Behavioral Thermoregulation of Brook and Rainbow Trout: Comparison of Summer Habitat Use in an Adirondack River, New York

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Abstract.—The body temperatures of 15 hatchery-origin and two wild brook trout Salvelinus fontinalis and 11 hatchery-origin rainbow trout Oncorhynchus mykiss were monitored with internally implanted, temperature-sensitive radio transmitters from June through September 1997 in a fifth-order Adirondack river (New York). The fish were released into a 12-km reach that during summer had maximum temperatures near those that are lethal for salmonids. Body temperatures were compared between species and with river temperatures. In 1997, the maximum river temperature was 26.4°C, and the highest average daily temperature was 25.0°C. The brook trout were usually cooler than the main river flow because they used two of five tributary confluences or groundwater discharge areas in two pools within the main river. The temperatures of the brook trout from June through September were an average of 2.3°C cooler than the main flow of the river and differed significantly (P = 0.002) from those of the rainbow trout, which were 1.5°C cooler than the river. When the river temperatures were 20°C or higher, the mean temperatures of the brook trout were 4.0°C cooler than the river and differed significantly (P = 0.002) from those of the rainbow trout, which were 2.3°C cooler than the river. Brook trout, and to a lesser extent rainbow trout, used localized coolwater areas to lower their body temperatures below that of the main river. Groundwater discharge areas within pools and some tributary confluences were critical habitats for behavioral thermoregulation because they provided refuge areas from warm river water during the summer.

The streams inhabited by brook trout Salvelinus fontinalis or rainbow trout Oncorhynchus mykiss may have summer water temperatures that approach or exceed lethal levels. Surprisingly, populations sometimes flourish in waters that appear marginal or even unsuitable based on maximum summer stream temperatures (e.g., Matthews and Berg 1997). The summer water temperature can increase in streams through local-scale habitat alterations such as vegetation removal (e.g., Barton et al. 1985), or as a result of climate change (e.g., Eaton and Scheller 1996). Temperature increases can also result from the natural longitudinal gradients within stream systems. Because of their sensitivity to warmwater temperatures, salmonid populations—especially those near the southern edge of their ranges—could be either reduced or eliminated by increases in summer temperatures (e.g., Meisner 1990a, 1990b).

Stream temperatures may differ at various locations and may include localized coolwater areas that could serve as thermal refuges, allowing the survival of fish that are sensitive to high temperatures. Water cooler than mainstream flows can also occur where tributaries or groundwater sources discharge cool water (Kaya et al. 1977; Bilby 1984; Nielsen et al. 1994; Bonneau and Scarnecchia 1996), or in pools where depth and flow conditions result in thermal stratification (Matthews et al. 1994).

Salmonids have been reported to thermoregulate behaviorally by detecting and maintaining position within localized areas of cool water in streams. Chinook salmon O. tshawytscha equipped with temperature-sensitive radio transmitters maintained body temperatures lower than the main flow temperature in the Yakima River, Washington (Berman and Quinn 1991). Similarly, juvenile bull trout S. confluence were found in the coldest water available in a pool that had a thermal gradient created by a tributary confluence (Bonneau and Scarnecchia 1996).

Brook trout are particularly sensitive and vul-

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Received September 10, 2002; accepted May 6, 2003
nerable to the negative effects of warmwater temperatures. Their abundance and distribution in streams is especially influenced by water temperature (e.g., McCormick et al. 1972). For example, the southern limit of brook trout in North America corresponds to a mean July air temperature of approximately 21°C or the 15°C groundwater temperature isotherm (MacCrimmon and Campbell 1969; Meisner 1990a). Their preferred temperature range is about 10–16°C (MacCrimmon and Campbell 1969; Cherry et al. 1977; Schofield et al. 1993). Maximum temperatures of about 24°C limit the occurrence of brook trout in streams (Ricker 1934; MacCrimmon and Campbell 1969; Meisner 1990b). Because brook trout require relatively cool summer water temperatures, cool-water refuges may be important for survival in streams that have lethal water temperatures (>25°C) during the summer. Although anglers report that trout use cool “spring holes” within rivers, a detailed description of the use of thermal refuges by adult brook trout is generally lacking (Hayes et al. 1998).

Rainbow trout have higher preferred temperatures than brook trout, although both species have similar upper lethal temperatures of about 25°C (Fry et al. 1946; Black 1953; Bidgood and Berst 1969; Hokanson et al. 1977). The maximum growth of rainbow trout juveniles occurs at 17–19°C (Hokanson et al. 1977). Although rainbow trout have higher optimal temperatures than brook trout, they have been reported to use cool refuges. For example, juvenile steelhead moved into cool-water refuges when water temperatures exceeded 23–28°C and adult steelhead (anadromous rainbow trout) were located in thermally stratified pools during summer when maximum temperatures were 26–29°C in California streams (Nielsen et al. 1994). In a California stream that had water temperatures up to 28.9°C, rainbow trout were found in the coolest portion of a pool that had groundwater discharge and were absent from an adjacent warmer pool (Matthews and Berg 1997). In the geothermally heated Firehole River, Wyoming, rainbow trout moved into cool tributary streams when the main river temperature exceeded 20°C (Kaya et al. 1977; Kaeding 1996).

In this study we compared the use of thermal refuge areas by brook and rainbow trout during the summer in a medium-sized river that experienced high water temperatures (>24°C). We hypothesized that trout would locate and use cool-water tributary confluences and waters influenced by groundwater discharges. The objectives of this study were to (1) determine if brook and rainbow trout thermoregulate behaviorally by comparing fish temperatures with river temperatures measured simultaneously, (2) compare the body temperatures of brook and rainbow trout during the summer, and (3) identify the types of thermal refuges used.

Study Site

This study was conducted on a 12-km reach of the South Branch of the Moose River (hereafter referred to as the Moose River), a fifth-order stream located in Hamilton and Herkimer counties, New York, in the west-central region of the Adirondack Mountains (Figure 1). The Moose River has an average gradient of 3.3 m/km and drains an area of 450 km². The mean annual discharge is 11 m³/s, and the base flow is about 2 m³/s; the average channel width is 40 m (range, 10–60 m). Low-gradient sections, interspersed with short sections of steep gradient, characterize the study reach. Boulder, cobble, and occasionally bedrock are the predominant substrates in steep-gradient sections. Low-gradient sections have a mix of sand, gravel, and cobble substrates. The watershed is almost completely forested with mature second-growth northern hardwoods and mixed northern hardwood–conifer forests. The stream is stocked annually with brook and rainbow trout in late spring. Naturally reproducing brook trout are common in some tributaries and are present in the Moose River. The primary tributaries within the study area have base flow discharges that range from 0.05 to 0.5 m³/s and widths that range from 3 to 10 m.

FIGURE 1.—Study reach where brook and rainbow trout implanted with temperature-sensitive radio transmitters were released in the South Branch of the Moose River, Adirondack region, New York.
The relatively wide and shallow channel of the Moose River results in summer water temperatures that can approach and sometimes exceed the maximum upper limits for salmonid survival (25°C). The Moose River is also subject to episodic acidification (pH < 5) during high-discharge events, especially during spring snowmelt (Baird 2000). The variation in temperature and pH make the Moose River a harsh environment for the survival of salmonids.

Methods

Temperature-sensitive radio transmitters were used to monitor the body temperature and location of 15 hatchery-origin and two wild brook trout and 11 hatchery rainbow trout from June through September 1997 in the Moose River. Fish temperatures measured with telemetry equipment were compared with recorded water temperatures.

Water temperatures.—Water temperatures were recorded with recording temperature loggers (Optic Stowaway and Hobo Temp models, Onset Corporation, Pocasset, Massachusetts) at hourly intervals at three sites in the main stem of the river and in five tributaries. The manufacturer’s stated accuracy was ±0.2°C for the Optic Stowaway logger, and ±0.7°C for the Hobo logger. The temperature loggers were compared with a mercury thermometer (calibrated against a NIST traceable standard) and all were within their stated accuracy. Main-stem river temperatures were measured with loggers placed at Bisby Bridge, Limekiln Pool, and Lunch Rock (Figure 1). The temperatures in all five major tributaries within the study reach were monitored with loggers placed 10–500 m upstream from their confluences with the Moose River. Limekiln Pool had a maximum depth of about 5 m and was monitored with a vertical array of four loggers at 0.3, 1.5, 3.0, and 4.2 m from the surface.

Thermal gradient maps of the confluences of the Combs and Otter brooks were developed to describe the areal extent of cool refuge areas. The location of trout within these areas on a typically warm summer day were then superimposed on the gradient maps. These measurements were made 1–2 July 1997, when maximum air temperatures were 26.8°C and 21.1°C, respectively. Direction and distances were measured from established reference points on shore to locations where water temperature, depth, and substrate type were recorded. Visual observation by snorkeling and from shore determined the locations of fish in the confluence areas on these dates.

Fish body temperatures.—Temperature-sensitive radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota) were placed in the body cavities of study fish. Each tag transmitted at a unique frequency from 150.014 to 150.304 MHz. Four transmitter models were used (weighing from 5.5 to 9.7 g each), with estimated battery lives of 20, 45, 70, and 130 d, respectively (Tables 1, 2). The transmitters ranged from 0.5% to 3% of body weight (Tables 1, 2). A regression function determined by the manufacturer was used to calculate the temperature from the time period required for 10 pulses. The accuracy of the temperature measurements for each transmitter was checked prior to implantation. Each transmitter was tested at two temperatures within the expected range of field temperatures. The average deviation between transmitter-measured temperature and water temperature was −0.1°C (SE = 0.04).

To implant the transmitters, the fish were anesthetized (MS-222 [tricaine methanesulfonate]; 100 mg/L) until the fish lost equilibrium and did not respond to physical stimuli. Length and weight were recorded, and the fish were marked with visible implant tags (Haw et al. 1990) and adipose fin clips during surgery, unless the fish had been previously marked. Hatchery-origin fish whose transmitters were implanted in the field had already received a visible implant tag and fin clip prior to stocking. General surgical procedures used for implantation are described by Wooster et al. (1993). The transmitters were inserted through an incision anterior to the left pelvic fin and the antenna trailed out of a small incision posterior to the pelvic fin (Brown and Mackay 1995).

The transmitters were implanted in both laboratory and field settings. Five hatchery brook trout and five hatchery rainbow trout were implanted at the Little Moose Field Station (Figure 1), located near the study site, and held 5–9 d before release on 9 June 1997 (Tables 1, 2). The fish implanted at the field station were released at Lunch Rock and near the mouth of Combs Brook (Tables 1, 2; Figure 1). Twelve brook trout (2 wild and 10 hatchery-origin) and 6 hatchery rainbow trout were implanted in the field from July through August. The fish implanted in the field were captured by angling. The hatchery-origin fish implanted in the field were released in late May or early June 1997 as part of a put-and-take management stocking program and were from the same source as the fish implanted at the field station in May and June (Baird 2000). The fish implanted in the field were released back into the river at their point of capture after a brief (<30 min) recovery period. The fish...
Table 1.—Details for brook trout implanted with temperature-sensitive radio transmitters and released in the South Branch of the Moose River, New York, in 1997. The disposition column indicates the fate of each fish after tag implantation. When “battery” is listed, the transmitter battery probably expired. Fish number 2, whose transmitter was found in spring 1998, was alive through November 1997 and probably died during the winter.

<table>
<thead>
<tr>
<th>Fish number</th>
<th>Transmitter weight (g)</th>
<th>Length (mm)</th>
<th>Weight (g)</th>
<th>Date implanted</th>
<th>Location transmitter implanted</th>
<th>Last day temperature observed</th>
<th>Number of temperature observations</th>
<th>Disposition and final location</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>9.7</td>
<td>389</td>
<td>770</td>
<td>31 May</td>
<td>Lab</td>
<td>16 Jul</td>
<td>16</td>
<td>Found transmitter at Lunch Rock; predation</td>
</tr>
<tr>
<td>2</td>
<td>9.7</td>
<td>415</td>
<td>990</td>
<td>1 Jun</td>
<td>Lab</td>
<td>10 Sep</td>
<td>44</td>
<td>Found transmitter upstream of Combs Brook in spring 1998</td>
</tr>
<tr>
<td>3</td>
<td>7.3</td>
<td>300</td>
<td>437</td>
<td>2 Jun</td>
<td>Lab</td>
<td>16 Jul</td>
<td>16</td>
<td>Found transmitter at Lunch Rock; predation</td>
</tr>
<tr>
<td>4</td>
<td>6.4</td>
<td>328</td>
<td>426</td>
<td>3 Jun</td>
<td>Lab</td>
<td>16 Sep</td>
<td>47</td>
<td>Unknown; battery; Otter Brook</td>
</tr>
<tr>
<td>5</td>
<td>6.4</td>
<td>297</td>
<td>316</td>
<td>4 Jun</td>
<td>Lab</td>
<td>8 Jul</td>
<td>17</td>
<td>Found transmitter at Combs Brook</td>
</tr>
<tr>
<td>6 (wild)</td>
<td>5.5</td>
<td>253</td>
<td>180</td>
<td>1 Jul</td>
<td>Combs Brook</td>
<td>17 Jul</td>
<td>9</td>
<td>Unknown; battery; Combs Brook</td>
</tr>
<tr>
<td>7</td>
<td>5.5</td>
<td>255</td>
<td>191</td>
<td>1 Jul</td>
<td>Combs Brook</td>
<td>21 Jul</td>
<td>10</td>
<td>Unknown; battery; Combs Brook</td>
</tr>
<tr>
<td>8</td>
<td>6.4</td>
<td>266</td>
<td>210</td>
<td>2 Jul</td>
<td>Otter Brook</td>
<td>17 Jul</td>
<td>8</td>
<td>Found transmitter 400 m upstream of Lunch Rock</td>
</tr>
<tr>
<td>9</td>
<td>6.4</td>
<td>445</td>
<td>1178</td>
<td>2 Jul</td>
<td>Otter Brook</td>
<td>30 Sep</td>
<td>39</td>
<td>Unknown; battery; Otter Brook</td>
</tr>
<tr>
<td>10</td>
<td>6.4</td>
<td>354</td>
<td>533</td>
<td>7 Aug</td>
<td>Lunch Rock</td>
<td>21 Aug</td>
<td>11</td>
<td>Found transmitter at Lunch Rock</td>
</tr>
<tr>
<td>11</td>
<td>5.5</td>
<td>279</td>
<td>205</td>
<td>7 Aug</td>
<td>Lunch Rock</td>
<td>18 Sep</td>
<td>23</td>
<td>Unknown; Combs Brook</td>
</tr>
<tr>
<td>12</td>
<td>6.4</td>
<td>404</td>
<td>840</td>
<td>12 Aug</td>
<td>Otter Brook</td>
<td>30 Sep</td>
<td>23</td>
<td>Unknown; battery; Otter Brook</td>
</tr>
<tr>
<td>13</td>
<td>5.5</td>
<td>278</td>
<td>210</td>
<td>26 Aug</td>
<td>Lunch Rock</td>
<td>9 Sep</td>
<td>8</td>
<td>Unknown; battery; 500 m downstream of Lunch Rock</td>
</tr>
<tr>
<td>14 (wild)</td>
<td>5.5</td>
<td>290</td>
<td>214</td>
<td>26 Aug</td>
<td>Limekiln Pool</td>
<td>4 Sep</td>
<td>6</td>
<td>Unknown; 500 m downstream of Combs Brook</td>
</tr>
<tr>
<td>15</td>
<td>5.5</td>
<td>281</td>
<td>206</td>
<td>27 Aug</td>
<td>Combs Brook</td>
<td>29 Aug</td>
<td>2</td>
<td>Unknown; Combs Brook</td>
</tr>
<tr>
<td>16</td>
<td>5.5</td>
<td>288</td>
<td>242</td>
<td>27 Aug</td>
<td>Combs Brook</td>
<td>5 Sep</td>
<td>6</td>
<td>Found dead at Combs Brook</td>
</tr>
<tr>
<td>17</td>
<td>6.4</td>
<td>423</td>
<td>950</td>
<td>28 Aug</td>
<td>Otter Brook</td>
<td>23 Sep</td>
<td>11</td>
<td>Unknown; battery; Otter Brook</td>
</tr>
</tbody>
</table>

caught and implanted with transmitters in the field were captured from the 6-km reach between the Combs and Otter brooks (Tables 1, 2; Figure 1).

Radio-tagged fish were located and temperatures recorded during daylight hours from 9 June through 30 September 1997, with a three-element yagi antenna and a model R2000 receiver (Advanced Telemetry Systems). Fish temperatures were recorded on 53 d during the duration of the study. Every day when observations were recorded, an attempt was made to locate and record the temperatures of every fish with an active transmitter. The entire 12-km study reach was searched with the receiver to locate fish. The 10-pulse time period was measured four or more times for each temperature observation. Locations were determined to within 5–10 m and recorded on 1:24,000 maps. If a fish was in the same location for five or more days, it was disturbed to determine whether it was still alive. In some cases, fish were found dead; in others, only transmitters were found. Temperature observations 1–7 d prior to the probable death of the fish were excluded from analysis. At least one fish (rainbow trout number 18) expelled its transmitter. This fish was subsequently caught by angling about a month after the transmitter was found. Observations made when snorkeling or angling indicated that transmitter-tagged fish were often seen with untagged trout and appeared to behave similarly.

Data analysis.—To determine thermal habitat use, the temperatures recorded from the fish with transmitters were compared with water temperatures. To analyze the deviations between fish and main river flow temperatures, the differences between fish temperatures and the nearest river temperature monitoring site were used (Bisby Bridge, Limekiln Pool, or Lunch Rock; Figure 1). The temper-
temperatures at the Bisby Bridge monitoring site were compared with the fish temperatures recorded in the reach downstream from Limekiln Pool. The temperature measurements made at the Lunch Rock site were used in the analyses to represent the river temperatures above Limekiln Pool. The Limekiln Pool monitoring site (0.3-m depth temperature) was used for comparison with the temperatures of the fish located in Limekiln Pool. The mean distance between the locations where the fish temperatures were recorded and the river temperatures at the Bisby Bridge monitoring site were 1.6 km (range, 0–9.6 km). We used t-tests to compare the mean temperatures between the brook and rainbow trout and the deviations between the trout and river temperatures. Analysis of variance (ANOVA) was used to compare the different sources of cool water (e.g., tributary or groundwater discharge) based on the temperatures measured by the transmitters in the trout at these locations. If the ANOVA indicated significant differences ($P \leq 0.05$), Tukey’s tests were used to make comparisons between the locations (Zar 1984).

Results

River Water Temperature

Based on measurements at Bisby Bridge (Figure 2), water temperatures above 20°C occurred periodically in the Moose River from mid-June through early September. The mean water temperature from June through September was 18.3°C (range, 9.1–26.4°C). The highest mean daily temperature was 25.0°C; the mean daily water temperature was greater than 20°C for 32 d. The mean water temperature of the Moose River in 1997 was 7.8°C.

Evidence of Behavioral Thermoregulation

Study fish moved to localized areas of cool water in the Moose River during June through August...
TABLE 3.—Temperatures (°C) of brook and rainbow trout and the main river flow simultaneously recorded from the Moose River, New York, June through September 1997. Differences are between fish body temperature and the main river flow temperature; negative numbers indicate that the body temperature was less than the temperature of the main river flow. Data are also displayed for those observations recorded when the main river flow exceeded 20°C. The letter N represents the total number of observations from the 17 brook and 11 rainbow trout.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>SE</th>
<th>Minimum</th>
<th>Maximum</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Brook trout</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body</td>
<td>17.1</td>
<td>0.16</td>
<td>9.1</td>
<td>25.4</td>
<td>296</td>
</tr>
<tr>
<td>River</td>
<td>19.4</td>
<td>0.16</td>
<td>11.8</td>
<td>26.3</td>
<td>296</td>
</tr>
<tr>
<td>Difference</td>
<td>−2.3</td>
<td>0.15</td>
<td>0.8</td>
<td>−17.3</td>
<td>296</td>
</tr>
<tr>
<td><strong>Rainbow trout</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body</td>
<td>17.7</td>
<td>0.23</td>
<td>11.7</td>
<td>23.9</td>
<td>117</td>
</tr>
<tr>
<td>River</td>
<td>19.2</td>
<td>0.25</td>
<td>12.6</td>
<td>25.1</td>
<td>117</td>
</tr>
<tr>
<td>Difference</td>
<td>−1.5</td>
<td>0.15</td>
<td>1.2</td>
<td>−6.7</td>
<td>117</td>
</tr>
</tbody>
</table>

**Comparison of Brook and Rainbow Trout**

The mean temperature of brook trout (17.1°C) during the summer study period was less than that observed for rainbow trout (17.7°C; P = 0.04; Table 3). Similarly, the mean deviation between the river and brook trout temperatures (2.3°C colder than the river) was different from that observed for rainbow trout (1.5°C colder than the river; P = 0.002; Table 3). When river temperatures were 20°C or higher, the mean temperature deviation for brook trout (4.0°C colder than the river) was also greater than the mean deviation for rainbow trout (2.3°C colder; P = 0.002; Table 3). The two wild brook trout did not differ from the stocked brook trout in mean temperature deviations from the main river (P = 0.9).

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**Figure 3.**—Brook trout temperatures versus temperatures of the main flow of the South Branch of the Moose River. Each data point represents one observation of a fish temperature and a simultaneous measurement of the river temperature. The dashed line indicates equal fish and river temperatures.

**Figure 4.**—Rainbow trout temperatures versus temperatures of the main flow of the South Branch of the Moose River. Each data point represents one observation of a fish temperature and a simultaneous measurement of the river temperature. The dashed line indicates equal fish and river temperatures.
Table 4.—Differences at specific coolwater locations between temperatures of the main river flow and of brook and rainbow trout in the Moose River, New York, during the summer of 1997. Negative numbers indicate that the body temperature was less than the temperature of the main river flow. “Other” locations include records of fish temperatures when the radio-tagged fish were >500 m from the four primary coolwater areas.

<table>
<thead>
<tr>
<th>Coolwater location</th>
<th>Habitat type</th>
<th>Mean difference from river</th>
<th>SE</th>
<th>Maximum difference</th>
<th>Minimum difference</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combs Brook pool</td>
<td>Tributary confluence</td>
<td>−2.9</td>
<td>0.20</td>
<td>−7.4</td>
<td>0.2</td>
<td>84</td>
</tr>
<tr>
<td>Otter Brook pool</td>
<td>Tributary confluence</td>
<td>−1.2</td>
<td>0.10</td>
<td>−4.8</td>
<td>0.8</td>
<td>119</td>
</tr>
<tr>
<td>Lunch Rock</td>
<td>Groundwater–shallow pool</td>
<td>−3.5</td>
<td>0.46</td>
<td>−17.3</td>
<td>0.7</td>
<td>79</td>
</tr>
<tr>
<td>Limekiln Pool</td>
<td>Groundwater–deep pool</td>
<td>−1.8</td>
<td>1.08</td>
<td>−7.0</td>
<td>−0.2</td>
<td>6</td>
</tr>
<tr>
<td>Other</td>
<td></td>
<td>−1.1</td>
<td>0.33</td>
<td>−2.6</td>
<td>0.3</td>
<td>8</td>
</tr>
<tr>
<td>Combs Brook</td>
<td>Tributary confluence</td>
<td>−2.0</td>
<td>0.26</td>
<td>−4.9</td>
<td>0.3</td>
<td>31</td>
</tr>
<tr>
<td>Otter Brook pool</td>
<td>Tributary confluence</td>
<td>−0.7</td>
<td>0.39</td>
<td>−3.0</td>
<td>1.2</td>
<td>10</td>
</tr>
<tr>
<td>Lunch Rock</td>
<td>Groundwater–shallow pool</td>
<td>−0.6</td>
<td>0.39</td>
<td>−3.9</td>
<td>0.5</td>
<td>16</td>
</tr>
<tr>
<td>Limekiln Pool</td>
<td>Groundwater–deep pool</td>
<td>−1.8</td>
<td>0.23</td>
<td>−6.7</td>
<td>0.2</td>
<td>53</td>
</tr>
<tr>
<td>Other</td>
<td></td>
<td>−0.2</td>
<td>0.18</td>
<td>−0.9</td>
<td>0.6</td>
<td>7</td>
</tr>
</tbody>
</table>

**Types of Coolwater Habitats**

Tributary confluences or instream groundwater discharge provided the coolwater habitats used by brook and rainbow trout to maintain body temperatures below the main river flow temperature. Four sources of cool water were occupied: the confluences of the Combs and Otter brooks, and two pools known as Lunch Rock and Limekiln (Figure 1). The temperature deviations observed between fish and river temperatures were dissimilar among sites (brook, $P < 0.001$; rainbow $P = 0.001$; Table 4).

Tributary confluences.—Large aggregations of stocked and wild trout occurred in the Moose River immediately downstream from the confluences of the Combs and Otter brooks (Figures 5, 6). On only one occasion was a trout with a transmitter observed out of the Moose River and up in one of these tributaries during the summer. Instead, fish positioned themselves downstream of the confluence where a coldwater plume from the tributary entered the main river. These confluence areas were used extensively by brook trout and, to a lesser extent, by rainbow trout. The mean temperature of Otter Brook was 13.4°C from 10 July through 12 August 1997, cooler than Combs Brook (mean temperature 14.2°C from 10 July through 12 August; $P < 0.001$). Both tributaries were much cooler than the average temperature of the main stem of the river over the same period (20.4°C).

Although Otter Brook was cooler than Combs Brook, brook trout at the Combs Brook confluence maintained a larger deviation from the river temperature than those at the Otter Brook confluence (Tukey’s test, $P < 0.05$; Table 4). Aggregations of approximately 30–50 trout often were located at the confluence of Combs Brook where the tributary water discharged into a stillwater, medium-depth reach of the Moose River (Figure 5). These aggregations included both stocked and wild brook trout, and occasionally a few stocked rainbow trout. Fish were positioned primarily beyond the edge of a small delta formed at the tributary mouth (Figure 5). In contrast, the Otter Brook confluence was located on the south side of the river in a shallow riffle with little cover in terms of deep water or woody material. A few brook trout were observed in the cool water at the confluence; however, most fish were located along the south side of the main river in a pool 80–160 m downstream that had a thermal gradient across the width of the pool, a result of the incomplete mixing of cool tributary water (Figure 6; Table 4).

No aggregations of trout or study fish were observed at the confluences of three other second- and third-order tributaries within the 12-km study reach. One tributary was warmer than the Moose River (mean, 20.4°C; range, 15.5–26.1°C; Figure 1). The two other tributaries were cooler than the Moose River and had mean temperatures of 18.0°C (Little Moose Outlet: range, 12.1–24.0°C) and 15.7°C (Pico Creek: range, 9.8–21.3°C) but were warmer than the Combs Brook (mean, 14.2°C; range, 9.6–18.4°C) and the Otter Brook (13.4°C; range, 9.2–17.3°C), the two streams with confluence areas used by trout. While Pico Creek had an average temperature nearly as cool as the Combs and Otter brooks, this stream was chronically acidic, with a
summer pH range of 4.2 to 5.0. Some untagged brook trout (<10 fish) were observed to use cool water at three other small, first-order tributaries within the study reach; however, radio-tagged trout were not observed in these areas.

Groundwater discharge.—The greatest difference between the body temperatures of the brook trout and the river temperatures occurred where groundwater upwelled at the bottom of Lunch Rock pool. Groundwater discharge in the pool was located at the bottom of a 2-m-deep, 4-m² area on the edge of the north side of the main channel and was protected from mixing with the main current flow at low discharge by a bedrock mass that jutted out and deflected the main flow away from the upwelling area. This physical arrangement allowed cool groundwater to accumulate in the bottom 30 cm of the pool. Aggregations of about 10–15 brook trout were observed by snorkeling in this area throughout the summer. At Lunch Rock, the brook
Figure 6.—Location of brook trout (shaded areas) in relation to surface temperature and depth at the confluence of Otter Brook with the South Branch of the Moose River on 2 July 1997. Few fish were located in the immediate confluence area. Most were located along the south bank in the pool downstream of the confluence, as indicated by shading. The trout location and temperature patterns depicted are representative of temperature conditions and fish distributions at this location throughout the summer during low-flow and warmwater periods.

trout with transmitter tags were an average of 3.5°C cooler than the river. The temperatures of the rainbow trout in this same pool were closer to the main river temperature and were only an average of 0.6°C cooler (Table 4).

The brook and rainbow trout also used a 5-m-deep pool with groundwater discharge (Limekiln Pool; Figure 1). The trout in this pool avoided the warm surface water, but neither did they use the coldest water at the bottom of the pool. Both species maintained similar temperatures and were an average of 1.8°C cooler than the river (Table 4). Bottom temperatures were an average of 5.8°C cooler than the surface of the pool, with a maximum of 13.7°C cooler. Except for one observation, radio-tagged fish were never found at temperatures cooler than those at the 3-m depth. At depths greater than 3 m in Limekiln Pool in August 1999, the concentrations of dissolved oxygen were approximately 2 mg/L (Baird 2000). During high discharge, thermal stratification ceased and the pool became isothermal. When base flows resumed, thermal stratification was reestablished within 48 h and the bottom became progressively cooler over time.

Discussion

Cool habitats created at two of five tributary confluences and by groundwater discharge in two large pools allowed trout in the Moose River to behaviorally thermoregulate and to avoid potentially stressful, warmwater temperatures during the summer. Radio-tagged fish, as well as other hatchery and wild trout, consistently used these areas during warm summer periods. However, radio-tagged brook trout were not always located in cool areas when the main river flow was greater than 20°C and were occasionally observed in the main river at temperatures up to 25.4°C. Feeding opportunities were likely limited in most coolwater areas as many fish were confined to a small refuge habitat. Some brook trout were observed actively feeding in the main river flow, while others were located nearby in an adjacent thermal refuge and appeared inactive. Individual trout may not constantly occupy coolwater areas but instead may periodically move out of refuge areas to feed and then return.

Interpretation of the statistical results of this study should be done cautiously because of autocorrelation of the observations, the imbalance in the number of observations per fish, and the small number of fish observed. Further, not all fish were observed for the same length of time over the same time period. Our observations of radio-tagged trout in coolwater areas in the Moose River in 1997 are consistent with other observations made from 1996 to 1999, and the pattern of trout use of the described areas of cool water during times of warm temperatures was a repeated pattern of fish behavior (Baird 2000).

The use of thermal refuge areas created by tributaries and groundwater discharges is probably a common behavioral means for the survival of adult brook trout in medium to large rivers that have warm summer temperatures. Brook trout have been reported to avoid warm temperatures in rivers and lakes elsewhere. For instance, brook trout in the Ford River, Michigan, moved upstream into a cool headwater tributary that rarely exceeded 20°C when the main-stem river warmed to maximum temperatures of 22–23°C (Hayes et al. 1998). Lake-dwelling, adult brook trout have been reported to move into deep, cool waters in the summer (e.g., Power 1980). However, most studies of brook trout movement in association with temperature have focused on young of the year (age-
0). Age-0 brook trout have been reported to use areas of cool groundwater discharge in streams (Gibson 1966) and lakes (Biro 1998). Age-0 brook trout were observed in areas of groundwater discharge where temperatures were 18–20°C when surface temperatures in an Ontario lake were 23–27°C (Biro 1998). In a California lake with surface temperatures up to 23°C, age-0 brook trout occupied shallow areas with groundwater discharge, while age-0 rainbow trout were located in the pelagic and littoral zones (Wurtsbaugh et al. 1975).

In our study the rainbow trout did not position themselves in cool areas to the same extent as did the brook trout. For example, the rainbow trout rarely used the Lunch Rock shallow pool with groundwater discharge, even though 10–15 brook trout were often located there. Rainbow trout instead occupied an adjacent riffle–run habitat a few meters away near the head and tail of the pool. Rainbow trout located near the Combs Brook confluence had body temperatures cooler than the main river; this, however, may have been coincidental with some other habitat feature they preferred that also may have been cooled by the tributary water. Rainbow trout have been reported to use coolwater refuges in other streams (Kaya et al. 1977; Nielsen et al. 1994, Kaeding 1996; Matthews and Berg 1997). Similar to the use of cool tributary water in the Moose River, at the confluence of a cool tributary with a warm stream in California, rainbow trout were located in the coolest water available and always had body temperatures less than 20°C (Baltz et al. 1987). In contrast, rainbow trout and brown trout Salmo trutta equipped with temperature-sensitive radio transmitters did not use cool water at the bottom of a thermally stratified pool in a California stream (Matthews et al. 1994), perhaps because the maximum temperature of the stream (19.3°C) was not warm enough to stimulate them to seek cooler water.

The rainbow trout in the Moose River may have used coolwater refuges less frequently than the brook trout because they prefer higher temperatures (e.g., Coutant 1977; Hokanson et al. 1977) or perhaps because the maximum temperatures rarely exceeded the lethal limits for rainbow trout (25°C; e.g., Bidgood and Berst 1969). Alternatively, the brook trout may have competitively excluded the rainbow trout from refuge areas. The timing, amount, and location of different water temperatures—when combined with the thermal preferences of a species—define their thermal habitat niche and can be considered a limiting ecological resource in space and time (Magnuson et al. 1979). For example, cool groundwater discharge areas considered limited habitat in the littoral zone of an Ontario lake resulted in brook trout defending positions within discharge areas (Biro 1998). The competitive exclusion of rainbow trout from the coolwater areas by brook trout may have occurred in the Moose River, although we observed no aggressive behavior either within or between species. Competition between species should intensify as the size of a coolwater refuge declines. In this study, at the smallest of the four areas of cool water (Lunch Rock) where tagged trout occurred, we observed the greatest differences between brook and rainbow trout temperatures. This could have been caused by competitive exclusion.

The physical attributes of a tributary confluence (such as orientation to the main flow, depth, and the location and type of substrate and bank materials) can influence the rate of mixing with warmer river water at base flows and thus determine how fish use the cooler tributary water. For example, at the confluence of Otter Brook, the channel configuration of the Moose River directed much of the main flow to the north bank at low flow, such that the cool tributary water on the south side mixed slowly, creating a large downstream refuge area (Figure 6). Presumably, if the main flow had been primarily on the south side of the channel, the downstream refuge would have been smaller because the tributary water would have mixed more rapidly. Bilby (1984) and Nielsen et al. (1994) reported that structures such as rocks or wood can slow the mixing of cooler water with warmer river water, thus increasing the area of cool water created by tributaries or groundwater sources.

Water depth at the tributary confluences was associated with refuge use. Fish were rarely observed in shallow (<45 cm) areas of cool water (e.g., at the mouth of Otter Brook) and instead were located in deeper areas. Tributaries in this study were shallow (<45 cm), which may explain their infrequent use by transmitter-tagged trout. Trout always aggregated in the Moose River near the confluences of Otter and Combs brooks in contrast to the Ford River, Michigan, where brook trout moved into cool headwater tributaries when the main river temperature was greater than 20°C (Hayes et al. 1998), possibly because these tributaries were larger than the Moose River tributaries.
Management Implications

Coolwater habitats for salmonids in thermally marginal streams may require special angling regulations in heavily fished areas where harvest is excessive. Many anglers who fished our study reach knew the exact locations of coolwater refuges along the 12-km reach where brook trout congregated during the summer. Their fishing sites included the two of five tributary confluences and the two specific pools with groundwater discharge that our study fish occupied. Although anglers may release the trout they catch, both immediate and delayed hooking mortality could be high if trout are caught from cool water, then physiologically stressed by being retrieved through adjacent warm water, and later released into warm water. The continual pursuit of trout over the summer by anglers might also discouraged the use of thermal refuges by fish.

The riparian zones within the drainage areas of marginal trout streams should be managed to protect the critical summer habitats provided by cool thermal refuges. Many habitat alterations—including the removal of vegetation—can result in an increase in water temperatures (e.g., Barton et al. 1985) and a decrease in the volume of coolwater areas created by tributaries and groundwater discharge. The natural thermal heterogeneity of stream systems provides important habitats for trout during the summer and should be maintained to promote the survival of salmonids in thermally marginal environments (Torgersen et al. 1999).

The physical manipulation of cool tributary confluences or groundwater sources to prevent mixing with the main river flow could increase the volume of cool water available for trout. The increased separation of cool tributary water from warm river water would increase the size of coolwater areas in the Moose River. In the littoral zone of an Ontario lake, Biro (1998) reported that creating 5-cm-deep depressions in areas of groundwater discharge increased the abundance of brook trout using such areas. In the Moose River or other similar streams, rocks or logs placed upstream of cool tributary confluences could redirect the warm stream water (under base flow conditions) to the opposite bank of the river channel, thus preventing cool tributary water from mixing. Such structures need to be effective only during low-flow periods because water temperatures cool during high-flow events. The water depth at confluence areas also could be increased to reduce mixing and provide protection from predators.

Cool thermal habitats created by tributaries and groundwater discharge will become more important for salmonid survival if global temperatures increase and cause stream temperatures to increase during the summer. If the atmospheric CO$_2$ concentration doubles, the maximum weekly average water temperatures of streams in northern New York State may increase by about 4°C (Eaton and Scheller 1996). In 1997, the maximum weekly average temperature in the Moose River was 22.5°C. An increase in the maximum weekly average to 26.5°C would be lethal for most trout (e.g., Fry et al. 1946) and would require all trout to use cool thermal refuge areas to survive. Groundwater temperatures would also increase by about 4°C, but cool refuges would still be created during the summer (Meisner 1990a, 1990b). If summer temperatures increase, the protection of groundwater and the watersheds of cool tributaries will be critical for brook trout survival in Adirondack rivers.

Acknowledgments

D. Josephson provided invaluable assistance and logistical support throughout this project. T. Patronski, T. Strakosh, T. Hughes, H. Barker Baird, P. Brown, and B. Weidel helped in the field and hatchery. The Adirondack League Club provided access to the study site and facilities to conduct this project. The Adirondack League Club, the Adirondack Fishery Research Fund, and a Kieckhefer Adirondack Fellowship provided funding for this project. M. Bain and B. Peckarsky of Cornell University provided helpful comments on an earlier version of this paper.

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