of dam removal on the differences (downstream minus upstream) in the three response variables associated with four station pairs on Halley Creek (Table 1). This second set of ANOVAs, for which the differences associated with the station pairs were response variables, consisted of three 4×2 factorial models (4 station pairs $\times$ 2 treatments). Analyses were conducted with the SAS®[3] System, and statistical significance was assessed at $P \leq 0.05$ for all tests.

Modeling of daily stream temperature cycles.—Daily stream temperature typically follows a sinusoidal pattern due to the high specific heat of water, which buffers against rapid temperature fluctuations. A sinusoidal time series model (Bingham et al. 1982; Chatfield 1989) was used to describe this diel pattern. Hourly stream temperatures were modeled as

$$y_i = M_j + \sum_{i=0}^{23} A_j \cos(\omega t_i + \phi_j) + e_i; \qquad (1)$$

y_i = water temperature at hour i;
M_j = daily mean water temperature for day j;
A_j = amplitude of temperature variation for day j (roughly one-half the range);
ω = angular frequency (radians);
t_i = hour ($i = 0, 1, \ldots, 23$);
ϕ_j = acrophase or time of maximum temperature on day j;
e_i = random error.

Substituting $\omega = 2\pi/24$, the frequency corresponding to a period of 24 h, and expanding the cosine term allows expression of equation (1) in linearized form:

$$y_i = M_j + \sum_{i=0}^{23} \left[A_j \cos\left(\frac{2\pi}{24} t_i\right) + \cos(\phi_j) \right] - \left[A_j \left(\sin \frac{2\pi}{24} t_i \right) + \sin(\phi_j) \right] + e_i. \qquad (2)$$

Equation (2) may then be rewritten by substituting

$$x_i = \cos\left(\frac{2\pi}{24} t_i\right),$$

$$z_i = \sin\left(\frac{2\pi}{24} t_i\right),$$

$$\beta_j = A_j \cos(\phi_j),$$

and

$$\gamma_j = A_j \sin(\phi_j),$$

and adding an additional term (λv_i, where $v_i = t_i - 11.5$) that forces each daily temperature trace to match up more closely that of the next day. In simplified notation, the final model has the form

$$y_i = M_j + \lambda v_i + \beta x_i + \gamma z_i + e_i. \qquad (3)$$

TABLE 1.—Distances between stations and total areas of beaver impoundments associated with thermograph station pairs on four northern Wisconsin streams. Site locations appear in Figure 1.

Station pair	Distance between stations (km)	Impounded area (ha)	Shade categories[a]
R2-R1	0.8	6	A-B
R3-R2	1.4	19	A-A
R5-R4	0.8	8	A-A
H3-H2	0.8	7	C-C
H4-H3	1.3	15	A-C
H5-H4	1.5	13	A-A
H6-H5	1.3	10	A-A
N2B-N2A	0.9	14	A-D
N2C-N2B	1.3	16	A-A

[a] Categories: A, 0–24%; B, 25–49%; C, 50–74%; D, 75–100%.

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[3] Reference to trademarks and trade names of manufacturers does not imply government endorsement of commercial products.

TABLE 2.—Correlations of lagged water temperatures with air and soil temperatures at each stream thermograph site for 1991. The phase shifts indicate the number of hours water temperature was lagged to achieve maximum R^2 in the water–air correlation, and they include differences in sampling times. All R^2 values are significantly different from zero (F-tests, $P < 0.05$) except those shown as NS.

Station combination							
Water	Air	Soil	Period of record	Phase shift (h)	Air partial R^2	Soil partial R^2	Multiple R^2
R1	A1	G1	Jul 19–Aug 05	2.3	0.85	0.05	0.90
R2	A3	G1	Jul 18–Sep 15	3.5	0.79	NS	0.79
R3	A3	G1	Jul 18–Sep 15	4.6	0.59	NS	0.59
R4	A3	G1	Jul 18–Sep 15	4.6	0.08	0.30	0.38
R6	A3	G1	Jul 18–Sep 15	3.7	0.68	NS	0.68
R7	A2	G1	Jun 22–Sep 15	3.7	0.72	0.07	0.79
R8	A4	G1	Jul 18–Sep 15	1.8	0.75	NS	0.75
H1[a]	A5	G2	Jun 05–Jul 14	4.1	0.47	0.28	0.76
H1[b]	A5	G2	Jul 18–Aug 19	5.1	0.48	NS	0.48
H2[a]	A5	G2	Jun 05–Jul 14	4.3	0.46	0.27	0.74
H2[b]	A5	G2	Jul 18–Aug 19	4.3	0.42	NS	0.42
H3[a]	A5	G2	Jun 05–Jul 14	3.9	0.22	NS	0.22
H3[b]	A5	G2	Jul 18–Aug 19	2.9	0.24	NS	0.24
H4[a]	A5	G2	Jun 05–Jul 14	3.4	0.47	0.23	0.70
H4[b]	A6	G2	Jul 19–Aug 19	1.2	0.18	NS	0.18
H5[a]	A5	G2	Jun 05–Jul 14	3.1	0.78	0.04	0.82
H5[b]	A6	G2	Jul 19–Aug 19	1.9	0.49	NS	0.49
H6[a]	A5	G2	Jun 05–Jul 14	2.5	0.80	NS	0.80
H6[b]	A6	G2	Jul 19–Aug 19	8+[c]	0.57	0.16	0.73
H7[a]	A5	G2	Jun 05–Jul 14	2.8	0.84	NS	0.84
H7[b]	A7	G2	Jul 18–Aug 05	1.7	0.78	NS	0.78
S1[a]	A5	G2	Jun 30–Jul 14	1.1	0.66	NS	0.66
S1[b]	A6	G2	Jul 19–Aug 19	0.1	0.67	NS	0.67
S2[a]	A5	G2	Jun 05–Jul 14	1.4	0.65	NS	0.65
S2[b]	A5	G2	Jul 18–Aug 19	1.4	0.71	0.12	0.84
N1A	A8	G2	Aug 07–Sep 15	1.5	0.73	NS	0.73
N1B	A8	G2	Aug 07–Sep 15	0.8	0.78	NS	0.78
N2A	A9	G2	Aug 07–Sep 15	1.7	0.82	0.06	0.88
N2B	A9	G2	Aug 07–Sep 15	6.6	0.51	NS	0.51
N2C	A9	G2	Aug 07–Sep 15	3.3	0.34	NS	0.34

[a] Before dam removal.

[b] After dam removal.

[c] The water–air R^2 at this site increased as lags increased from 0 to 8 h; statistics listed are for the 8-h lag.

Using equation (3), we estimated the rhythm characteristics (the set of coefficients λ, β, and γ describing the shape of the temperature trace) for each day by ordinary least-squares regression. Thus the shape of the temperature pattern for day j at any given location is accurately characterized, and the temperature (y_i) at any hour (t_i) may be approximated from the ordinary least-squares estimators of λ, β, and γ. Hourly temperatures approximated with equation (3) rarely differed more than 0.1°C from the observed temperatures. Besides simplifying data visualization and management, the time series model also allowed us to calculate a rate of heating at any given hour by taking the first derivative of equation (2) with respect to t_i (dy/dt), which is equivalent to the slope of the line tangent to the temperature curve at hour i. We chose to use the rate of heating at solar noon (midway between sunrise and sunset) as a variable for comparison among stream thermograph sites, because the rate of temperature change was usually near its maximum at that time.

Results

Water–Air–Soil Temperature Associations

Although there was little variability in mean daily air temperatures among the nine air stations (mean, 16.5°C; SD, 0.69) during mid-July to mid-September 1991, there were significant differences in daily maximum air temperatures (F-test; $P < 0.0001$) associated with shading differences. Mean daily maxima at air sites in shade categories A and B (sites A1, A3, A6, and A7) were more than 2°C higher than those in shade categories C and D (sites A2, A4, A5, A8, and A9). Soil temperatures remained within a range of 12–14°C for much of summer 1991; site G1 averaged about 0.5°C cooler than site G2.

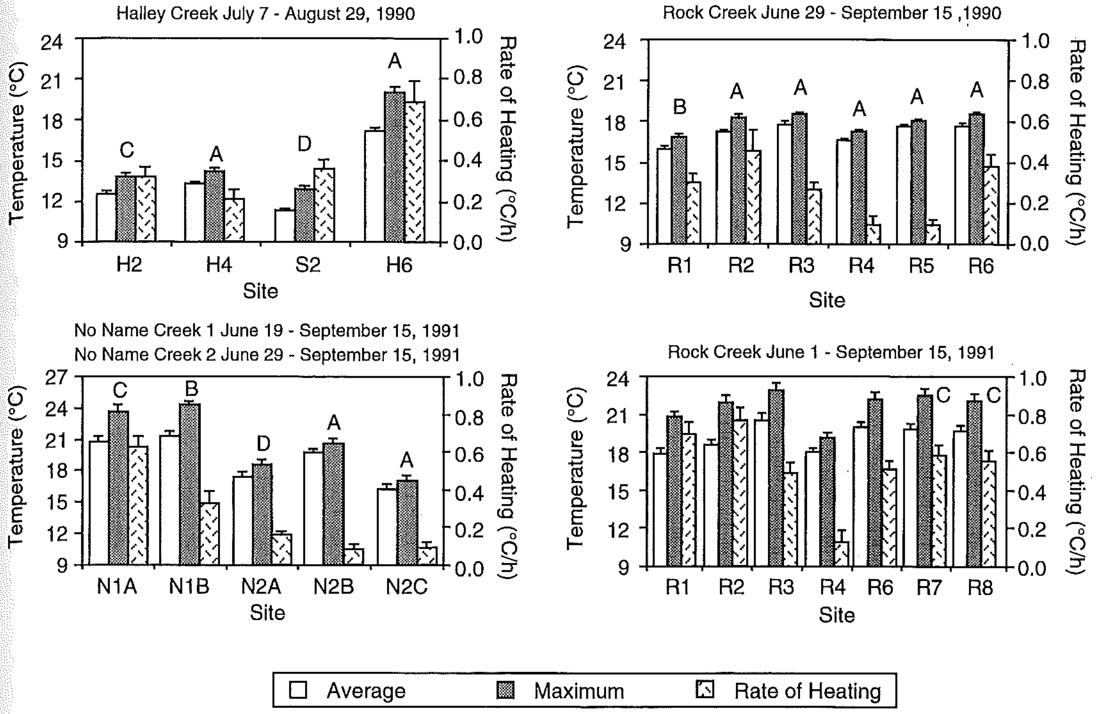

FIGURE 2.—Average daily mean and maximum stream temperatures and average noon rate of heating at the study sites. Letters above bars represent shade categories (A = 0–24%, B = 25–49%, C = 50–74%, D = 75–100%), and error bars indicate one-half of the simultaneous 95% confidence intervals derived from Bonferroni significant differences. Sites are listed in downstream order from left to right and locations appear in Figure 1.

Air temperature accounted for an average of 63% of the variability in lagged water temperature (exclusive of site H6 after dam removal; mean R^2, 0.63; SD, 0.20; Table 2). The phase shift between water and air temperature ranged from 0.1 to 6.6 h (exclusive of site H6 after dam removal; mean, 2.81 h; SD, 1.49). The water–air phase shift could not be determined at site H6 following dam removal because dramatic cooling effectively dampened the sinusoidal nature of the water temperature trace (discussed below). Phase shifts were particularly low and coefficients of determination relatively high for the two spring sites (S1, S2), where the entire flow was derived from subsurface inflow exposed to the atmosphere for a fairly short period of time. The addition of soil temperatures generally improved the fit of the multiple-correlation model for stations in the upper reaches of Rock and Halley Creeks (R1, H1, H2, and H3), but offered little improvement for stations in the lower reaches of these creeks or for any of the stations on either of the No Name creeks. Only one station, R4 on the west arm of Rock Creek, showed a stronger association between water and soil temperatures than between water and air temperatures (Table 2).

The removal of dams on Halley Creek was associated with an increase in the responsiveness of water temperature to air temperature at sites H3, H4, H5, and H7, as indicated by the decreased phase shifts (Table 2). The correlation between water temperature and air temperature was substantially less following dam removal at three sites in the midreaches of Halley Creek (H4, H5, and H6). Only site H6 showed a higher correlation between air and soil temperatures after dam removal than before. Dam removal had no substantial effect on either the phase shift or the fit of the correlation model at the two spring sites, which are off the main channel of Halley Creek (Figure 1).

Beaver Impoundments and Thermal Regimes

Limited sampling on Halley Creek in 1990 indicated that the thermal character of the midreaches was similar to that of the upstream section (Figure 2) despite the presence of five beaver ponds between sites H2 and H4. Daily mean and max-

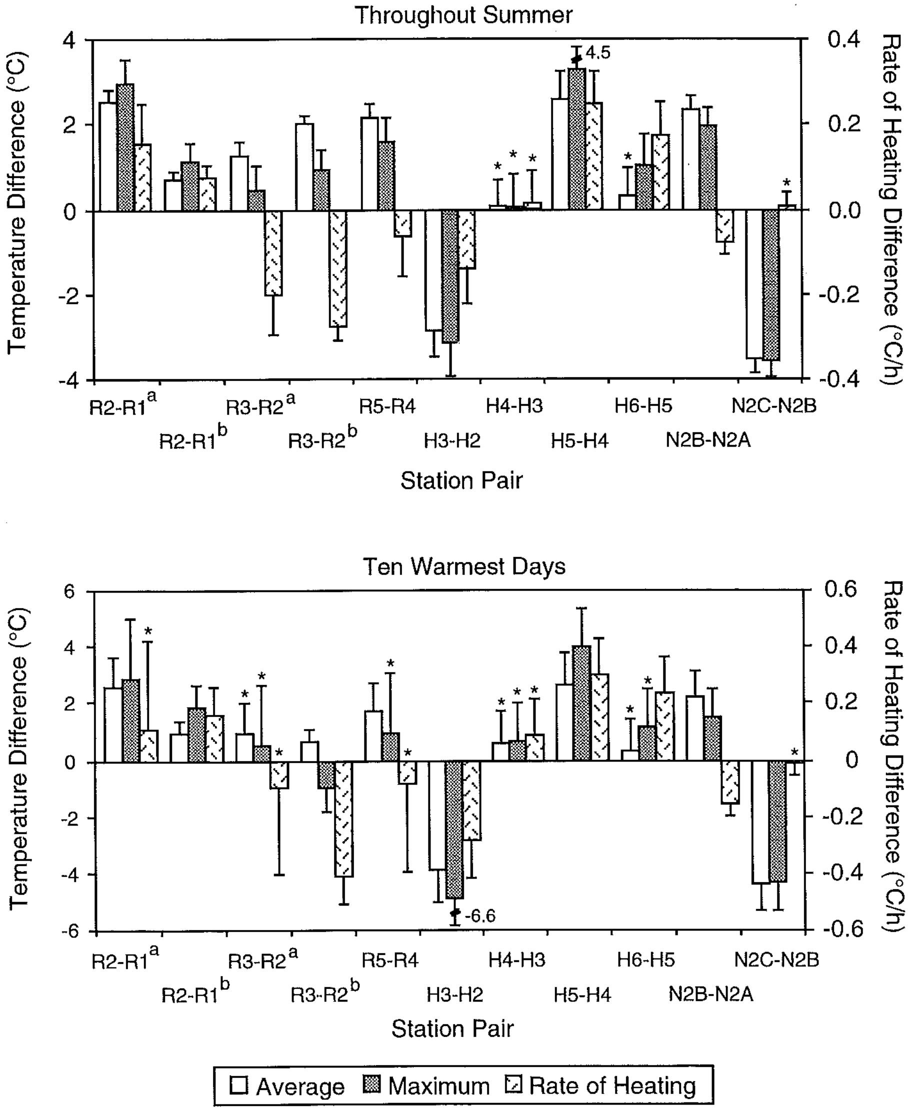

FIGURE 3.—Average differences between downstream and upstream sites for thermograph station pairs on three of the study streams throughout summer 1991 and on the 10 warmest days during the period of record. Error bars indicate one-half of the simultaneous 95% confidence intervals derived from Bonferroni significant differences (bars with asterisks are not significantly different from zero, $P > 0.05$). Superscript "a" on a station pair indicates 1990 records; superscript "b" indicates 1991 data. Impounded areas and distances between stations are listed in Table 1 and periods of record appear in Figure 2.

imum stream temperatures at these two sites were generally only 1–2°C higher than those at the spring site, S2. However, temperatures had increased substantially, and the stream was warmed at nearly twice the rate of the midreaches (as indicated by the rate of heating: Figure 2) by the time the water reached site H6.

The general thermal pattern was similar in Rock Creek in 1990 and 1991 (Figure 2). In the east branch, temperatures increased gradually from sites R1 to R3, and the rate of heating at site R3, which was immediately downstream of a series of three impoundments, was significantly lower (BSD, $P < 0.05$) than that at site R2 immediately upstream of the ponds. Stream temperatures in the upper west arm of Rock Creek (site R4) were significantly lower than those below the confluence of the two branches (sites R6–R8) during both years, and sites R4 (1990) and R5 (1990–1991) warmed at significantly lower rates than stations elsewhere on the creek.

Stream temperatures at the two stations below the large pond on No Name Creek 1 were very similar in summer 1991 (Figure 2). However, the downstream station warmed at a slower rate than the upstream station.

In No Name Creek 2, temperatures were significantly higher at site N2B, which was directly below a pair of beaver ponds, than at either the upper (N2A) or lower (N2C) station (Figure 2). However, the downstream site (N2C), situated immediately below a similar pair of ponds, was significantly cooler than either of the upstream stations. In general, the sites on No Name Creek 2 warmed relatively slowly (<0.2°C/h), and the upstream station warmed slightly faster than the other sites.

Examination of the differences in temperature associated with nine station pairs (Table 1) revealed no clear relationship between either the distance between stations or the intervening impoundment area and the degree of downstream warming (Figure 3). This conclusion held true even when a subset of the 10 warmest days (as defined by maximum daily air temperature) were considered. Station pairs R3-R2 and N2C-N2B, despite being separated by similar distances and impoundment areas, displayed opposite patterns of differences in daily average and maximum temperatures. A similar phenomenon occurred with the R2-R1 and the H3-H2 station pairs. Three station pairs contained sites in different shade categories (Table 1); in each case the downstream site was more shaded than the upstream site. In two cases (R2-R1 and N2B-N2A) temperatures were significantly higher downstream of the impoundment(s), whereas the stations in the third pair (H4-H3) were statistically identical both on the warmest days and throughout the summer of 1991 (Figure 3).

Only the Rock Creek station pairs, in which the downstream stations were significantly warmer on average than those upstream throughout the summers of 1990–1991, consistently showed warming below impoundments (Figure 3). Differences in the three response variables associated with the R2-R1 station pair were greater on the warmer days, but average daily temperatures associated with the R3-R2 station pair were actually lower downstream during the warmest periods. Differences associated with the R5-R4 station pair displayed a pattern similar to those of the R3-R2 pair, with higher average temperatures and lower rates of heating downstream of the impoundment.

The relationships within the four station pairs on Halley Creek were less consistent than those on Rock Creek (Figure 3). In the H3-H2 station pair, mean daily downstream temperatures averaged more than 3°C lower than the upstream station despite the two intervening impoundments. The stations of the H4-H3 station pair, which were separated by three impoundments, showed no significant differences in the temperature variables. The two station pairs on the lower reaches of Halley Creek, H6-H5 (separated by two impoundments) and H7-H6 (with no intervening impoundment) showed significant downstream warming and increases in the rate of heating.

The station pairs of No Name Creek 2 showed opposite temperature relationships even though the distances between stations and the intervening impoundment areas were similar. The middle station (N2B) warmed less rapidly than the upstream station (N2A), and there was no significant difference in the heating rate between the middle and lower (N2C) sites.

Dam Removal

Removal of the dam on the west branch of Rock Creek in 1990 had no identifiable effect on the mean daily average or maximum temperatures at sites R4 or R5 (Figure 4). However, daily average and maximum stream temperatures decreased by 1.6°C and 2.3°C, respectively, at site R6 following dam removal. The heating rate at site R4, which was upstream of the former pond, increased by more than a factor of seven following dam removal, but it decreased by more than 0.2°C/h at site R6.

Average daily mean and maximum stream temperatures were cooler at all sites in the period following the large-scale dam removal on Halley Creek in 1991 (Figure 4). These differences were generally less pronounced in the upper reaches (upstream of site H3) than in the lower portion of the creek. Average heating rates before and after dam removal were not significantly different for those stations upstream of H5, but there were large declines at sites H6 and H7, where the average values were 0.8°C/h and 0.2°C/h lower, respectively, in the period following dam removal.

Removal of the dams on Halley Creek was associated with a decrease in the temperature differences in the H3-H2 and H5-H4 station pairs (Figure 5). However, the differences associated with the H4-H3 and H6-H5 station pairs increased

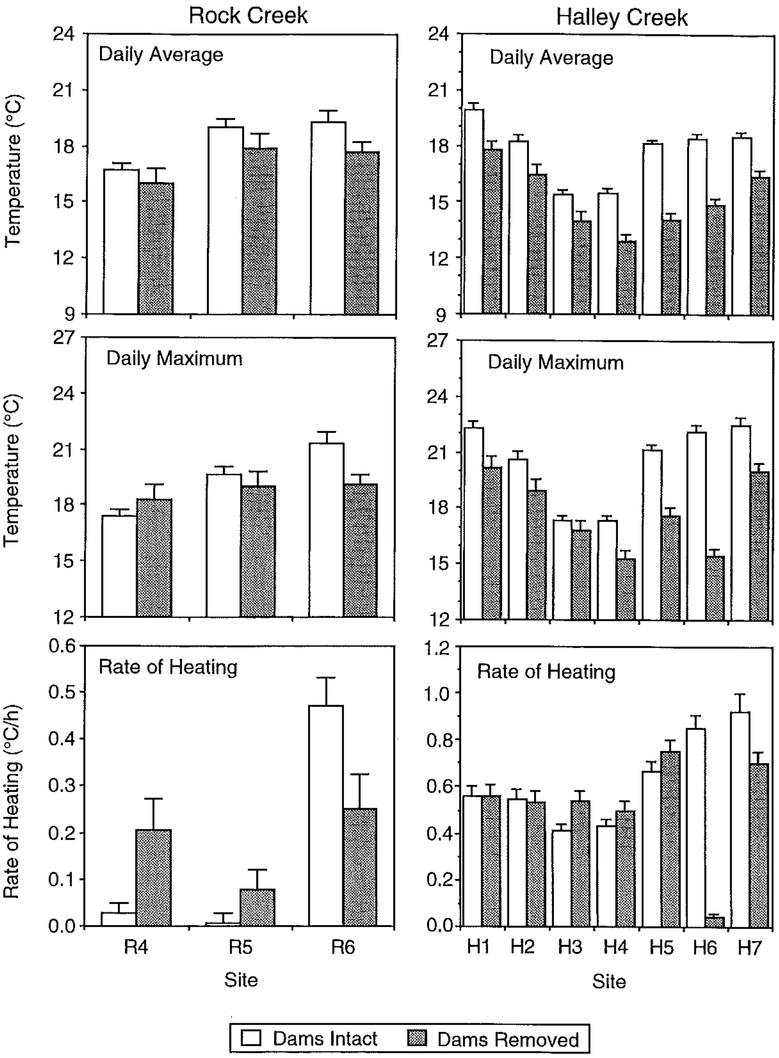

FIGURE 4.—Average daily mean and maximum stream temperatures and average noon rate of heating before and after beaver dam removal on Rock and Halley Creeks, Wisconsin. Sampling dates were June 24–August 13, 1990 (dams intact), and August 16–September 15, 1990 (dams removed), for Rock Creek, and June 5–July 14, 1991 (dams intact), and July 18–August 19, 1991 (dams removed), for Halley Creek. Sites are listed in downstream order from left to right, and error bars represent one-half of the simultaneous 95% confidence intervals derived from Bonferroni significant differences.

slightly in the period after dam removal. The differences in average heating rate associated with the Halley Creek station pairs differed little before and after dam removal, except the downstream station of the H6-H5 pair warmed much less rapidly than did the upstream station in the period following dam removal.

Thermal Habitat Suitability

Stream temperatures in Rock Creek were most commonly in the 17–23°C range, although the two uppermost stations on the east branch (sites R1 and R2) maintained temperatures in the optimum range for extended periods of time (Table 3). In 1990, lethal temperatures occurred for at least part of the day at sites R2 and R6 several times in late June and early July, and temperatures remained in the lethal zone for an entire 24-h period at site R3 in early July. In 1991, the warmer of the two years, lethal temperatures occurred for at least part of the day at all sites in Rock Creek (Table 3). Elevated temperatures tended to persist longer at

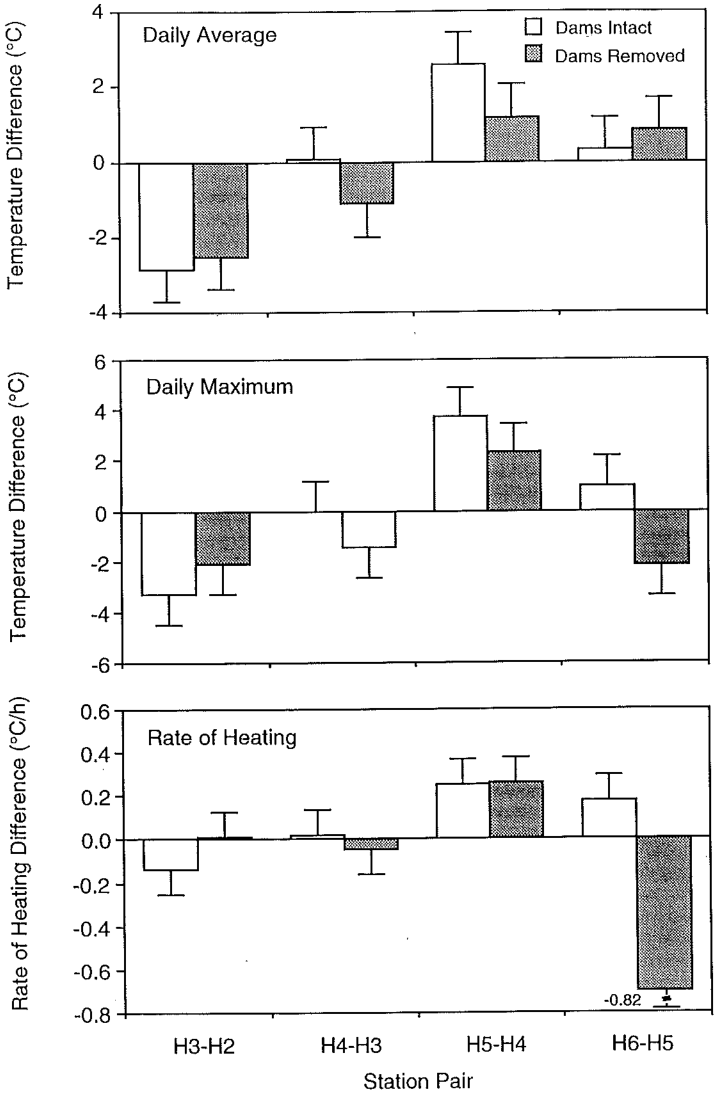

FIGURE 5.—Average differences between downstream and upstream sites for four thermograph station pairs on Halley Creek before (June 5–July 14) and after (July 18–August 19) beaver dam removal on Halley Creek in 1991. Error bars represent one-half of the simultaneous 95% confidence intervals derived from Bonferroni significant differences. Impounded areas and distances between stations appear in Table 1.

site R3 and at the stations below the confluence of the two branches (sites R6–R8). In general, the stations directly below impoundments (R2, R3, and R5) tended to maintain temperatures within a narrower range than did those stations immediately above ponds.

Temperatures at sites R4, R5, and R6 were generally cooler and more variable following removal of the dam on Rock Creek in 1990. The percentage of time in which temperatures were in the optimum zone increased substantially at these three stations following dam removal.

Stream temperatures in Halley Creek tended to be lower and less varible in the middle portion of the creek (Table 3). In 1990, the two upper stations (sites H2 and H4) maintained temperatures in the optimum range for much of the summer, while temperatures at site H6 fluctuated in the 17–23°C range for much of July and August. Before dam removal on Halley Creek in 1991, the two

TABLE 3.—Percentage of time summer stream temperatures fell into one of four temperature ranges in four headwater streams in northeastern Wisconsin. The optimal zone for brook trout is 11–16°C, and sustained temperatures above 24°C are lethal. Site locations appear in Figure 1 and sampling periods appear in Figure 2.

Thermograph site	Total hours sampled	Percent of total hours in temperature range (°C): <11	11–16	17–23	≥24
Rock Creek 1990					
R1	1,896	1	68	31	0
R2	1,896	0	28	69	3
R3	1,896	0	8	89	3
R4[a]	1,104	0	31	69	0
R4[b]	720	3	48	49	0
R5[a]	1,104	0	0	100	0
R5[b]	744	0	20	80	0
R6[a]	1,104	0	6	88	6
R6[b]	744	0	22	78	0
Total	11,208	0	27	71	2
Rock Creek, 1991					
R1	2,568	0	28	69	3
R2	2,568	0	22	72	6
R3	2,568	0	4	84	12
R4	2,568	0	10	89	1
R6	2,568	0	8	84	8
R7	2,568	0	9	82	9
R8	2,568	0	10	83	7
Total	17,976	0	13	80	7
Halley Creek, 1990					
H2	1,008	11	89	0	0
H4	1,008	1	99	0	0
H6	1,008	0	25	75	0
Total	3,024	4	71	25	0
Halley Creek, 1991					
H1[a]	960	0	7	86	7
H1[b]	792	0	32	64	4
H2[a]	960	0	21	78	1
H2[b]	792	1	47	51	1
H3[a]	960	1	64	35	0
H3[b]	792	19	56	25	0
H4[a]	960	0	62	38	0
H4[b]	792	26	61	13	0
H5[a]	960	0	23	76	1
H5[b]	792	15	61	24	0
H6[a]	960	0	24	73	3
H6[b]	792	0	84	16	0
H7[a]	960	0	24	71	5
H7[b]	792	1	47	51	1
Total[a]	6,720	0	32	66	2
Total[b]	5,544	9	55	35	1
No Name Creek 1, 1991					
N1A	2,136	0	2	77	21
N1B	2,136	0	4	80	16
Total	4,272	0	3	79	18
No Name Creek 2, 1991					
N2A	1,896	0	27	73	0
N2B	1,896	0	0	98	2
N2C	1,896	0	51	49	0
Total	5,688	0	26	73	1

[a] Before dam removal.

[b] After dam removal.

sites in the middle portion of the creek (H3 and H4) generally remained within the optimum zone longer than the other stations. In 1991, lethal temperatures persisted for an extended period of time only at sites H1 and H7, the uppermost and lowermost sites, respectively. Lethal temperatures did not persist for an entire 24 h period at any of the stations in Halley Creek in 1991.

Removal of the beaver dams on Halley Creek in 1991 affected the thermal character of stations H6 and H7 most profoundly; the dramatic cooling effect at site H6 resulted in a substantial increase in the duration of optimal temperatures (Table 3). These changes occurred even though the large impoundment immediately downstream of site H5 was left intact.

Periods of several days in which temperatures reached the lethal zone were common at both stations in No Name Creek 1 in 1991 (Table 3). The thermal character of these stations was nearly identical throughout the summer, and temperatures reached the optimum zone briefly and only at night on a few occasions in late July, late August, and early September.

In No Name Creek 2, the upper (N2A) and lower (N2C) stations generally showed cooler and more variable thermal patterns than did the middle station (N2B; Table 3). Lethal temperatures were reached only for very short periods at site N2B early in the summer. Temperatures at site N2B were very stable, remaining in the narrow range of 17–23°C throughout most of the summer.

Discussion

As water moves downstream, its temperature seeks an equilibrium with air temperature, a process influenced by local environmental factors such as stream shading and subsurface inflow (Sullivan et al. 1990). The rate at which water temperature changes as it approaches equilibrium depends on stream size (Edinger and Geyer 1968). Because of the high specific heat of water, large volumes of water change temperature relatively slowly. Downstream of large beaver impoundments, the stream channel was often wider and deeper than in areas without beaver ponds. The lower rates of heating associated with the stations immediately downstream of large impoundments (R3, R4, and N2B; Figure 2) may reflect the buffering influence of increased volume. These same three stations also exhibited a great degree of thermal consistency (Figure 2; Table 3) throughout the summer and were less responsive to air temperature in general, as indicated by the longer phase shifts and lower air partial R^2 values in Table 2. The buffering effect of increased volume is particularly important in low-flow situations. Anderson and Miyajima (1975) constructed pools on a Colorado stream to buffer water temperature in periods of low flow. Stream temperatures were 0.6–2.2°C lower and peak temperature duration (above 22.2°C) was substantially shorter in the pools than in upstream riffles.

The opposite effect of reduced volume is evident in the correlation analyses for the two spring sites on Halley Creek. The small volumes of water in the spring channels, which were generally less than 1 m wide and 0.5 m deep, were very responsive to changes in air temperature, as indicated by the short phase shifts and relatively high air partial R^2 values (Table 2). Although water at these sites was derived entirely from groundwater, it was rapidly warmed by the atmosphere upon emerging above ground. The lack of a ground term effect in the correlation models for the two spring stations (Table 2) also supports the contention that the influence of the spring source diminishes quickly. Thus the cooling effect of concentrated groundwater discharges may not persist in downstream reaches unless additional subsurface inflow or sufficient shading exists to temper local air temperatures.

Air temperature is the single most important determinant of stream temperature in the absence of other thermal inputs (Bartholow 1989), and it is particularly important for small exposed streams (Ward 1985). This relationship is complicated in headwater streams in summer because cooler subsurface inflow typically contributes a substantial percentage of total flow. We found generally strong positive relationships between lagged water and air temperatures (Table 2) indicating that air temperature plays a dominant role in regulating stream temperatures even when the thermal regimes are driven by groundwater discharge. Addition of the ground temperature term improved the fit of the correlation models only for sites at the upper reaches of Rock and Halley Creeks (R1 and H1–H3). Given the location of these generally well-shaded stations, it seems likely that a higher portion of the base flow at these sites was due to groundwater inflow that had not yet warmed to surrounding temperatures.

Local differences in the degree of shading, groundwater inflow, and stream volume make it difficult to generalize about the effect of beaver impoundments on stream temperature, even within the scope of a single headwater stream. Each of the study streams had fairly unique longitudinal temperature patterns. In Rock Creek, temperatures tended to be fairly constant among thermograph stations, gradually increasing in daily maxima from headwaters to mouth (Figure 2). However, average maximum daily temperatures differed by only 1.3°C between R1 and R8 throughout summer 1991, representing an average increase of only 0.03°C/100 m of stream. This rate of increase is less than that observed between the two sites on No Name Creek 1, which were not separated by any beaver ponds (Figure 1). In terms of daily maxima, site N1B averaged 0.7°C warmer than N1A throughout the summer of 1991, which translates to an average increase of 0.1°C/100 m of stream.

Halley and No Name 2 Creeks generally exhibited a greater degree of thermal heterogeneity than the other two creeks. The uppermost stations were generally warmer than the lower stations on both Halley and No Name 2 Creeks. The relatively poor correlations between air and water temperatures at sites H1–H4 and N2B–N2C indicate that some other factor, most likely subsurface inflow, accounted for a large portion of the variability in water temperature in the midreaches of Halley Creek and the lower part of No Name Creek 2. These observations corroborate those of Threinen and Poff (1963), who noted that thermal discontinuity is common in Wisconsin trout streams.

The longitudinal temperature patterns in the study streams agree well with inferences based on surficial geology. The amount of groundwater discharge to a stream depends on the area contributing recharge to the aquifer and the rate of recharge (Todd 1983). In northern Wisconsin, aquifers are often found along watercourses where glacial meltwaters removed fine material and left behind permeable deposits of sand and gravel. These materials have high hydraulic conductivities and thus recharge and release groundwater rapidly (Todd 1983; Simpkins et al. 1987). In many low-lying areas, these alluvial deposits are overlain by a layer of peat, which tends to form where groundwater inflow far exceeds the outflow. These areas of peat, which generally lie at or near the water table (Simpkins et al. 1987), proved to be excellent indicators of groundwater sources, and they related fairly well to the longitudinal temperature patterns on the study streams. Site R4 on the west arm of Rock Creek, which is underlain by a large bed of peat (Simpkins et al. 1987), showed a stronger association between water and ground temperatures than between water and air temperatures (Table 2). Each of the lower two sites on No Name Creek 2 are underlain by beds of peat (Simpkins et al. 1987), which implies that substantial groundwater input may have mitigated any warming effect due to the four impoundments. Similarly, large expanses of peat in the midreaches of Halley Creek (between H2 and H5) indicate that these stations were likely receiving substantial amounts of subsurface inflow in addition to that originating from the two spring sites.

The potential for evaluating brook trout habitat suitability based on geological principles has been examined in detail by Dean et al. (1991). These researchers coined the term "geofisheries" to describe an algorithm that determines brook trout habitat suitability based on the geological structures from which groundwater is derived. We did not attempt such an evaluation in the present study; however, the paradigm followed by this technique has potential applicability in the management of trout streams occupied by beaver. A geofisheries perspective could be used to identify those streams or sections of streams that are likely to have stable groundwater input throughout the summer and thus are more likely to support brook trout populations. Identification of combinations of features, particularly the contiguous occurrence of large areas of unsorted glacial till, which are important recharge areas, and well-sorted alluvium, which form excellent conduits to the stream beds (given sufficient hydraulic gradient), as well as expanses of peat would indicate areas with the highest potential for stable groundwater flows. The thermal effect of beaver impoundments could then be more accurately evaluated in relation to the location of coolwater discharges.

The tendency for brook trout to seek out areas of cooler inflow for spawning (Brasch et al. 1958; Webster and Eiriksdottir 1976; Becker 1983) and to avoid high temperatures (Huntsman 1942; Gibson 1966) has been well documented. In the present study, we found maximum daily temperature differentials above and below beaver impoundments to be quite variable, ranging from −2.1°C for the H3-H2 station pair to more than 4.5°C for the H5-H4 station pair (Figure 3). These temperature differentials appeared to be independent of intervening impoundment area and distance between stations. In such heterogenous thermal environments, at least equal concern should be given to the potential for beaver dams to block access to coldwater refuges during the summer. Identification of these coolwater refuges through a process analogous to the geofisheries algorithm would undoubtedly lead to more focused brook trout management on streams with substantial beaver activity.

Removal of beaver dams, particularly those established for several decades, can have profound effects on the ecology of downstream reaches. Stock and Schlosser (1991) reported that a catastrophic collapse of a beaver dam and ensuing flood resulted in more than a 90% decrease in benthic insect density downstream and altered the structure of the fish community by causing a short-term influx of pond species. Mean insect density 1 d after the collapse (1,632/m^2) was only 8% of the pre-flood density, and 60 d after the flood mean insect density in downstream riffles was only 62% of pre-flood values. These results, combined with those of the present study, suggest that losses in downstream diversity may outweigh the thermal benefits of dam removal in many cases. The large-scale dam removal on Halley Creek was associated with a substantial thermal decline (>2.5°C change in average daily maxima) only at site H6. The temperature decline at site H6 occurred even though the large impoundment below site H5 was left intact. The localized nature of the temperature decline suggests that the cooling effect of subsurface inflow, which may have been suppressed by the pond upstream of H6, could have been responsible for this anomaly. This suggestion is supported by the presence of a band of peat that extends from Valley Lake, a seepage lake about 0.5 km south of H6 (Figure 1), to Halley Creek just upstream of H6. If this speculation is correct, the same degree of cooling at sites H6 and H7 may have been attained by removing only the dam immediately upstream of H6, rather than all the dams upstream of H5.

Temperature comparisons associated with beaver dam removal in this study were confounded with seasonal effects as air temperatures decreased and soil temperatures increased toward the end of the summer. Average daily maximum air temperatures (measured at A2) were slightly less during the period following dam removal (mean, 21.6°C; SD, 3.49) than before (mean, 22.0°C; SD, 2.65), but the difference was not statistically significant (t-test, $P = 0.18$). Average daily soil temperatures at G1 were slightly but significantly higher (t-test, $P = 0.0001$) after dam removal (mean, 11.7°C; SD, 0.54) than before (mean, 11.0°C; SD, 0.56). These factors, along with others associated with seasonality such as decreasing day length, likely accounted for a portion of the temperature decreases following dam removal.

The headwater streams in this study represented typical, heterogenous thermal environments dominated by groundwater inflow and regulated by local air temperatures. This heterogeneity caused the thermal effect of beaver impoundments to be highly site dependent. Our results suggest that large ponds act as thermal buffers, raising downstream water temperatures slightly in some cases, but also dampening the diel fluctuation. It was also demonstrated that dam removal was generally not effective in reducing downstream temperatures substantially. However, following careful study of the geological and topographical attributes of the watershed, judicious removal of a few key beaver impoundments may have a strong effect on downstream temperatures without the loss of diversity associated with large-scale dam removal. A thorough understanding of the attributes leading to surface expressions of groundwater and subsequent identification of the areas that are important thermal refuges for trout will enhance the information base necessary for management of beaver, trout, and waterfowl populations along headwater streams.

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