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# Classifying Regional Variation in Thermal Regime Based on Stream Fish Community Patterns

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*Abstract.*—Although the importance of water temperature to the ecology of stream fishes is well documented, relatively little information is available on the extent of regional variation in thermal regime and its influence on stream fish distribution and abundance patterns. In streams draining the heterogeneous glacial landscape of Michigan's Lower Peninsula, regional variation in summer mean temperature and temperature fluctuation is among the highest reported in the literature. We developed a habitat classification to simplify the description of thermal regimes and to describe the relationships between available thermal regimes and distribution patterns of stream fishes. Changes in community composition, species richness, and standing stocks of key fish species occurred across gradients in mean temperature and temperature fluctuation. These changes were used to identify three mean temperature categories (cold, <19°C; cool, 19–<22°C; and warm, ≥22°C) and three temperature fluctuation categories (stable, <5°C; moderate, 5–<10°C; and extreme, ≥10°C). The combination of these categories resulted in a 3 × 3 matrix with nine discrete thermal regimes. The classification developed in this study provides a framework for descriptions of the realized thermal niche of stream fishes, and can be used as a baseline for measurement of changes in distribution patterns associated with future climate warming. Our results suggest that observed differences in community structure among sites are largely attributable to spatial variation in mean temperature and temperature fluctuation. Thus, accounting for the linkage between regional variation in thermal regime and fish community structure should improve our ability to effectively assess and manage stream resources.

In streams and rivers, quantifying temporal and spatial variation in key lotic habitat features is critical to understanding mechanisms regulating species assemblage structure and to evaluating the impacts of environmental perturbations (Poff and Ward 1990; Schlosser 1990). Despite a large body of literature documenting the importance of temperature on the physiology (Fry 1971; Sweeney and Schnack 1977; Sweeney 1978; Cech et al. 1990), life histories (Vannote and Sweeney 1980; Ward and Stanford 1982; Haro and Wiley 1992), and distribution patterns (Huet 1959; Matthews 1987; Rahel and Hubert 1991; Hawkins et al. 1997) of stream biota, relatively little information is available regarding the regional variation of stream thermal regimes. The paucity of regional studies is partly attributable to the historical focus on longitudinal patterns within individual streams and to the general lack of systematic collections of stream temperature data across relatively broad geographic regions.

Thermal regimes in stream reaches have been traditionally described in terms of coldwater, coolwater, and warmwater categories, based on the dominant fish species present. For example, the classical longitudinal zonation schemes developed near the turn of the 20th century (Thienemann 1912, 1925; Carpenter 1928) divided a river longitudinally into coldwater zones dominated by salmonids and cottids, and warmwater zones dominated by centrarchids, ictalurids, and cyprinids. Numerous classifications of this type have been developed for systems arising in mountainous regions, where species composition changes abruptly across altitude-related gradients in water temperature (Burton and Odum 1945; Huet 1959; Hynes 1970; Hawkes 1975; Cech et al. 1990; Rahel and Hubert 1991).

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Streams draining lower-elevation regions can also exhibit considerable variation in thermal regime. In the upper Midwest, spatial variation in thermal regime is maintained primarily by differences in groundwater accrual among catchments and stream segments (Meisner et al. 1988; Wiley et al. 1997; Wehrly et al. 1998a; Wehrly 1999). Classifications have been proposed for streams draining lower-elevation regions, including streams in Michigan (Anonymous 1967), Ontario (Ricker 1934), and Wisconsin (Lyons 1996). As in mountainous regions, these classifications described stream reaches in terms of coldwater, coolwater, and warmwater categories, based on the dominant fish species present.

Although specific thermal requirements of individual fish species have been used to group fish into coldwater, coolwater, and warmwater categories (Hokanson 1977; Magnuson et al. 1979), such classifications have had limited utility in lotic systems. This partly results from inconsistencies between laboratory and field observations and from regional differences in available thermal habitat across a given species' range. For example, summer thermal regimes available to warmwater fishes in Michigan are substantially different from those available to similar species in Alabama. Furthermore, a growing number of observations suggest that finer-scale spatial differences in thermal regime within these broad categories can have important consequences for species composition (Matthews 1987; De Staso and Rahel 1994; Smale and Rabeni 1995; Wehrly 1999). Finally, most studies describing changes in species composition as a function of water temperature have focused on the effects of average or maximum stream temperatures. However, both laboratory (Hokanson et al. 1977; Biette and Geen 1980; Diana 1984) and field (Matthews 1987; Smale and Rabeni 1995; Hinz and Wiley 1997; Wehrly et al. 1998b; Wehrly 1999) observations suggest that the extent of diel temperature fluctuation is also important. We believe that effective ecological assessment and management of lotic ecosystems requires a more detailed understanding of the linkage between variations in thermal regime and the distribution and abundance patterns of stream biota.

The goal of this study was to describe the relationship between regional variation in thermal regime and community structure of stream fishes. To simplify the description of thermal regimes across the heterogeneous, glaciated region of study (the Lower Peninsula of Michigan), we developed a thermal habitat classification. This classification provides a common language for communication among managers, researchers, and interested user groups (Hudson et al. 1992). In addition, it provides a framework for evaluating the influence of thermal regime as a factor controlling species assemblage structure at sites distributed across a relatively broad geographic region. In this paper, we seek to (1) describe a novel approach for classifying regional variation in thermal regime that includes both mean temperature and temperature fluctuation and (2) illustrate the potential uses of this classification approach by describing the relationships between available thermal regimes and observed distribution patterns for selected riverine fish species.

## Methods

*Water temperature data.*—Temperature data were collected with maximum–minimum thermometers and digitally recording thermographs during the first three weeks of July at 171 sites in lower Michigan. The temperature data were collected over several years (1989, 1990, 1994, and 1996), but in this analysis, we used only one observation (year) per site. When data for more than one year were available for a site, we arbitrarily chose the earliest record for inclusion in this analysis. For each site, we determined the maximum weekly July stream temperature as the average of the three weekly maximum readings; similarly, we determined the minimum weekly July stream temperature as the average of the three weekly minimum readings.

We also described summer thermal characteristics at 499 additional lower Michigan sites, based on predictive models developed by Wehrly et al. (1998a). The models predict average July weekly maximum and minimum stream temperatures as a function of catchment-scale and reach-scale landscape attributes, and account for 70–81% of the spatial variation in measured July stream temperatures across lower Michigan. Models were constructed with temperature data (from the 171 sites) that represented the range of July thermal characteristics observed in lower Michigan rivers. Channel characteristics, riparian forest cover, and local and network groundwater contributions were primary factors controlling spatial distribution of stream temperatures across lower Michigan (Wehrly et al. 1998a).

For this classification analysis, we combined measured and predicted maximum and minimum stream temperatures into one dataset ($N$ = 670). For each site, weekly mean July temperature was calculated as the average of the weekly maximum and minimum temperatures for that site. Mean July temperatures calculated with this method are typically within 1°C of the true weekly mean temperature calculated from continuous temperature records (K. E. Wehrly, unpublished data). We also calculated the average weekly July fluctuation as the difference between weekly maximum and minimum stream temperatures. Hereafter, we will refer to mean weekly July temperature as the mean temperature, and to mean July weekly fluctuation as the temperature fluctuation.

*Fish data*.—Information on distribution and abundance of stream fishes were obtained from a database contained in the Michigan Rivers Inventory (MRI) program (Seelbach and Wiley 1997). The MRI database consists of fish abundance data from rotenone, mark–recapture, and multiple-pass depletion surveys conducted from 1960 to 1995. Seelbach and Wiley (1997) and Seelbach et al. (1988) provide greater detail regarding fish sampling techniques and computation of abundance estimates. For this analysis, we used standardized fish abundance estimates based on the weight of individual species per unit sampling area:

$$z_i = (d_{ij} - x_i)/\mathrm{SD}_i \tag{1}$$

where $z_i$ is the standardized standing stock for species $i$, $d_{ij}$ represents the standing stock of species $i$ at site $j$, $x_i$ is the statewide average standing stock (kg/ha) of species $i$, and $\mathrm{SD}_i$ represents the standard deviation of all standing stocks for species $i$ (Sokal and Rohlf 1995). The $z$-score facilitated comparisons between various species without the need to correct for differences in body size.

Fish abundance data were available for 307 of the 670 sites in the temperature database. Therefore, both temperature and fish abundance analyses were based on a sample size of 307. Presence–absence data were available for another 95 sites. Presence–absence and abundance data were combined to generate estimates of species richness for a total of 402 sites.

### *Approach to Classification*

Development of a thermal classification required the identification of criteria for assigning sites to a limited number of discrete thermal categories. Given that temperatures at sites across lower Michigan represent a more or less continuous gradient in mean temperature and temperature fluctuation, objective categorization of these data was desirable. Therefore, our approach was to examine the degree of change in fish community composition across gradients of both mean temperature and temperature fluctuation. Distinct changes in community composition across these gradients were assumed to reflect community-level responses to differences in mean temperature and temperature fluctuation. Changes in species richness and abundance patterns of key species across these gradients were also assumed to reflect community- and species-level responses to differences in temperature, and were used to corroborate (fine-tune) the thermal boundaries identified in the similarity analysis.

*Classification methodology*.—To examine changes in fish species composition across gradients of both mean temperature and temperature fluctuation, we used Sorensen's index of similarity:

$$C_s = 2j/(a + b), \tag{2}$$

where $C_s$ represents the similarity coefficient, $j$ is the number of species found at sites A and B, $a$ represents the number of species at site A, and $b$ is the number of species at site B. Sorensen's index provides a simple measure of similarity between two sites; $C_s$ values range from 0 (sites are dissimilar and have no species in common) to 1 (sites are completely similar with identical sets of species present) (Magurran 1988).

To compute similarity coefficients, we first placed sites into one of 12 mean temperature categories and one of eight temperature fluctuation categories. For example, sites with mean temperatures ranging from 20.0°C to 20.9°C were assigned to the 20°C category. Similarity coefficients were calculated for all pairwise combinations of sites, based on a measure of presence–absence generated from standardized fish abundance estimates. To minimize the effects of rare occurrences, we considered a species as present at a site only if its abundance exceeded the statewide average standing stock ($z > 0$).

We used the software program Mathcad (version 6.0) to generate a matrix containing the similarity coefficients for all pairwise site combinations. We then computed the average similarity of sites using similarity coefficients generated from within and among temperature category comparisons. For example, we determined the average similarity of sites at 20°C by first calculating the similarity among all sites within the 20°C category and then averaging those values. Likewise, the average similarity between sites at 20°C and at 21°C was determined by calculating the pairwise similarity be-

TABLE 1.—Guild membership (Eaton et al. 1995) of fish species used to evaluate thermal classification, presented with the number (*N*) of sites where each species was present, the maximum weekly average temperature tolerance (Eaton and Scheller 1996), and the optimal thermal category determined in this study by habitat suitability analysis.

| Guild and species | *N* | Maximum tolerance (°C) | Optimal thermal regime |
|---|---|---|---|
| Coldwater guild | | | |
| Brook trout *Salvelinus fontinalis* | 78 | 22.4 | Cold–table |
| Rainbow trout *Oncorhynchus mykiss* | 64 | 24.0 | Cold–moderate |
| Brown trout *Salmo trutta* | 115 | 24.1 | Cold–moderate |
| Slimy sculpin *Cottus cognatus* | 16 | | Cold–moderate |
| Mottled sculpin *Cottus bairdi* | 63 | 24.3 | Cold–moderate |
| Coolwater guild | | | |
| Longnose dace *Rhinichthys cataractae* | 21 | 26.5 | Cool–moderate |
| Creek chub *Semotilus atromaculatus* | 174 | 27.1 | Cold–extreme |
| Blacknose dace *Rhinichthys atratulus* | 77 | 27.2 | Cold–moderate |
| White sucker *Catostomus commersoni* | 209 | 27.4 | Cool–moderate |
| Northern pike *Esox lucius* | 128 | 28.0 | Cool–extreme |
| Central mudminnow *Umbra limi* | 142 | | Cool–moderate |
| Burbot *Lota lota* | 24 | | Cool–extreme |
| Warmwater guild | | | |
| Rock bass *Ambloplites rupestris* | 176 | 29.3 | Warm–extreme |
| Smallmouth bass *Micropterus dolomieu* | 115 | 29.5 | Warm–moderate |
| Green sunfish *Lepomis cyanellus* | 156 | 34.0 | Cool–moderate |
| Common carp *Cyprinus carpio* | 126 | 35.0 | Warm–stable |
| Channel catfish *Ictalurus punctatus* | 44 | 35.0 | Warm–stable |

tween all sites in the 20°C category with those in the 21°C category, and subsequently calculating the average of those values. In this example, average similarity measured the similarity in species composition among 20°C sites and between 20°C and 21°C sites. If temperature is an important environmental attribute shaping community structure, then species composition should correspond more closely among sites with the same temperature than between sites characterized by different temperatures.

We plotted the average similarity of sites for each temperature category against the gradients in mean temperatures and temperature fluctuations. This resulted in a series of similarity curves that together illustrate the rate of change in community composition across the temperature gradients. Curves showing similar patterns of change were grouped together; these groupings were then used to identify discrete thermal categories. Changes in species richness and abundance patterns of key species were also used as decision tools for delineation of discrete thermal categories, and helped fine-tune the boundaries identified in the similarity analysis.

### *Thermal Distribution of Selected Fish Species*

In order to quantify patterns of fish distribution and abundance, we generated a habitat suitability score within each category for 17 species representative of coldwater, coolwater, and warmwater thermal guilds (Table 1). Guild membership was based on information from Eaton et al. (1995). First, we calculated both the average standing stock of a species within each category and the proportion of sites within each category where that species was present. Average standing stocks and proportions were calculated from sites with standing stocks that equaled or exceeded the statewide average. For this analysis, standing stocks were reported in standard deviations above the mean ($z = 0$). Next, within each category, the average standing stock of a particular species was multiplied by the proportion of sites where the species was present. Finally, the resulting product in each category was then divided by the maximum product calculated for that species. Habitat suitability scores ranged from 0 to 1, and for this analysis, thermal regimes were considered either optimal (habitat suitability score = 1.00) or suitable (habitat suitability score ≥ 0.10).

To examine the distribution of selected species across thermal categories, we plotted sites with standing stocks that equaled or exceeded the statewide average of each species across gradients of both mean temperature and temperature fluctuation. This provided a graphical description of the realized thermal niche. Because the plots were based on sites having relatively high population standing stocks, we assumed that they represented

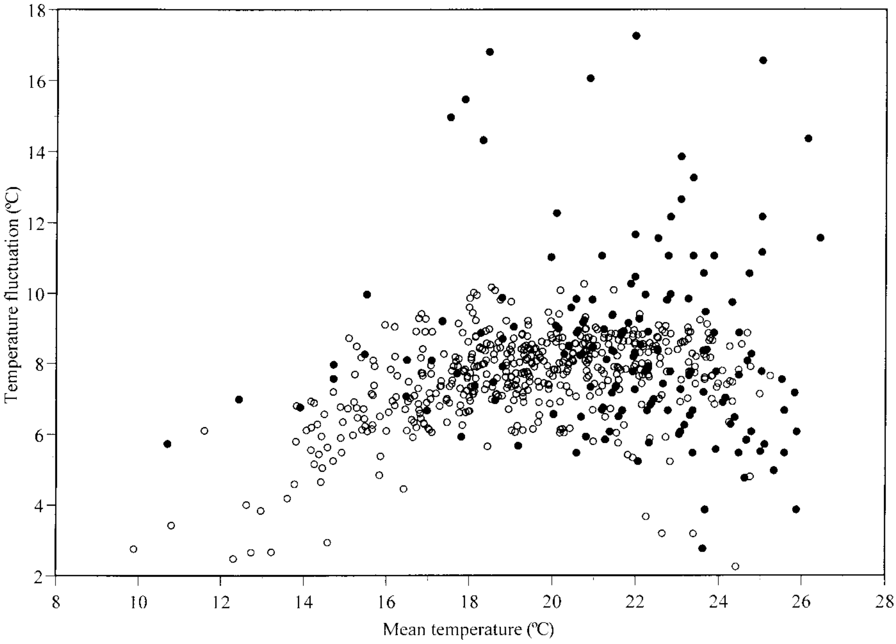


FIGURE 1.—Measured (closed circles) and predicted (open circles) July mean temperature and temperature fluctuations for 667 sites on lower Michigan rivers.

thermal conditions leading to optimal performance of each species.

## Results

### *Variation in July Temperatures*

Sites across lower Michigan exhibited considerable variation in summer thermal conditions (Figure 1). Mean temperatures ranged from 10°C to 26°C, with the majority of sites displaying mean temperatures between 16°C and 24°C. Temperature fluctuations ranged from 2°C to 17°C, with the majority of sites exhibiting fluctuations between 6°C and 9°C. Relatively low temperature fluctuations (<5°C) occurred at sites having either cold (<17°C) or warm (>22°C) mean temperatures. Relatively large temperature fluctuations were observed at sites having mean temperatures of 17°C or greater.

### *Fish Community Response to Mean Temperature Gradient*

Fish community composition changed dramatically at two points along the gradient of mean temperature (Figure 2). These transitions suggest three distinct regions of the gradient, each having a relatively distinct community composition: a coldwater group (14–17°C), a coolwater group (18–21°C), and a warmwater group (22–26°C). The similarity curve for sites at 18°C was interpreted as a transition between coldwater and coolwater categories; likewise, the similarity curve for sites at 21°C was interpreted as a transition between coolwater and warmwater categories.

The relation between average species richness and mean temperature demonstrated a general trend of increasing species richness with increasing mean temperature (Figure 3). However, the rate of change in species richness appeared to increase at temperatures greater than 18°C, then decrease at temperatures greater than 22°C. Stream size (catchment area) was also positively correlated with mean water temperature ($r = 0.60$; $P < 0.001$). To evaluate the potential effect of stream size on species richness, we divided our dataset into thirds based on catchment area, then reexamined the relation between species richness and mean temperature. Average species richness and mean temperature were highly correlated in small ($r = 0.95$; $P < 0.01$), medium ($r = 0.85$; $P < 0.01$), and large streams ($r = 0.78$; $P < 0.05$). However, species richness values at a particular mean temperature increased with increasing stream size.

The mean temperature was related to standardized standing stocks of selected fish species representing coldwater and warmwater guilds (Figure

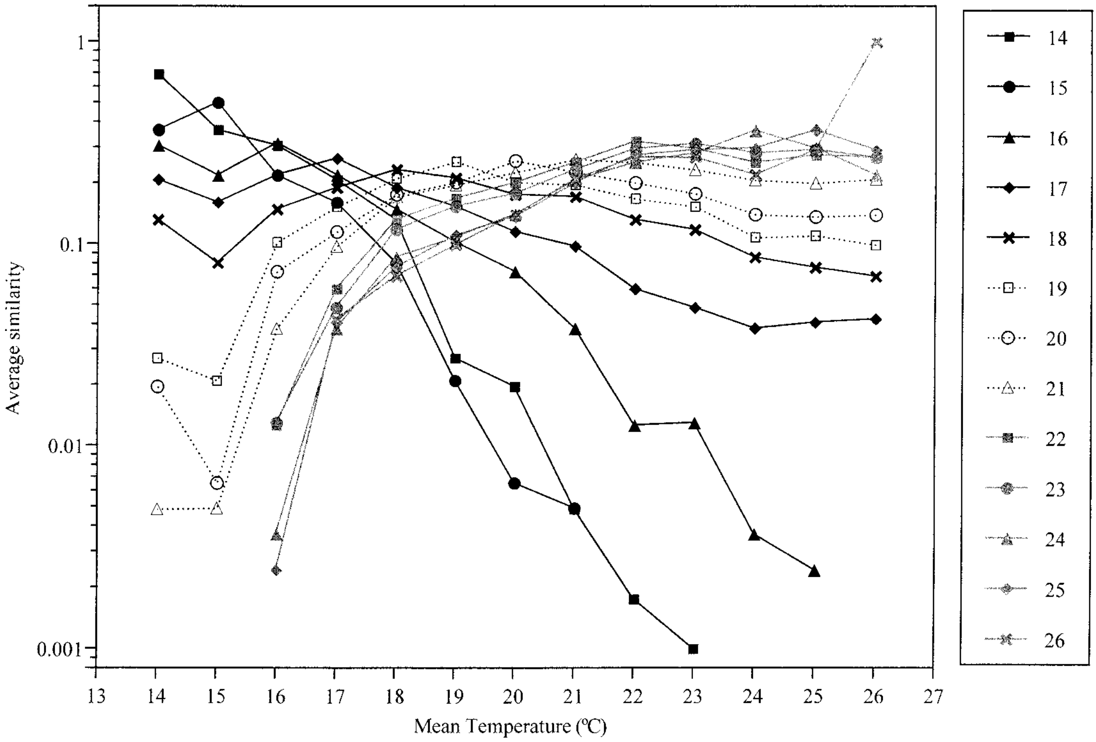


FIGURE 2.—Community similarity plots illustrating the extent of similarity in species composition among sites across a gradient of mean temperature. For each line, maximum similarity occurs where species composition was compared among sites with the same mean temperature. Changes in individual lines represent differences in community similarity that are attributable to among-site differences in mean temperatures. Truncated lines result from the exclusion of average similarity values equal to 0.

4). Mean temperatures at sites having the highest standing stocks of brook trout, brown trout, and rainbow trout ranged from 15°C to 19°C, and mean temperatures at sites where these species were present at average or above-average standing stocks ranged from 10°C to 22°C. Mean temperatures at sites with the highest standing stocks of common carp, channel catfish, and smallmouth bass ranged from 22°C to 26°C, and mean temperatures at sites where these species were present at average or above-average standing stocks ranged from 18°C to 26°C. Sites characterized by mean temperatures ranging from 19°C to 21°C exhibited relatively low standing stocks of any of these six coldwater or warmwater fishes. These results agreed with the patterns observed in the similarity and species richness plots.

We identified major ecological transitions in streams with mean temperatures between 18°C and 19°C and between 21°C and 22°C, resulting in three thermal categories based on mean temperatures: (1) 18°C or lower, (2) 19–21°C, and (3) 22°C or higher. Hereafter, these groupings will be referred to as cold, cool, and warm mean temperature categories.

### *Fish Community Response to Temperature Fluctuation Gradient*

Community composition changes with respect to temperature fluctuations suggested two distinct groups: a low fluctuation category (<5°C) and a high fluctuation category (5–18°C; Figure 5). Although some differences in community composition were evident for sites with relatively large temperature fluctuations (i.e., 10°C or greater), distinct groupings were difficult to identify.

Temperature fluctuation was also related to standardized standing stocks of selected fish species representing coldwater and warmwater guilds (Figure 6). Temperature fluctuations at sites with the highest standing stocks of brook trout, brown trout, and rainbow trout ranged from 6°C to 10°C, and fluctuations at sites where these species were present at average or above-average standing

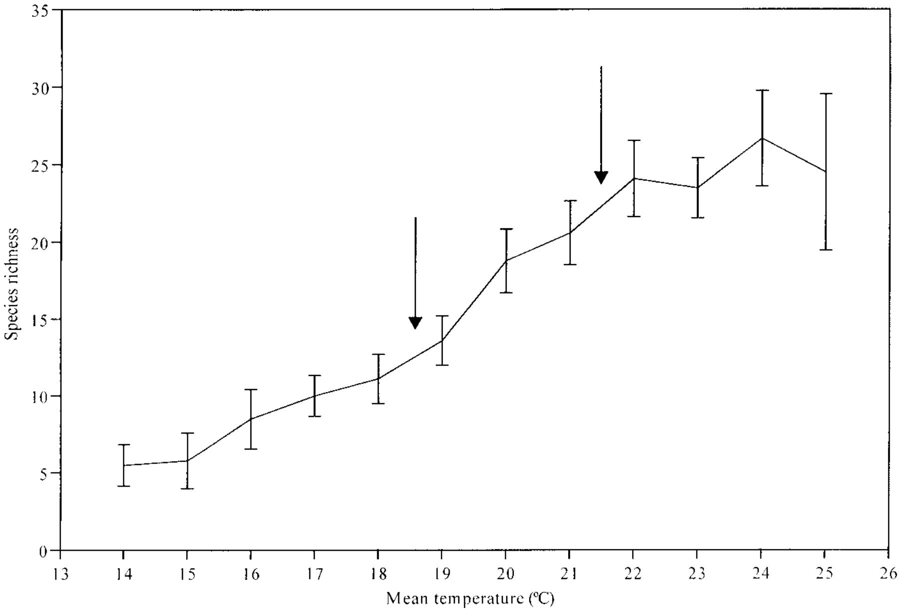


FIGURE 3.—Relationship between species richness (mean ±2 SE) and mean temperature categories. Arrows indicate transitions identified in similarity analysis (Figure 2).

stocks ranged from 2°C to 10°C (only one location exhibited a fluctuation >10°C). Temperature fluctuations at sites with the highest standing stocks of common carp, channel catfish, and smallmouth bass ranged from 4°C to 11°C, and fluctuations at sites where these species were present at average or above-average standing stocks ranged from 2°C to 17°C. Coldwater fishes were absent from sites with temperature fluctuations greater than 10°C, with the exception of one location. However, some warmwater fishes were present at relatively high standing stocks at sites exhibiting temperature fluctuations of 10°C or greater.

Based on changes in warmwater and coldwater fish presence at sites with above-average fish standing stocks, we identified an additional transition at 10°C, which resulted in three thermal categories based on temperature fluctuations: (1) less than 5°C (stable), (2) from 5°C to less than 10°C (moderate), and (3) 10°C or greater (extreme).

### *A Thermal Habitat Classification*

Mean temperature and temperature fluctuation categories were combined to create a 3 × 3 matrix with nine discrete thermal regimes (Figure 7). The majority of MRI sites (92%) occurred in the moderate fluctuation category at cold, cool, and warm mean temperatures. Relatively few sites were categorized as possessing stable (3% of sites) or extreme (5%) fluctuations. The total number of sites were fairly evenly distributed among cold (36% of sites), cool (36%), and warm (28%) mean categories.

We found a general increase in species richness and total standing stock from cold to warm sites (Table 2). Average species richness ranged from 6 (average standing stock = 69.9 kg/ha) in the cold–stable regime to 31 (standing stock = 304.5 kg/ha) in the warm–stable regime. Within the cold and cool mean categories, species richness and standing stock increased with increasing levels of temperature fluctuation. We observed the opposite trend within the warm categories, with the lowest species richness and standing stock occurring at high fluctuation (Table 2).

### *Habitat Suitability*

Brook trout was the only species whose optimum suitability occurred in the cold–stable regime (Table 3). Sites in the cold–moderate regime were also suitable for brook trout. Sites in the cold–stable regime were suitable, but not optimal, for brown trout and mottled sculpin and were unsuitable for rainbow trout and slimy sculpin. Optimum suitability scores for the remaining coldwater species corresponded to the cold–moderate regime. Distributions of suitability scores for rainbow trout, brown trout, and mottled sculpin extended into the cool–moderate regime and were much broader than those observed for brook trout and slimy sculpin.

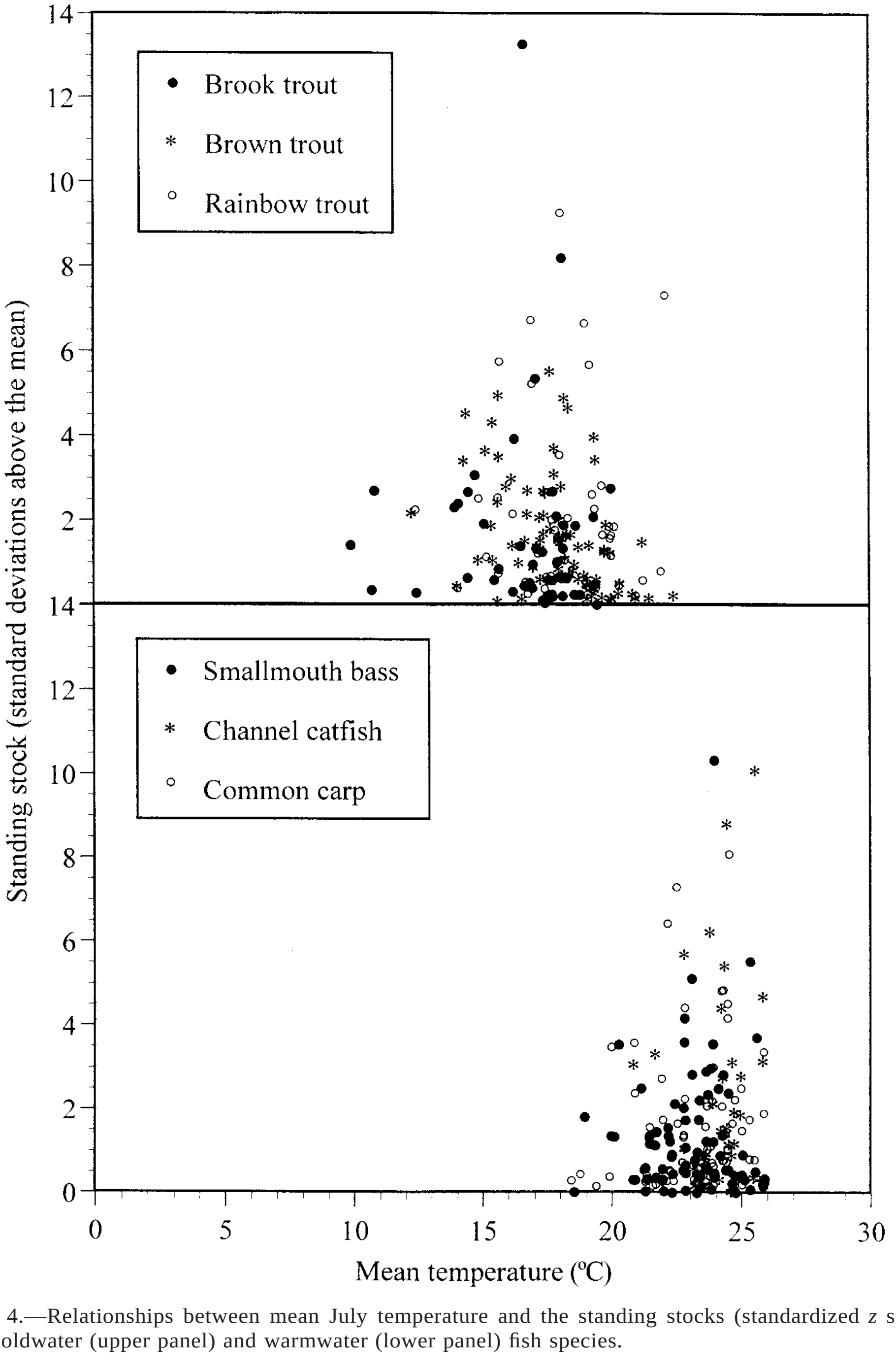


FIGURE 4.—Relationships between mean July temperature and the standing stocks (standardized *z* scores) of selected coldwater (upper panel) and warmwater (lower panel) fish species.

The distributions of habitat suitability scores were much more variable for selected coolwater fish than for coldwater fish (Table 3). Optimum suitability scores for coolwater fish encompassed several thermal regimes, including cold–moderate (blacknose dace), cold–extreme (creek chub), cool–moderate (longnose dace, white sucker, and central mudminnow), and cool–extreme (northern pike and burbot). With the exception of longnose dace and burbot, the habitat suitability distributions for coolwater species were relatively broad.

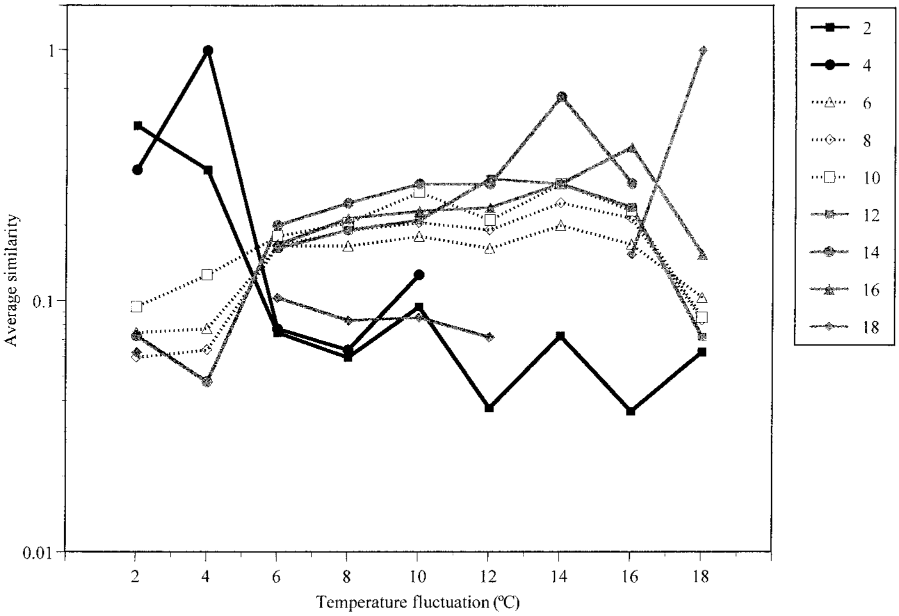


FIGURE 5.—Community similarity plots illustrating the extent of similarity in species composition among sites across a gradient of temperature fluctuation. For each line, maximum similarity occurs where species composition was compared among sites with the same temperature fluctuation. Changes in individual lines represent differences in community similarity that are attributable to among-site differences in temperature fluctuations. Truncated lines result from the exclusion of average similarity values equal to 0.

The distributions of habitat suitability scores for selected warmwater species were also variable (Table 3). Optimum suitability scores for fish in this group occurred in cool–moderate (green sunfish), warm–stable (common carp and channel catfish), warm–moderate (smallmouth bass), and warm–extreme (rock bass) thermal regimes. In all cases, the distributions of habitat suitability scores for warmwater fishes were relatively broad.

### *Thermal Distributions of Selected Fish Species*

Fish representing different thermal guilds showed considerable overlap, and in all cases, species were distributed across more than one thermal regime (Figures 8–10). coldwater species (Figure 8) had the narrowest distributions and were limited to cold and cool mean thermal categories. Distributions of coolwater (Figure 9) and warmwater species (Figure 10) were broader, and fish in these guilds were present across a greater number of thermal categories. In general, guild membership (Table 1) corresponded poorly with fish presence within a thermal category. For example, although coolwater species such as white sucker and northern pike (Figure 9) were present in cool mean thermal categories, they also occupied a large number of warmwater sites.

Differences in species distribution patterns were also observed for fish within each thermal guild, indicating that individual species within a guild occupied different thermal habitats. For example, within the coldwater guild, mottled sculpin were found more often in the cool–moderate regime than were either brook trout or slimy sculpin (Figure 8). In the coolwater guild, sites containing northern pike were distributed across both coolwater and warmwater categories, whereas creek chub were primarily distributed across coolwater and coldwater categories (Figure 9). In the warmwater guild, green sunfish were found in habitats cooler than those occupied by channel catfish (Figure 10).

## Discussion

The regional variation in stream thermal regimes found in this study is among the highest reported in the literature. Hawkins et al. (1997) found that the July mean temperature ranged from 9°C to 21°C and that the daily temperature fluctuation ranged from 6°C to 17°C across 45 montane

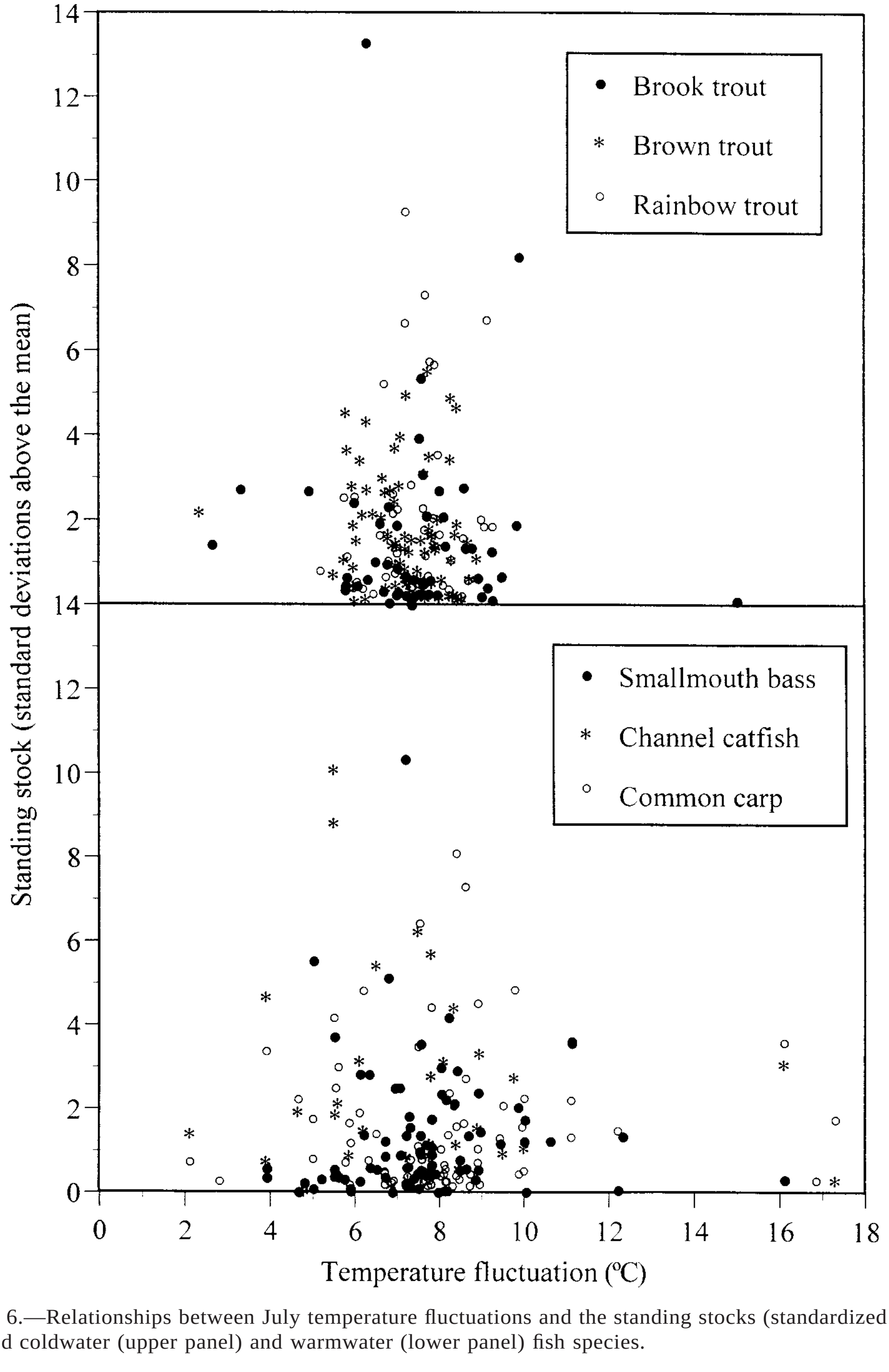


FIGURE 6.—Relationships between July temperature fluctuations and the standing stocks (standardized *z* scores) of selected coldwater (upper panel) and warmwater (lower panel) fish species.

streams in California. Ward (1985) summarized longitudinal differences in summer temperatures of several large rivers in the Southern Hemisphere. Mean temperatures ranged from 11.4°C to 25.0°C in the Purari River, New Guinea, and from 8.0°C to 23.5°C in the La Trobe River, Australia. These studies illustrate that spatial variation in thermal regime can result from a variety of factors, including regional differences in channel morphology (Hawkins et al. 1997), elevation (Ward 1985),

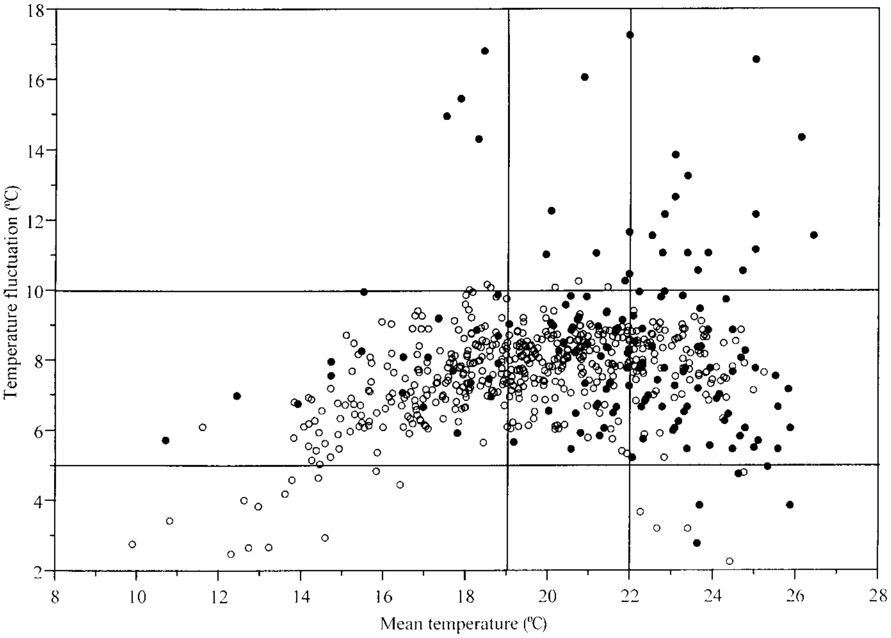


FIGURE 7.—The distribution of Michigan Rivers Inventory sites ($N = 667$) within each thermal regime. Regimes are defined by the intersection of thermal category boundaries (solid lines) from each axis. Thermal category boundaries for each axis are defined as cold (<19°C), cool (19°C to <22°C), and warm (≥22°C) mean temperatures, and stable (<5°C), moderate (5°C to <10°C), and extreme (≥10°C) temperature fluctuations. Closed circles indicate sites where temperatures were measured, and open circles indicate sites where temperatures were predicted.

and groundwater accrual (Wehrly et al. 1998a; Wehrly 1999).

### *Coldwater, Coolwater, and Warmwater Classifications*

A comparison of the coldwater, coolwater, and warmwater categories developed in this study with those proposed by Magnuson et al. (1979) and Lyons (1996) is shown in Table 4. In general, coldwater temperature ranges were similar across studies. However, the temperature ranges for coolwater and warmwater categories were somewhat lower for Michigan rivers (our study) than for Wisconsin streams (Lyons 1996) or laboratory thermal preference determinations (Magnuson et al. 1979).

Discrepancies among these classification systems partially result from different methodological approaches to classification. Magnuson et al. (1979) used laboratory preference data to define coldwater, coolwater, and warmwater guilds, and characterized both narrow and broad fundamental thermal niches of representative fish in each guild as the average final preference temperature ±2°C and ±5°C, respectively. Thus, this type of classification can be used to delimit the temperature range that an individual species should select to maximize

TABLE 2.—Average species richness (±2 SE) and (in brackets) average standing stock (±2 SE) in kg/ha within sites ($N = 402$) from each thermal regime.

| | Mean | | | |
|---|---|---|---|---|
| Fluctuation | Cold | Cool | Warm | Total |
| Extreme | 17 ± 10.4<br>[138.5 ± 56.5] | 24 ± 5.8<br>[281.3 ± 245.0] | 18 ± 2.0<br>[228.1 ± 114.8] | 20<br>[126.0] |
| Moderate | 9 ± 0.8<br>[102.2 ± 15.8] | 18 ± 1.2<br>[146.2 ± 26.2] | 25 ± 1.4<br>[285.6 ± 53.2] | 12<br>[178.0] |
| Stable | 6 ± 2.0<br>[69.9 ± 20.8] | | 31 ± 6.6<br>[304.5 ± 172.7] | 19<br>[187.3] |
| Total | 11<br>[103.6] | 21<br>[213.7] | 25<br>[272.7] | |

TABLE 3.—Habitat suitability scores for species within thermal regimes where species were present. Only sites having average or above-average standing stocks were included in the analysis. Thermal categories were considered optimal when scores equaled 1.00 and suitable when scores were greater than 0.10.

| | Cold | | | Cool | | | Warm | | |
|---|---|---|---|---|---|---|---|---|---|
| Guild and species | Stable | Moderate | Extreme | Stable | Moderate | Extreme | Stable | Moderate | Extreme |
| Coldwater | | | | | | | | | |
| Brook trout | 1.00 | 0.38 | 0.01 | | 0.02 | | | | |
| Rainbow trout | | 1.00 | | | 0.37 | | | 0.16 | |
| Brown trout | 0.28 | 1.00 | | | 0.17 | <0.01 | | <0.01 | <0.01 |
| Slimy sculpin | | 1.00 | | | 0.04 | | | | |
| Mottled sculpin | 0.45 | 1.00 | <0.01 | | 0.76 | | | <0.01 | <0.01 |
| Coolwater | | | | | | | | | |
| Longnose dace | | 0.25 | | | 1.00 | | | 0.09 | |
| Creek chub | | 0.39 | 1.00 | | 0.73 | 0.05 | | 0.03 | 0.15 |
| Blacknose dace | | 1.00 | 0.54 | | 0.63 | <0.01 | | <0.01 | 0.04 |
| White sucker | | 0.28 | 0.04 | | 1.00 | <0.01 | 0.01 | 0.44 | 0.68 |
| Northern pike | | <0.01 | 0.29 | | 0.51 | 1.00 | 0.03 | 0.54 | 0.17 |
| Central mudminnow | | 0.41 | 0.07 | | 1.00 | 0.44 | | <0.01 | 0.41 |
| Burbot | | | | | 0.48 | 1.00 | <0.01 | 0.20 | |
| Warmwater | | | | | | | | | |
| Rock bass | | 0.20 | 0.20 | | 0.17 | 0.97 | 0.00 | 0.96 | 1.00 |
| Smallmouth bass | | 0.02 | 0.00 | | 0.14 | 0.31 | 0.11 | 1.00 | 0.92 |
| Green sunfish | | 0.10 | 0.07 | | 1.00 | 0.36 | | 0.52 | 0.02 |
| Common carp | | 0.00 | 0.02 | | 0.09 | 0.83 | 1.00 | 0.78 | 0.49 |
| Channel catfish | | | | | 0.02 | 0.38 | 1.00 | 0.44 | 0.05 |

physiological performance (e.g., growth) (Brett 1971; Beitinger and Magnuson 1979; Magnuson et al. 1979). However, biotic interactions, availability of food, and availability of appropriate temperatures can influence observed thermal distributions (i.e., realized thermal niches) of fishes. For example, based on a final preferendum of 31°C (Coutant 1977) ±5°C, the fundamental thermal niche of adult green sunfish ranged from 26°C to 36°C. In Michigan, however, mean July stream temperatures rarely exceed 26°C (Figure 1), and the realized thermal niche of green sunfish (Figure 10) is considerably cooler than that expected from laboratory data. Consequently, inconsistencies between laboratory (fundamental niche) and field (realized niche) observations limit the utility of classifying stream reaches based on thermal preference data.

In a different approach, Lyons (1996) proposed threshold temperatures for classifying Wisconsin streams into coldwater, coolwater, and warmwater categories based on field observations of indicator species (e.g., trout). Similar classifications have been developed elsewhere (Ricker 1934; Van-Duesan 1954; Anonymous 1967), and allow identification of stream reaches that may potentially support important game fish species. However, because such classifications are based on distributions of a few key species, they may not reflect the range of thermal conditions available to other species, especially non-game fishes. In addition, the boundaries proposed do not necessarily represent community-level responses to temperature. Classifications of this nature have limited utility for predicting species composition at sites with similar thermal characteristics.

### *A Thermal Habitat Classification for Michigan Rivers*

We based our classification on July thermal regimes, because Michigan streams typically approach the lethal upper thermal limit for some taxa during this month, and differences in thermal regime among sites are also most pronounced in July (Hinz and Wiley 1997). The use of summer temperatures is common in stream classifications proposed for other regions (see references in Hynes 1970; Hawkes 1975; Hudson et al. 1992). However, classifications are usually based on maximum summer temperatures (e.g., Ricker 1934). To our knowledge, no prior classification has incorporated temperature fluctuations.

Within the MRI database, the number of sites having either stable or extreme July temperature fluctuations was relatively low. This scarcity may be explained, in part, by the relative rarity of certain thermal habitats. Stream size, groundwater accrual, and riparian shading are major landscape-scale factors controlling spatial variation in July temperatures among sites in lower Michigan rivers (Wehrly et al. 1998a; Wehrly 1999). Different catchment-specific combinations of these variables

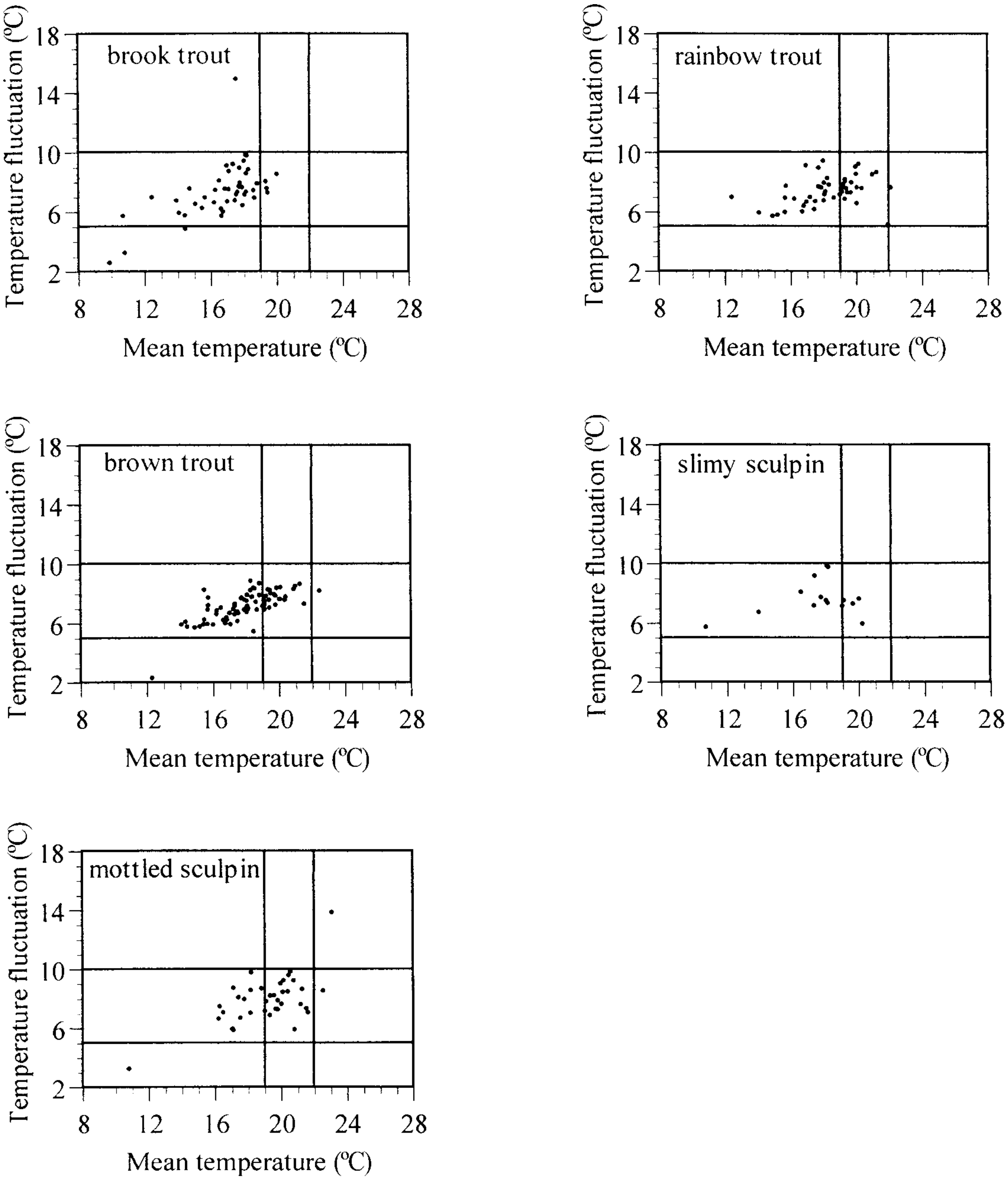


FIGURE 8.—Thermal distributions of coldwater fishes within each thermal regime in lower Michigan rivers. See Figure 7 for definition of thermal regimes.

give rise to the thermal characteristics observed in each regime. For example, sites in the cold–stable regime tend to be small, groundwater-dominated reaches draining forested landscapes. Relatively large groundwater contributions and extensive forest cover buffer these systems against diel changes in meteorological conditions (e.g., direct solar radiation and air temperature). In contrast, sites in the warm–extreme regime tend to be small, surface-runoff-dominated reaches draining agricultural landscapes. The relatively small volumes of water and the lack of shading in these systems result in thermal regimes that typically mimic daily air temperature patterns. Based on our experience in Michigan rivers, we believe that the combination of variables that are necessary to achieve certain thermal characteristics may be either relatively rare (cold–stable and warm–stable) or absent (cool–stable) in lower Michigan.

Sampling bias may be partially responsible for the limited number of sites exhibiting either very low or very high temperature fluctuations. The majority of sites within the MRI database are wadeable streams with the potential to support harvestable populations of game fish. As a result, certain sites such as small, warm headwaters (typical of sites in the warm–extreme regime) were underrepresented (Seelbach and Wiley 1997). Additional sampling in these areas will help clarify the relationships between temperature and patterns of fish distribution and abundance.

### *Relationships between Species Richness and Temperature*

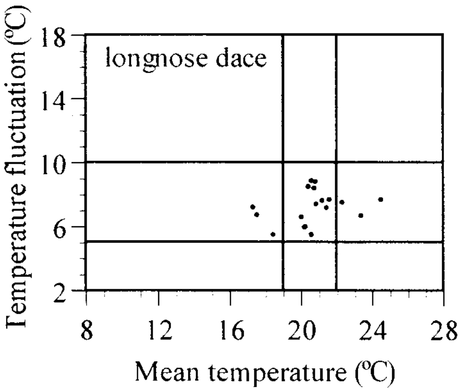
Differences in mean temperature strongly influenced species richness across sites, with a general increase in species richness from coldwater to warmwater categories. The gradient from coldwater to warmwater regimes has been shown to play a vital role in structuring both regional patterns of fish species richness (Lyons 1996; Zorn et al. 2002) and longitudinal changes in species richness within individual streams (Burton and Odum 1945; Huet 1959; Hynes 1970; Hawkes 1975; Rahel and Hubert 1991). Species richness can also increase as a function of stream size (Fausch et al. 1984; Angermeier and Schlosser 1989; Lyons 1996; Angermeier and Winston 1999; Newall and Magnuson 1999). Michigan rivers, however, do not exhibit the classical longitudinal pattern of small, cold headwaters grading into large, warm downstream reaches (Zorn et al. 2002). Although large rivers tend to be warm, smaller streams can be either warm or cold, depending upon groundwater inputs (Wiley et al. 1997; Wehrly et al. 1998; Wehrly 1999). If stream size were the dominant factor structuring species richness, then we would expect small, warmwater sites to have species richness values comparable to those of small, coldwater sites. Rather, we found that species richness was positively correlated with mean temperature *within* size-classes of streams. Our results suggest that temperature is important in structuring the overall trend depicted in Figure 3, and that stream size contributes to the variability in species richness among sites having the same mean temperature (represented by error bars in Figure 3).

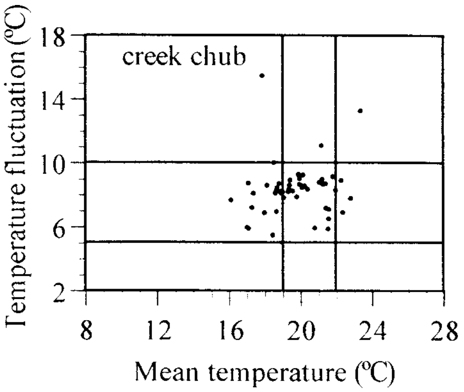
Differences in the extent of temperature fluctuation also appeared to influence patterns in species richness across sites. At cold and cool temperatures, increased fluctuation correlated with higher species richness. One possible explanation for this trend is that species less adapted to coldwater habitats require the warmer periods within the diel temperature cycle. Several studies have documented the exploitation of fluctuating thermal environments by certain fish species and the effects of cyclic temperatures on the metabolism and growth of fish (Brett 1971; Hokanson et al. 1977; Biette and Geen 1980; Diana 1984; Coutant 1987) and aquatic invertebrates (Sweeney and Schnack 1977; Sweeney 1978).

At sites having warm mean temperatures, increased fluctuation was correlated with lower species richness. This may result from the inability of certain species to tolerate even short-term exposure to temperatures exceeding the species' lethal limits. Large diel changes in temperature (and associated changes in dissolved oxygen content) are important limiting factors structuring the species composition of certain warm, headwater reaches (Matthews 1987; Smale and Rabeni 1995). However, the influence of large temperature fluctuations on fish assemblage structure in Michigan rivers remains poorly understood.

Temperature can also indirectly affect differences in species richness across sites. For example, the presence of competitively superior species may restrict the distributions of some fish species to thermally suboptimal habitats. Several authors have documented the importance of temperature-mediated competition on the distribution and abundance patterns of certain riverine fishes (Baltz et al. 1982; De Staso and Rahel 1994; Taniguchi et al. 1998). Stream temperatures also have been shown to affect the productivity of benthic invertebrates (Hinz and Wiley 1998) in Michigan. Consequently, differences in fish species richness among thermal regimes may reflect temperature-dependent differences in food availability.

The potential for temperature to influence patterns of species richness among sites has important implications for ecological assessment and monitoring methodologies (e.g., Index of Biotic Integrity [IBI]; Karr et al. 1986). Failure to acknowledge the influence of thermal regime on species richness could result in erroneous assessments of ecological integrity among sites having naturally occurring differences in thermal characteristics. For example, based solely on species richness, sites having warm mean temperatures and high


longnose dace
Temperature fluctuation (°C)
18
14
10
6
2
8
12
16
20
24
28
Mean temperature (°C)


creek chub
Temperature fluctuation (°C)
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14
10
6
2
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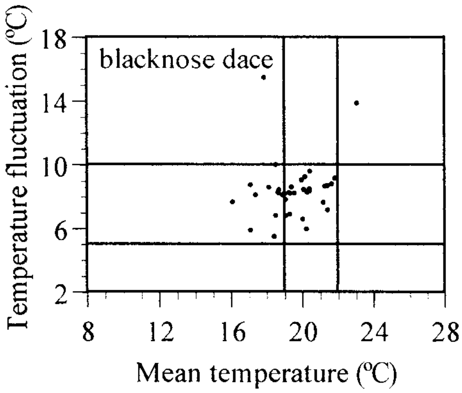
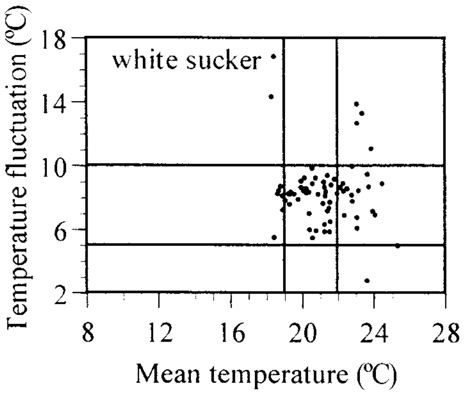
12
16
20
24
28
Mean temperature (°C)


blacknose dace
Temperature fluctuation (°C)
18
14
10
6
2
8
12
16
20
24
28
Mean temperature (°C)


white sucker
Temperature fluctuation (°C)
18
14
10
6
2
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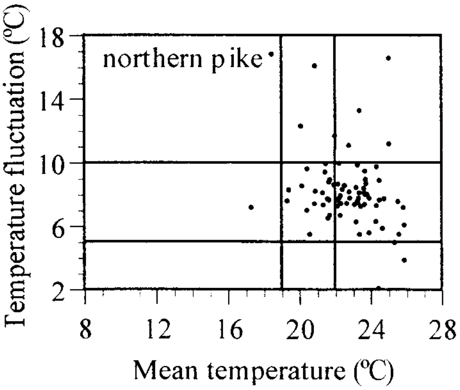
16
20
24
28
Mean temperature (°C)


northern pike
Temperature fluctuation (°C)
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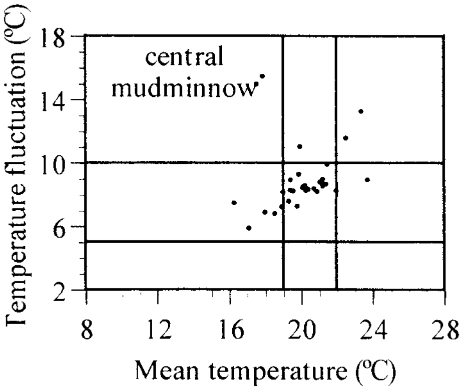
28
Mean temperature (°C)


central mudminnow
Temperature fluctuation (°C)
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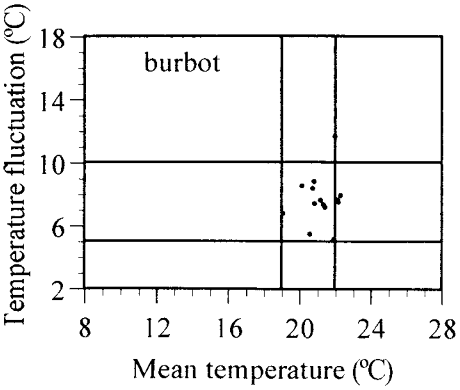
24
28
Mean temperature (°C)


burbot
Temperature fluctuation (°C)
18
14
10
6
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12
16
20
24
28
Mean temperature (°C)

temperature fluctuations would appear degraded when compared with sites having similar means and lower fluctuations. The IBI has been modified to account for broad-scale temperature differences (e.g., Coldwater IBI; Lyons et al. 1996) across sites. However, we found a continuous increase in species richness with increasing temperature (Figure 3), which suggests that relatively small differences in temperature between sites may inflate observed differences in ecological integrity. Further modifications to the IBI and other assessment metrics that incorporate the effects of both temperature fluctuation and finer-scale spatial differences in temperature on expected species richness should improve our ability to effectively assess and manage stream resources (e.g., Wiley et al. 2002).

### *Thermal Niche of Michigan Fishes*

The fact that most species were distributed across more than one thermal category reflects the ability of temperate fishes to function physiologically over a relatively broad range of temperature conditions. Based on laboratory and field observations, Magnuson et al. (1979) concluded that the range of temperatures typically occupied by fishes (niche width) is 10°C, regardless of guild membership. In Michigan, the average niche width (calculated from mean temperatures) was 10.3°C for coldwater fishes (95% confidence interval [CI] = 8.9–11.8°C), 6.8°C for coolwater fishes (95% CI = 6.0–7.7°C), and 7.3°C for warmwater fishes (95% CI = 6.1–8.5°C). The reduced range of temperatures occupied by warmwater fishes probably results from the limited range of warmwater habitats available in lower Michigan rivers. We hypothesize that the limited availability of warmwater habitats increases the overlap (and potential for biotic interactions) between coolwater and warmwater fishes, and contributes to the reduction in niche width for coolwater fishes. Interactions with coldwater fishes (Baltz et al. 1982; Taniguchi et al. 1998), differences in food availability among sites (Hinz and Wiley 1998), and the need to satisfy other habitat requirements may also explain the reduced range of temperatures occupied by coolwater fishes.

In this study, we found an increase in the average range of temperature fluctuation occupied by coldwater (7.6°C; 95% CI = 4.1–11.1°C), coolwater (9.8°C; 95% CI = 7.0–12.5°C), and warmwater (13.2°C; 95% CI = 11.6–14.8°C) fishes. Although little information is available on the thermal niches based on temperature fluctuations, the observed trend is consistent with Hokanson's (1977) observations that the range of temperatures to which the physiology and life history of fishes are adapted progressively increases from coldwater (stenothermal) to warmwater (eurythermal) species.

Relative performance (e.g., growth) of individuals and subsequent population dynamics are expected to vary across a species' realized thermal niche. Although we did not directly measure fish performance, differences in standing stocks (Figures 4, 6) and habitat suitability scores (Table 3) suggest that certain thermal regimes are more energetically profitable (Crowder and Magnuson 1983) than others. For example, smallmouth bass were present in six of nine thermal categories (Figure 10). However, habitat suitability scores indicate that smallmouth bass occur most frequently and in high numbers in only two thermal categories: warm–moderate and warm–extreme (Table 3). Differences in profitability across a species' thermal niche may have important management implications if, as suggested by Hokanson (1977), the mechanism of population regulation and the resiliency of populations to exploitation and environmental perturbations also differ as a function of thermal regime.

### *Limitations*

Development of our classification required that discrete boundaries be placed on gradients of mean temperature and temperature fluctuations, which are actually continuous variables. Although we attempted to draw boundaries that corresponded to distinct changes in community composition across sites, often the distribution of a given species exhibited a continuum across thermal categories. These extended distributions make it difficult to assign individual species to only one of the nine thermal categories, and therefore limit our ability to generate accurate expectations of assemblage structure, species richness, and standing stocks at sites with similar thermal characteristics. Nonetheless, the classification provides a useful means

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FIGURE 9.—Thermal distributions of coolwater fishes within each thermal regime in lower Michigan rivers. See Figure 7 for definition of thermal regimes.

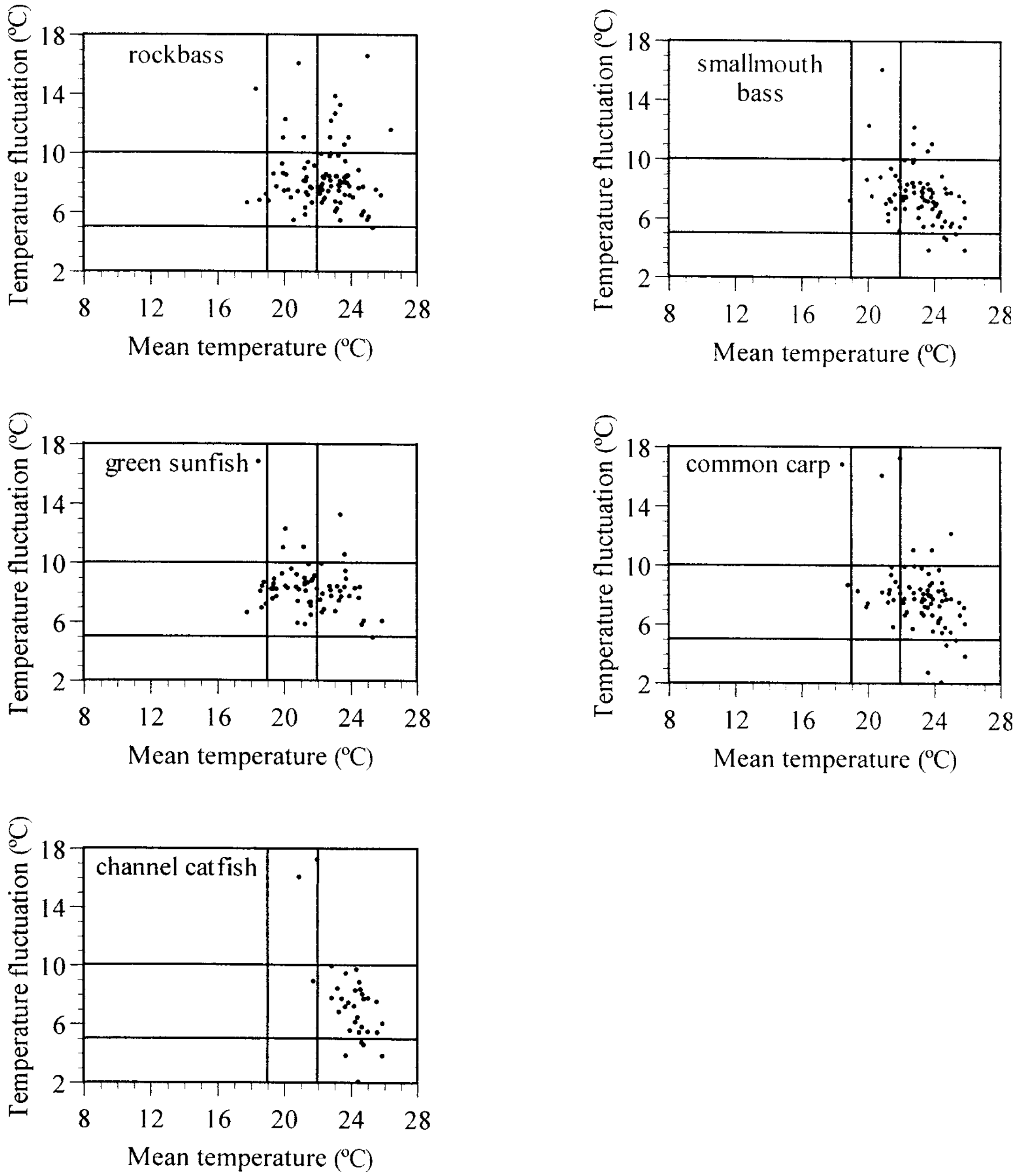

FIGURE 10.—Thermal distributions of warmwater fishes within each thermal regime in lower Michigan rivers. See Figure 7 for definition of thermal regimes.

for summarizing spatial variation in thermal regimes, and gives a general model for describing the influence of temperature on fish assemblage structure in lower Michigan rivers.

Development of the classification was limited by the quality of water temperature data. We used predicted temperatures for 62% of the sites (*N* = 307) included in the similarity analysis. Our ability to accurately classify stream types was therefore limited by the predictive ability of the models used to estimate maximum and minimum stream temperatures. The land cover attributes used to estimate temperatures were based on data from a single year (1978) and were assumed to be invariant

TABLE 4.—Comparison of proposed temperature ranges for coldwater, coolwater, and warmwater categories.

| | Temperature category | | |
|---|---|---|---|
| Source | Coldwater | Coolwater | Warmwater |
| Magnuson et al. (1979)[a] | | | |
| 4°C niche | 11–15°C | 21–25°C | 27–31°C |
| 10°C niche | 8–18°C | 18–28°C | 24–34°C |
| Lyons (1996)[b] | <22°C | 22–24°C | >24°C |
| This study[c] | 10–18°C | 19–21°C | 22–26°C |

[a] Average final preference temperatures.

[b] Mean maximum weekly summer temperatures.

[c] July weekly mean temperatures.

through time. However, changes in land cover attributes over the period for which fish data were collected (1960–1995) was a potential source of error in our temperature predictions. In addition, the temperature models tend to overestimate temperatures at colder sites and underestimate temperatures at warmer sites (Wehrly et al. 1998a). Because of this constraint, estimated temperature fluctuations were biased towards the moderate fluctuation category, and sites exhibiting either low (<5°C) or high (>10°C) temperature fluctuations were therefore underrepresented in the present analyses. Consequently, our ability to accurately characterize distribution and abundance patterns for individual fish species was also limited. Users of this classification should be aware that the number of sites exhibiting either stable or extreme temperature fluctuations would likely increase, and patterns of fish distribution and abundance might change, if additional measured temperatures were incorporated into the dataset.

Observed and predicted temperatures used in our study were based on a limited number of observations at each site and do not account for year-to-year variation in stream temperature. We expect that interannual variation in precipitation and air temperature would lead to variation in stream temperatures at a given site; sites showing large July fluctuations would also be expected to show the greatest variation in temperature across years. Based on 14 sites with more than one year of available temperature data, the average year-to-year difference was 1.9°C (95% CI = 1.4–2.4°C) for mean temperature and 2.4°C (95% CI = 1.6–3.2°C) for temperature fluctuation. Sites on or near the boundary between thermal regimes could therefore change from one regime to another in any given year. Ideally, a classification of this type would be based on long-term records (e.g., 40-year normals) similar to those used in hydrologic and climatologic analyses. However, in Michigan (as in other regions), long-term temperature records are available for only a few stream reaches.

Our results also may be limited by the quality of fish data used in this study. Abundance data were based on single estimates of standing stock at each site and were collected over several years. We assumed that these single values represented the average performance of fish populations over time. We also assumed that the single measures or estimates of temperature at each site were representative of the average thermal habitat experienced by fish over time. These assumptions contribute additional variation to already noisy data. We attempted to reduce the noise by modifying presence–absence data so as to minimize the influence of rare species occurrence at a site. Further analyses of temperature and fish data collected in the same year would result in a more accurate depiction of the relationship between temperature and fish community structure.

We assumed that thermal conditions were spatially homogeneous across a fish sampling reach and that measured temperatures at a single site within a reach represented the thermal characteristics throughout the sampled length of stream. Spatial variability in groundwater accrual or riparian cover within a reach, however, could result in finer-scale spatial differences in temperature. Fine-scale differences in temperature may have confounded our results and contributed to the relatively broad thermal distributions observed for some species.

Finally, the classification presented in this paper was based exclusively on temperature and fish data collected in lower Michigan rivers. Consequently, the extent to which it can be applied to streams in other regions is unknown. Factors that could potentially limit the widespread use of this classification include regional and local differences in (1) available thermal habitats, (2) species assemblages, (3) thermal niche partitioning, and (4) physiological adaptations. Evaluations of the classification outside lower Michigan are necessary to determine its transferability to streams in other regions.

## Conclusions

Our results suggest that streams draining low-elevation, glaciated landscapes can exhibit considerable spatial variation in summer thermal regime. Our classification approach provides a useful means to summarize this spatial variation and may be transferable to numerous other physiographic settings. In addition, the classification provides a framework for describing the realized thermal niche of stream fishes and can be used as a baseline from which to measure changes in distribution patterns associated with future climate warming (e.g., Eaton and Scheller 1996; Keleher and Rahel 1996). Finally, our results suggest that observed differences in community structure among sites are largely attributable to spatial variation in mean temperature and temperature fluctuation. Thus, accounting for the linkage between regional variation in thermal regime and fish community structure should improve our ability to effectively assess and manage stream resources.

## Acknowledgments

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