A Thermal Habitat Classification
for Lower Michigan Rivers

Kevin E. Wehrly,
Michael J. Wiley
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Paul W. Seelbach

MICHIGAN DEPARTMENT OF NATURAL RESOURCES
FISHERIES DIVISION

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Kevin E. Wehrly, Michael J. Wiley

School of Natural Resources and Environment
The University of Michigan
Ann Arbor, Michigan 48109

and

Paul W. Seelbach

Institute for Fisheries Research
Michigan Department of Natural Resources
212 Museums Annex Building
Ann Arbor, Michigan 48109

*Abstract.–*We developed a thermal classification for Lower Michigan rivers that characterizes the spatial variation in summer (July) temperatures in terms of both mean temperatures and temperature fluctuations. We used patterns of change in community composition, species richness, and abundance of key species to partition continuous gradients of mean temperature and temperature fluctuation to identify discrete thermal categories.

We identified three mean temperature categories (cold <19°C; cool 19 to 21 °C; and warm > 21°C) and three temperature fluctuation categories (stable < 5°C; moderate 5 to 9°C; and extreme > 9°C). These categories were combined to create a 3 x 3 matrix with 9 discrete thermal regimes. Species distribution data were plotted on this 3 x 3 matrix to examine how selected species were distributed across thermal regimes. In order to quantify patterns of distribution and abundance, we calculated both the average density of a species within each thermal regime and the proportion of sites within each thermal regime where that species was present. We also generated habitat suitability scores within each thermal regime for each species in order to identify appropriate thermal habitats for individual species.

Within the MRI database, 92% of 667 sites occurred in the categories exhibiting moderately fluctuating temperatures. Relatively few sites occurred in the stable (3%) or extreme fluctuation categories (5%). The total percentages of sites were evenly distributed in cold (36%), cool (36%), and warm (28%) mean categories.

We found a continuous increase in species richness from sites with cold to warm mean temperatures. Species richness ranged from 6 in the cold-stable regime to 31 in the warm-stable regime. Within the cold and cool mean categories, species richness increased with increasing levels of temperature fluctuation. The opposite trend was observed within the warm categories with the lowest richness occurring at high fluctuations.

Distributions of fish representing distinct thermal guilds showed considerable overlap and in all cases species were distributed across more than one thermal category. 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. In general, there was poor correspondence between guild membership and fish presence within a thermal category.

The classification developed in this study provides a framework to describe the summer thermal distribution of stream fishes, and can be used to generate expectations of species assemblage structure and standing stocks of key species at sites having similar thermal characteristics. Biologically meaningful patterns in fish species assemblage and abundance of selected species were observed across gradients. This suggests that summer thermal regime may be an important factor structuring fish communities in Lower Michigan rivers.

In lotic ecosystems, physical habitat is an important factor structuring patterns of species distribution and abundance for both fishes (Gorman and Karr 1978; Schlosser 1982) and aquatic insects (Richards et al. 1996; Wright 1995). This has been attributed to the characteristically large variation that exists among sites in variables such as streamflow, thermal regime, and substratum (Poff and Ward 1990). This variation in habitat can be viewed as a template (sensu Southwood 1977) that directly constrains life-history attributes and also can modify the influence of biotic interactions in regulating species assemblage structure. In addition, spatial and temporal variation in habitat quality can influence the resiliency of biota subjected to perturbations. For example, fish that naturally experience large diel fluctuations in temperatures and oxygen concentrations are less likely to be sensitive to human-induced impacts and are more likely to re-colonize disturbed areas than fish occupying more benign habitats (Matthews 1987). Consequently, quantifying temporal and spatial variation in key 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).

Water temperature is a key habitat feature that affects both fishes (Huet 1959; Matthews 1987; Cech et al. 1990; Rahel and Hubert 1991) and aquatic insects (Vannote and Sweeney 1980; Ward and Stanford 1982; Haro and Wiley 1992; Hawkins et al. 1997). Temperature can affect stream biota directly by controlling rates of feeding, metabolism, and growth (Fry 1971; Brett 1979); or indirectly by mediating biotic interactions (Baltz et al. 1982; DeStaso and Rahel 1994; Hinz and Wiley 1998). As a result,

spatial and temporal variation in stream temperature is likely an important factor contributing to the observed differences in species assemblages between sites.

Thermal regimes in stream reaches have been traditionally described in terms of cold-, cool-, and warmwater categories based on the dominant fish species present. Numerous studies have described changes in species composition along longitudinal temperature gradients from cold, headwater reaches to warm, downstream reaches (Burton and Odum 1945; Huet 1959; Hynes 1970; Moyle and Nichols 1973; Hawkes 1975; Cech et al. 1990; Rahel and Hubert 1991). Recently, ecological assessment protocols have been developed that incorporate the influence of these broad-scale temperature categories on differences in expected species assemblage structure across sites (e.g., development of a coldwater index of biotic integrity: Lyons et al. 1996).

Although specific thermal requirements of individual fish species have been used to formally group fish into cold-, cool-, and warmwater categories (Hokanson 1977; Magnuson et al. 1979), such classifications have had limited utility in lotic systems. This has been, in part, a result of inconsistencies between laboratory and field observations, and also in regional differences in available thermal habitat across a species' range. For example, summer thermal regimes available to warm-water fishes in Michigan are substantially different than those available to similar species in Alabama. Furthermore, a growing number of observations suggest that finer-scale differences in temperature within these broad categories also affect species composition (Matthews and Styron 1981; Matthews 1987; DeStaso and Rahel 1994; Smale and Rabeni 1995). We

believe that effective ecological assessment and management of lotic ecosystems requires a more detailed understanding of the linkages between spatial variation in water temperature, and distribution and abundance patterns of stream biota.

Lotic ecosystems range from smaller tributary to larger mainstem reaches that can vary in terms of both average temperatures and the magnitude of diel fluctuations (Macan 1958; Crisp and LeCren 1970; Webb and Walling 1986; Webb and Nobilis 1994). Most studies describing changes in species composition as a function of water temperature have focused on the effects of average (Rahel and Hubert 1991) or maximum (Bowlby and Roff 1986; Meisner 1990; Smale and Rabeni 1995) stream temperatures. However, the extent of diel temperature fluctuation can also affect stream biota. For example, exposure to relatively low (± 4°C about the mean) diel temperature cycles can enhance the growth rates of certain species of fish (Brett 1971; Hokanson et al. 1977; Biette and Geen 1980; Diana 1984) and aquatic insects (Sweeney 1976; Sweeney and Schnack 1977; Sweeney 1978) in laboratory settings. This response results from a relative increase in feeding rates during the warmer part of the cycle, and a relative decrease in metabolic demands during the cooler part of the cycle. In addition, relatively large diel changes in temperature (and associated changes in dissolved oxygen content) have been shown to be important limiting factors structuring the species composition of certain warm, headwater reaches (Matthews 1987; Smale and Rabeni 1995). Thus, spatial variation in diel temperature fluctuations may help to explain observed patterns of species distribution and abundance in lotic systems.

The goal of this study was to develop a thermal habitat classification for streams across a hydrologically heterogeneous geographic region. Our approach was to: 1) identify the extent of variation in temperature that exists among catchments in the Lower Peninsula of Michigan; 2) classify stream reaches into distinct, ecologically-relevant types based on response thresholds of both entire fish communities and key fish species; and 3) describe the relationships between available temperatures and observed distribution patterns for selected riverine fish species. Development of a thermal habitat classification would provide a method to describe the extent of spatial variation in stream temperatures, simplify the observed complexity of thermal characteristics, allow for generalizations across relatively homogeneous habitat units, and provide a common language for communication among managers, researchers and various user groups. In addition, it would provide a framework for evaluating the influence of temperature as a factor controlling species assemblage structure at sites across a relatively broad geographic region (Hudson et al. 1992).

Methods

Water Temperature Data

Temperature data were collected during the first 3 weeks of July at 171 sites in Lower Michigan using maximum/minimum thermometers and digitally recording thermographs. Temperature data were collected over several years (1989, 1990, 1994, and 1996), but in this analysis, we used only 1 observation (year) per site. When data for more than one year were available for a site, we arbitrarily chose the earliest record to include in this analysis. For each site, we determined the maximum weekly July stream temperature as the average of the 3 weekly maximum readings and the minimum weekly July stream temperature as the average of the 3 weekly minimum readings.

We also characterized summer thermal characteristics at 599 additional Lower Michigan sites using predictive models developed by Wehrly et al. (1998). These models predict average July weekly maximum and minimum stream temperatures as a function of catchment- and reach-scale landscape attributes and account for 70 to 81% of the spatial variation in measured July stream temperatures across Lower Michigan. Models were constructed using 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

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ground water contributions were primary factors controlling spatial distribution of stream temperatures across Lower Michigan (Wehrly et al. 1998).

For this analysis, we combined measured and predicted maximum and minimum stream temperatures into one data set (N=670). For each site, we calculated the weekly mean July temperature as the average between the weekly maximum and minimum temperatures for that site. We also calculated the average weekly July fluctuation as the difference between weekly maximum and minimum stream temperatures. From this point forward, we will refer to mean weekly July temperature as the mean July temperature, and to average July weekly fluctuation as the July fluctuation.

Fish Data

We obtained information on distribution and abundance of stream fishes from a database contained in the Michigan Rivers Inventory (MRI) program (Seelbach and Wiley 1997). This database consists of fish abundance data from rotenone, mark-recapture, and multiple-pass depletion surveys conducted from 1960-95. 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:

$$z_i = (x_i - d_{ij})/(SD_i); \qquad (1)$$

where z_i = standardized density for species i; x_i = statewide average density (lbs/acre) of species i; d_{ij} = density of species i at site j; and SD_i = the standard deviation of all densities for species i (Sokal and Rohlf 1995). This z-score facilitated comparisons between various species regardless of differences in body size.

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

Approach to Classification

Development of a thermal classification requires the identification of criteria for assigning sites into a limited number of discrete thermal categories. Given that temperatures at sites across Lower Michigan represent a more or less continuous gradient in average temperature and temperature fluctuation (Figure 1), categorization of these data should be as objective as possible. Our approach to this problem was to examine the degree of change in fish community composition across gradients of both mean temperature and temperature fluctuation. Patterns of change 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) 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:

$$C_s = 2j / (a + b); \qquad (2)$$

where C_s = the similarity coefficient; j = number of species found in both sites; a = number of species in Site A; and b = number of species in Site B. Sorensen's index provides a simple measure of similarity between 2 sites with C_s values ranging 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).

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To compute similarity coefficients, we first placed sites into 1 of 12 mean temperature categories and 1 of 8 temperature fluctuation categories. For example, sites having mean temperatures from 20.0 to 20.9°C were assigned the 20°C category. Similarity coefficients were calculated for all pair-wise combinations of sites using a measure of presence-absence generated from standardized fish abundance estimates. In order to minimize the effects of rare occurrences, a species was considered present at a site only if the abundance of that species exceeded the statewide average density $(Z > 0)$.

We used the software program Mathcad (version 6.0) to generate a matrix containing the similarity coefficients for all pair-wise site combinations. We then computed the average similarity of sites using similarity coefficients generated from within and among temperature category comparisons. For example, the average similarity between sites at 20°C was determined by first calculating the similarity between all sites within the 20°C category and then taking the average of those values. Likewise, the average similarity between sites at 20°C and sites at 21°C was determined by first calculating the pair-wise similarity between all sites in the 20°C category with all sites in the 21°C category, and then taking the average of those values. In this example, average similarity provided a measure of how similar sites at 20°C are to themselves and how similar sites at 20°C are to sites at 21°C. If temperature is an important attribute of the environment which shapes community structure, we would expect species composition at sites having the same temperature to be more similar to one another than to the species composition at sites having different temperatures.

We then plotted the average similarity of sites for each temperature category against the gradient in mean temperatures and the gradient in temperature fluctuations. This procedure 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 and 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 boundaries identified in the similarity analysis.

Thermal Distribution of Selected Fish Species

To examine how selected species (Table 1) were distributed across thermal categories, we plotted sites having densities 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 densities, we assumed that they represented thermal conditions leading to the optimal performance of each species.

In order to quantify patterns of distribution and abundance, we calculated both average density of a species within each category and proportion of sites within each category where that species was present. Average density and proportion calculations were made using two sets of data. The first set represented thermal conditions leading to optimal performance of each species and included only those sites having densities that equaled or exceeded the statewide average. For this analysis, densities were reported in standard deviations above the mean $(z = 0)$. The second set represented the entire range of thermal conditions experienced by each species throughout Lower Michigan and included all sites where population estimates were available. For this analysis, densities were reported in pounds/acre. We also generated 2 habitat suitability scores within each category for each species. Within each category, we multiplied average density of a particular species by proportion of sites where that species was present. The resulting product in each category was then divided by the maximum product calculated for that species. Habitat suitability scores ranged from 0 (low suitability) to 1 (high suitability).

Results

Variation in July Temperatures

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

Classification Results Based on Mean Temperature

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). Similarity curves for sites at 18 and 21°C were interpreted as transitions between cold- and coolwater, and cool- and warmwater categories respectively.

The relationship between average species richness and mean temperature had 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 and then decrease at temperatures greater than 21°C.

The mean temperature was related to standardized densities of selected fish species representing cold- and warmwater guilds (Figure 4). Mean temperatures at sites having the highest densities of brook, brown, and rainbow trout ranged from 15 to 19°C, and mean temperatures at sites where coldwater fishes were present ranged from 10 to 22°C. Mean temperatures at sites having the highest densities of carp, channel catfish, and smallmouth bass ranged from 22 to 26°C, and mean temperatures at sites where warmwater fishes were present ranged from 18 to 26°C. Sites with mean temperatures from 19 to 21°C had relatively low densities of either cold- or warmwater fishes. These results were consistent with the patterns observed in the similarity and species richness plots.

Based on these observations, we identified major ecological transitions in streams with July mean temperatures between 18 and 19°C and between 21 and 22°C. This resulted in 3 thermal categories based on mean temperatures: 1) ≤ 18°C; 2) 19 to 21°C; and 3) ≥ 22°C. Hereafter, these groupings will be referred to as cold, cool, and warm mean temperature categories.

Classification Results Based on Temperature Fluctuation

Changes in community composition 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 having relatively large temperature fluctuations (i.e. 10°C and greater), distinct groupings were difficult to identify.

Temperature fluctuation was also related to standardized densities of selected fish species representing cold- and warmwater guilds (Figure 6). Temperature fluctuations at sites having the highest densities of brook, brown, and rainbow trout ranged from 6°C to 10°C, and fluctuations at sites where coldwater fishes were present ranged from 2°C to 10°C. Temperature fluctuations at sites having the highest densities of carp, channel catfish, and smallmouth bass ranged from 4°C to 11°C, and fluctuations at sites where warmwater fishes were present ranged from 2°C to 17°C. With the exception of one location, coldwater fishes were absent at sites having temperature fluctuations greater than 10°C. However, some warmwater fishes were present in relatively high densities at sites

having temperature fluctuations of 10°C and greater.

Based on these changes in warmwater and coldwater fish presence at sites with above average fish density, we identified an additional transition at 10°C. This resulted in 3 thermal categories based on temperature fluctuations: 1) < 5°C; 2) 5 to < 10°C; and 3) ≥ 10°C. Hereafter, these categories will be referred to as stable, moderate, and extreme fluctuation.

General Classification Attributes

We combined mean temperature and temperature fluctuation categories to create a 3 x 3 matrix with 9 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 occurred in the stable (3%) and extreme fluctuation categories (5%). The total percentages of sites were evenly distributed among cold (36%), cool (36%), and warm (28%) mean categories.

We found a general increase in species richness and total standing stock (lbs/acre) from cold to warm sites (Table 2). Species richness ranged from 6 (standing stock = 62.4) in the cold-stable regime to 31 in the warm-stable regime. Within the cold and cool mean categories, species richness and standing stock increased with increasing levels of temperature fluctuation. The opposite trend was observed within the warm categories with the lowest richness occurring at high fluctuations.

Thermal Distribution of Selected Fish Species

Distributions of fish representing different thermal guilds showed considerable overlap and in all cases, species were distributed across more than one thermal regime (Figures 8 – 24). Coldwater species (Figures 8 – 12) had the narrowest distributions and were limited to cold and cool mean categories. Distributions of coolwater (Figures 13 – 19) and warmwater species (Figures 20 – 24) were broader, and fish in these guilds were found across a greater number of thermal categories. In general, there

was poor correspondence between guild membership (Table 1) and fish presence within a thermal category. For example, although cool-water species such as white sucker (Figure 16) and northern pike (Figure 17) were present in cool mean 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 (Figure 12) were found more often in the cool-moderate regime than either brook trout (Figure 8) or slimy sculpin (Figure 11). In the coolwater guild, sites containing northern pike (Figure 17) were distributed across both cool- and warmwater categories whereas the distribution of creek chubs (Figure 14) was centered on cool- and coldwater categories. In the warmwater guild, green sunfish (Figure 22) were found in cooler habitats than those occupied by channel catfish (Figure 24).

Fish Abundance and Temperature

Most species showed relatively high densities and high frequency of occurrence in more than one thermal regime (Tables 3 – 6). Species such as slimy sculpin, longnose dace, and burbot were relatively rare, occurring at only a few sites. In contrast, white suckers and rock bass were found at nearly every site within 3 or more thermal categories. In general, coldwater species were present at high densities in relatively fewer thermal categories compared to cool- and warmwater species.

Habitat Suitability

Overall, habitat suitability scores, because they integrated both density and probability of occurrence of a species within a thermal category, were the most useful in identifying appropriate thermal habitats for individual species. Habitat suitability scores based either on data from sites having average or above average densities (Table 7), or on data from all sites (Table 8) showed similar patterns for most

species. Brook trout was the only species whose optimum suitability occurred in the cold-stable regime (Tables 7 and 8). 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 not suitable for rainbow trout and slimy sculpin. Optimum suitability scores for the remaining coldwater species fell within the cold-moderate regime. Distributions of suitability scores for rainbow trout, brown trout, and mottled sculpin ranged into the cool-moderate regime and were much broader than those observed for brook trout and slimy sculpin (Tables 7 and 8).

The distributions of habitat suitability scores for selected coolwater fish were much more variable (Tables 7 and 8). Optimum suitability scores for fish in this group occurred in several thermal regimes including cold-moderate (blacknose dace), cold-extreme (creek chub), cool-moderate (longnose dace, white sucker, and mudminnow), and cool-extreme (northern pike and burbot). With the exception of longnose dace and burbot, the distribution of habitat suitabilities for coolwater species were relatively broad.

The distributions of habitat suitability scores for selected warmwater species were also variable (Tables 7 and 8). Optimum suitability scores for fish in this group occurred in cool-moderate (green sunfish), warm-stable (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 warm- water fishes were relatively broad.

Discussion

Numerous stream classifications have been developed (reviews in Hynes 1970; Hawkes 1975; Hudson et al. 1992), yet surprisingly few have considered water temperature to be an important habitat feature. For example, only 20% of the stream classifications reviewed by Hudson et al. (1992) included water temperature as a key habitat variable. The reasons for this are unclear but may relate to the fact that temperature has only recently been emphasized as an ecological resource (i.e. that temperature is habitat) (Magnuson et al. 1979; Coutant 1987; Magnuson and DeStasio 1996).

On the other hand, water temperature was incorporated into most of the classical longitudinal zonatin schemes developed near the turn of the century (Borne 1877, Thienemann 1912, 1925, Carpenter 1928; cited in Hawkes 1975). Typically, these classifications broke a river longitudinally into coldwater (dominated by salmonids and cottids) and warmwater (dominated by centrarchids, ictalurids, and cyprinids) zones. Classifications of this type have typically been developed for systems arising in mountainous regions where distinct changes in species composition occur across altitude-related gradients in water temperature (Burton and Odum 1945; Illies 1953, 1958, Huet 1959; Hynes 1970; Moyle and Nichols 1973; Hawkes 1975; Rahel and Hubert 1991; Keleher and Rahel 1996). Similar thermal classifications have been proposed for streams draining lower elevation regions including Michigan (Anonymous 1967), Ontario (Ricker 1934), and Wisconsin (Lyons 1996). Spatial variation in stream temperatures in these regions is maintained by differences in groundwater accrual among catchments and stream segments.

Water temperature has also been used to develop predictive stock models. These studies used regression analysis to develop models that predict standing stock of key species from habitat variables which include maximum water temperature, channel shape, and substrate characteristics (Binns and Eiserman 1979; Layher and Maughan 1985; Bowlby and Roff 1986; Layher et al. 1987; Fausch et al. 1988).

A Thermal Habitat Classification for Michigan Rivers

Our classification summarizes the spatial variation in July mean temperatures and temperature fluctuations that exist in Lower Michigan rivers. It provides both a framework to describe the thermal distribution of individual species and a method to generate expectations about community structure and standing stocks of key species at sites having predictable thermal characteristics. We based our

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

Based on community- and species-level analyses we identified three mean temperature categories (cold, cool, and warm) and three temperature fluctuation categories (stable, moderate, and extreme). Cold-, cool-, and warmwater groupings traditionally have been recognized by fisheries biologists. A comparison of cold-, cool-, and warmwater categories developed in this study with those proposed by Magnuson et al. (1979) and Lyons (1996) is shown in Table 9. In general, coldwater temperature ranges were similar across studies. However, temperature ranges for cool- and warmwater designations in Michigan rivers were somewhat lower.

Discrepancies among these classification systems at least partially result from different methodological approaches to classification. Magnuson et al. (1979) defined cold-, cool-, and warmwater guilds using laboratory preference data and characterized both narrow and broad fundamental thermal niches of representative fish in each guild as the average final preference temperature plus and minus 2°C and 5°C. Thus, this type of classification can be used to delimit the temperature range that an individual species should select in order to maximize physiological performance (e.g., growth) (Brett 1971; Beitinger and Magnuson 1979; Magnuson et al. 1979; Jobling 1981). However, biotic interactions, availability of food, and availability of appropriate temperatures can influence observed thermal distributions (i.e. realized thermal niche) of fishes. For example, based on final preferendum (31°C: Coutant 1977) plus and minus 5°C, the fundamental thermal niche of adult green sunfish ranges from

26 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 22) is considerably cooler than 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.

Using a different approach, Lyons (1996) proposed threshold temperatures for classifying Wisconsin streams into cold-, cool-, and warmwater categories based on field observations of indicator (e.g., trout) species. Classifications of this type have been developed elsewhere (Ricker 1934; VanDuesan 1954 cited in Hawkes 1975; Anonymous 1967) and can be used to identify stream reaches that have the potential to support important game fish species. However, because these classifications are based on distributions of a few key species, they may not reflect the range of thermal conditions that are available to other species, especially nongame fishes. In addition, the boundaries proposed in these classifications do not necessarily represent community-level responses to temperature. Classifications of this type have limited utility in predicting species composition at sites having similar thermal characteristics.

We identified nine thermal regimes that are likely to have distinct fish species composition based on summer thermal characteristics. However, within the MRI database, the number of sites having either stable or extreme July temperature fluctuations was relatively low. This 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. 1998). Different catchment-specific combinations of these variables give rise to the thermal characteristics observed in each regime. For example, sites in the cold-stable regime tend to be small, ground water-dominated reaches draining forested landscapes. Relatively large contributions of ground water 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. Consequently, relatively small volumes of water in the channel and a lack of shading in these systems result in thermal regimes that typically track 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).

The limited number of sites exhibiting either very low or very high temperature fluctuations can also be partially attributed to sampling bias. The majority of sites within the MRI database are wadeable streams that have the potential to support harvestable populations of game fish. As a result, sites of little fisheries interest such as small, warm headwaters (typical of sites in the warm-extreme regime) were under-represented (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 July mean temperature strongly influenced species richness across sites, with a general increase in species richness from cold- to warmwater categories. Numerous authors have reported increases in species richness across longitudinal gradients of stream temperature (Burton and Odum 1945; Huet 1959; Hynes 1970; Moyle and Nichols 1973; Hawkes 1975; Rahel and Hubert 1991; Keleher and Rahel 1996). Increased species richness typically correlates with addition of new species in the transition from cold- to coolwater habitats and with continued species additions and replacement of rare, cold-adapted fish (e.g., trout) in the transition from cool- to warmwater habitats. Inspection of Figures 8 to 24 illustrates this pattern of species addition and replacement from cold- to warm- water categories.

Differences in the extent of July temperature fluctuation also appeared to influence patterns of 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 are able to take advantage of the warmer portions of 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 both fish (Brett 1971; Hokanson et al. 1977; Biette and Geen 1980; Diana 1984; Coutant 1987) and aquatic insects (Sweeney 1976; Sweeney and Schnack 1977; Sweeney 1978).

At sites having warm mean temperatures, increased fluctuation correlated with lower species richness. This may result from the inability of certain species to tolerate even short-term excursions above their lethal temperature limits. Large diel changes in temperature (and associated changes in dissolved oxygen content) have been shown to be important limiting factors structuring the species composition of certain warm, headwater reaches (Matthews and Styron 1981; 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 affect differences in species richness across sites through indirect pathways. For example, distributions of some species may be restricted to thermally sub-optimal habitats due to the presence of competitively superior species. Several authors have documented the importance of temperature mediated competition on the distribution and abundance patterns of certain riverine fishes (Baltz et al. 1982; DeStaso and Rahel 1994). The relatively low abundance of tolerant species such as the mudminnow (Becker 1983) in warm sites having moderate and low fluctuations supports such a mechanism (Figure 18). This hypothesis, however, remains untested.

Stream temperatures also have been shown to affect the productivity of benthic invertebrates (Hinz and Wiley 1998). Consequently, differences in fish species

richness among thermal regimes may reflect temperature-dependent differences in food availability.

The local- and landscape-scale factors controlling stream temperatures can also directly affect species composition at a site. For example, in Michigan rivers large downstream reaches tend to be in the warm-stable regime due to the buffering capacity associated with large volumes of water. Thermal stability may be an important factor contributing to the relatively high species richness observed in this habitat type. However, large downstream reaches are also characterized by relatively stable flow regimes, a comparatively large number of micro-habitat types (pool-riffle, substratum), connections downstream to the Great Lakes, and connections to upstream portions of the catchment with abundant wetlands and lakes. These factors, among others, have been shown to influence species composition at a site independent of temperature (Horwitz 1978, Gorman and Karr 1978, Schlosser 1982, Angermeier and Schlosser 1989, Osborne and Wiley 1992) . Consequently, our classification does not allow us to separate the effects of temperature from the effects of other co-varying habitat features.

Limitations and Weaknesses

Development of the classification required that we place discrete boundaries on gradients of mean temperature and temperature fluctuations that are actually continuous variables. The thermal regimes that we identified were intended to provide a descriptive summary of species presence, abundance, and richness across these continuous variables. Although we attempted to draw boundaries that corresponded to distinct changes in community composition across sites, the distribution of individual species showed considerable overlap. Thus, the utility of our classification may be limited at sites on or near the boundaries between thermal categories.

In our analyses, we assumed that changes in community composition and species abundance across gradients of mean temperature and temperature fluctuations reflected community-

and species-level responses to differences in temperature. However, variables that often co-vary with stream temperature (e.g., stream flow, channel area, and network position) have also been shown to be important factors affecting species composition and may have led to classification errors for some sites. Consequently, our classification does not allow us to identify the mechanisms controlling patterns of species distribution and abundance across thermal categories.

The development of our classification was limited by the quality of water temperature data. We used predicted temperatures for 62% of the sites (N=307) included in our 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. These models explain from 70 to 81% of the spatial variation in July stream temperatures, and tend to overestimate temperatures at colder sites and underestimate temperatures at warmer sites (Wehrly et al. 1998). Because of this, estimated temperature fluctuations were biased towards the moderate fluctuation category and the number of sites exhibiting either low ($<5^{o}$C) or high ($>10^{o}$C) temperature fluctuations was therefore underrepresented in our analyses. Consequently, our ability to accurately characterize distribution (Figures 8-24) and abundance patterns (Tables 3-8) for individual fish species was also limited. Users of our classification should be aware that the number of sites exhibiting either low or high temperature fluctuations would likely increase, and that patterns of fish distribution and abundance might change if more measured temperatures were incorporated.

Observed and predicted temperatures used in this study were based on a limited number of observations at a site and do not account for year to year variation in stream temperature. It is expected that inter-annual variation in precipitation and air temperature would lead to variation in stream temperatures at a site; sites showing large July fluctuations would also be expected to show the greatest variation in temperature across years. Sites on or near the boundary between thermal regimes therefore could be misclassified or could 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 were also 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 using a variety of sampling methods. We assumed that these single values represented the average performance of fish populations over time. We also assumed equal confidence in population estimates among species regardless of gear type or catchability. These assumptions contribute additional variation to already noisy data. We attempted to reduce some of this noise by modifying presence-absence data to reduce the influence of rare occurrence of a species at a site.

Our classification summarizes the spatial variation in summer thermal characteristics observed in Lower Michigan rivers. However, it does not capture potential seasonal or annual temperature effects (e.g., growing degree days, overwinter survival). It also does not account for finer spatial- and temporal-scale differences in temperature among sites. In addition, the classification has limited utility in identifying the specific mechanisms linking temperature to observed patterns of fish distribution and abundance.

The predictive power of our classification could be enhanced by using independent data sets to determine the extent to which our thermal groupings represent ecologically-relevant categories. Testing and refinement of the classification will improve our ability to characterize relationships between temperature and fish, and will increase its utility as a mangement tool.

Finally, our classification 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 our classification include regional an 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.

Management Implications

Sites across Lower Michigan exhibit a broad range of summer thermal conditions in terms of both mean temperature and temperature fluctuation. The range of warmwater habitats, however, is relatively low with mean temperatures rarely exceeding 26°C. This suggests that many warmwater species experience suboptimal thermal conditions.

The classification developed in this study summarizes the spatial variation in summer stream temperatures across the Lower Peninsula and provides a framework to describe the summer thermal distribution of stream fishes. The classification can also be used to generate expectations of species assemblage structure and standing stocks of key species at sites having similar thermal characteristics. These types of information can then be used by fishery managers and researchers to identify stream reaches that: 1) should receive special protection (e.g., coldwater rivers); 2) are most appropriate for stocking particular species; 3) are most appropriate for habitat rehabilitation; and 4) should fall under similar management regulations.

Biologically meaningful patterns in fish species assemblage structure and abundance of selected species were observed across gradients of both mean temperatures and temperature fluctuations. This suggests that summer thermal regime may be an important factor structuring fish communities in Lower Michigan rivers. However, the mechanisms linking temperature to observed patterns of fish species distribution and abundance in Michigan rivers remains poorly understood. Additional research is needed to determine both the direct and indirect effects of temperature on the performance (e.g., growth, survival, and reproduction) of stream fishes.

Overlaying suitability scores on our classification provides a useful management tool that can be used to identify appropriate thermal habitats for individual fish species. For example, sites having cold-moderate temperatures appear to be the most suitable for brown trout (Table 8). Relatively high densities of brown trout in the cold-stable regime (Tables 4 and 6) indicate that this thermal habitat is also suitable. However, brown trout occur at only 10% of the sites in this category suggesting that factors other than temperature (e.g., competition with brook trout) limit their distribution at cold sites that fluctuate less than 5°C. On the other hand, brown trout were present at more than 30% of the sites having cool-moderate temperatures (Table 6). However, densities at these sites are generally low suggesting that temperatures above 19°C limit the production of brown trout.

This classification can also be used to generate hypotheses relating temperature to observed patterns of fish growth, survival, and reproduction, and to community-level attributes such as distribution, abundance, and diversity (Seelbach et al. 1997; Zorn et al. 1997). Information gained from field and laboratory investigations designed to test such hypotheses will improve our understanding of the effects of temperature on fish species assemblage structure and performance in lotic systems.

Temperature appeared to influence patterns of species richness and total production among sites. This has important implications on ecological assessment and monitoring methodologies (e.g., Index of Biotic Integrity (IBI): Karr et al. 1986) that incorporate species richness as a metric. Not accounting for the influence of temperature regime on species richness could result in erroneous assessments of ecological integrity among sites having *different* thermal characteristics. For example, based solely on species richness, sites having warm mean temperatures and high temperature fluctuations would appear degraded compared with sites having similar means and lower fluctuations. Modifying the IBI and other assessment metrics to account for the effects of temperature on species richness should improve our ability to effectively assess and manage stream resources.
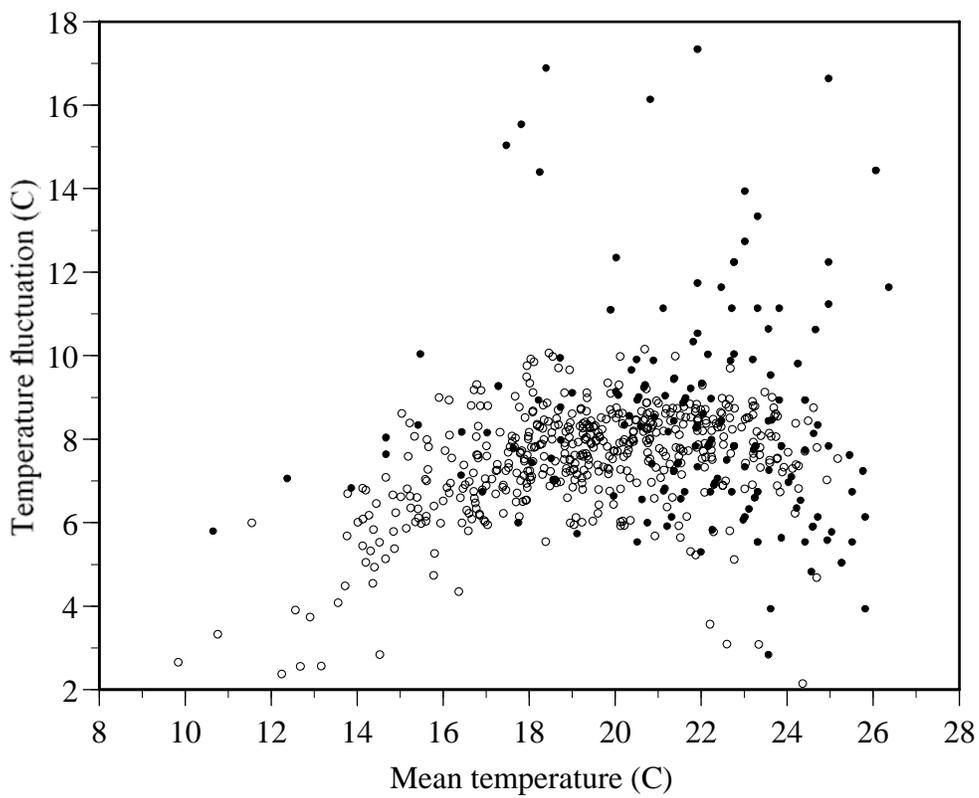
Figure 1.–Measured (closed circles) and predicted (open circles) July mean temperature and temperature fluctuations for 667 sites on lower Michigan rivers.
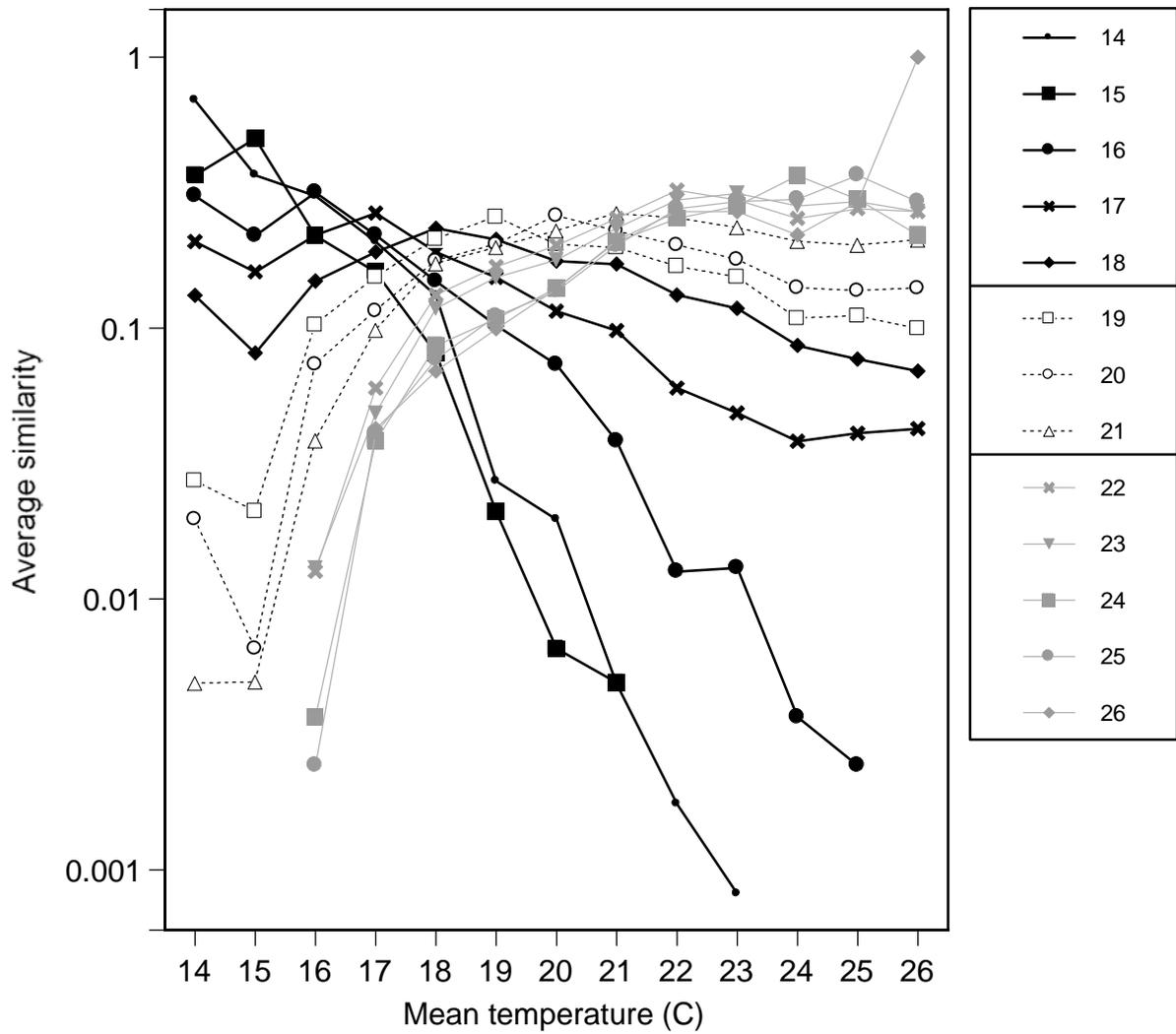
Figure 2.–Community similarity plots illustrating the extent of similarity in species composition among sites across a gradient of mean temperature. For each line, maximum similarity occurs where species composition at sites having the same mean temperature were compared with one another. Changes in individual lines represent difference in community similarity that are attributable to among site differences in mean temperatures.
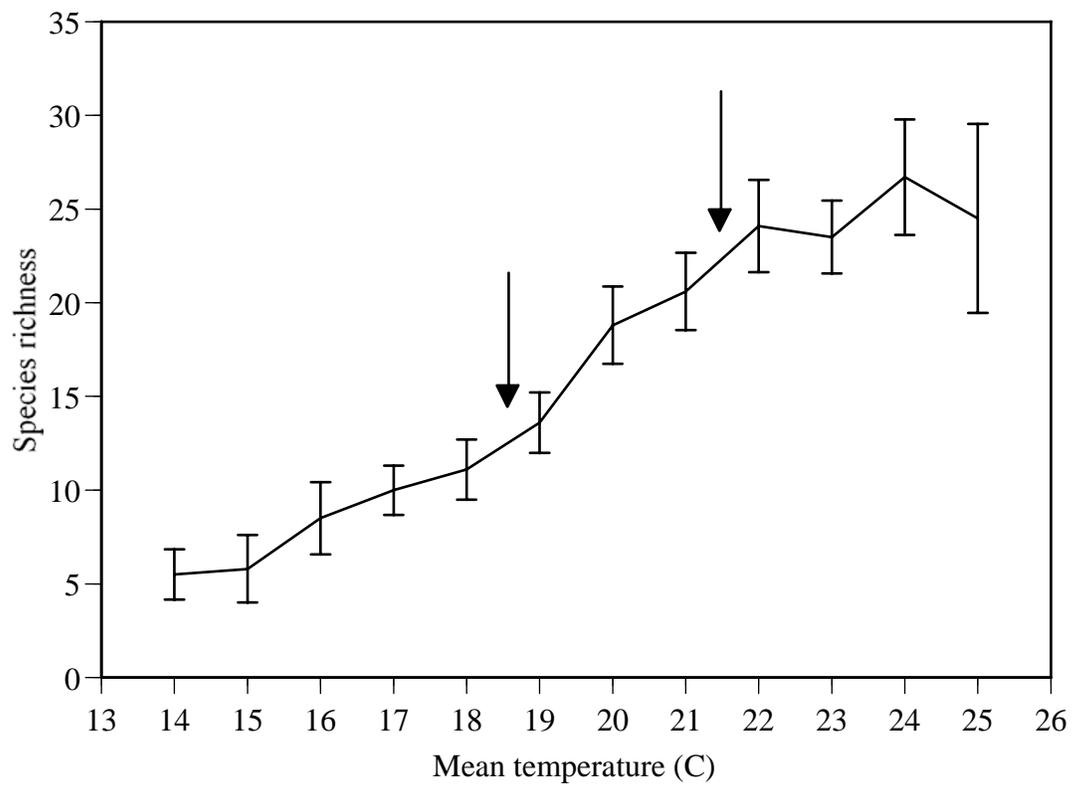
Figure 3.–Relationships between average species richness (mean plus or minus 2 SE) and mean temperature codes. Arrows indicate inflection points.
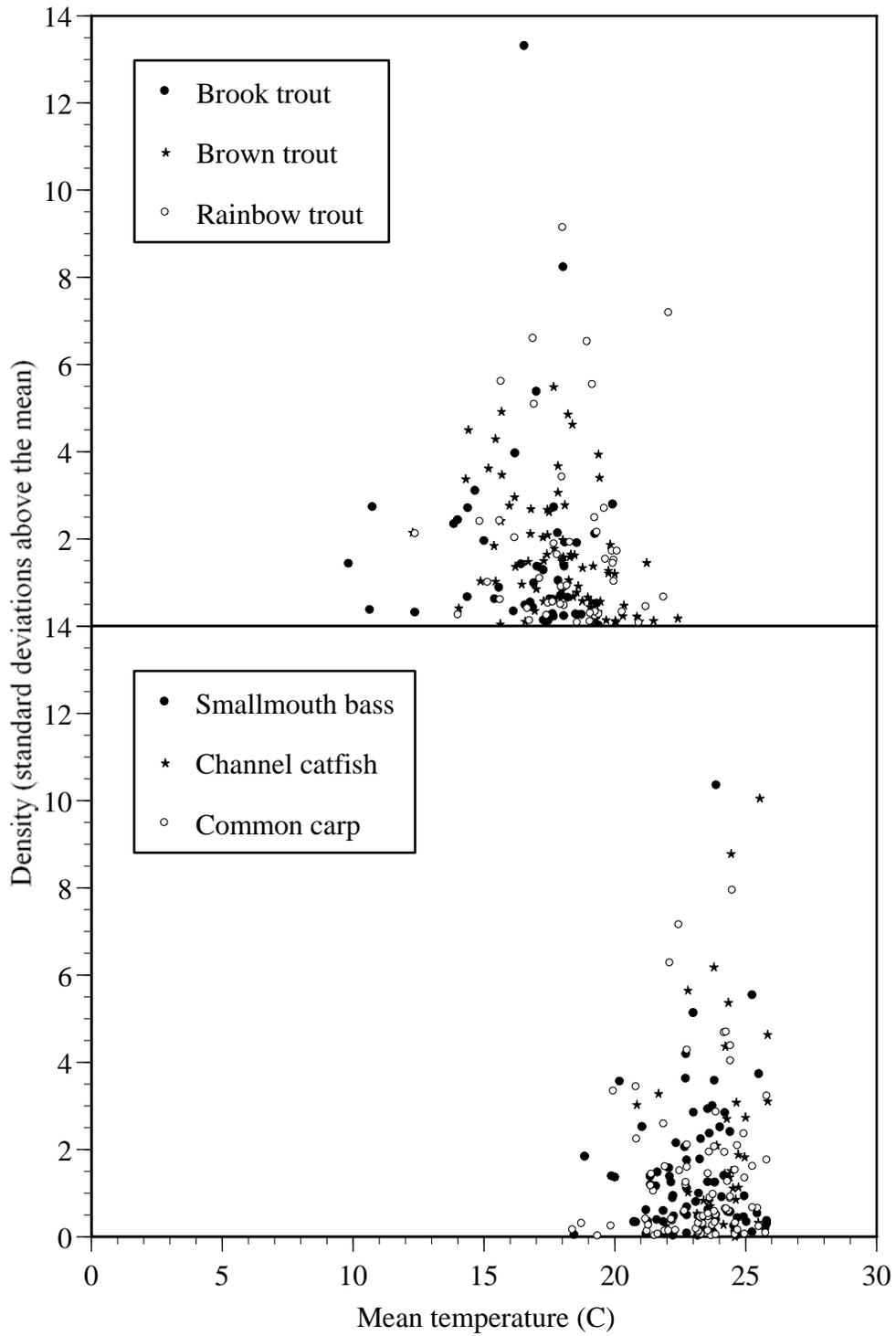
Figure 4.–Relationships between the density (standardized z scores) of selected cold water (upper) and warm water (lower) species and mean July temperature.
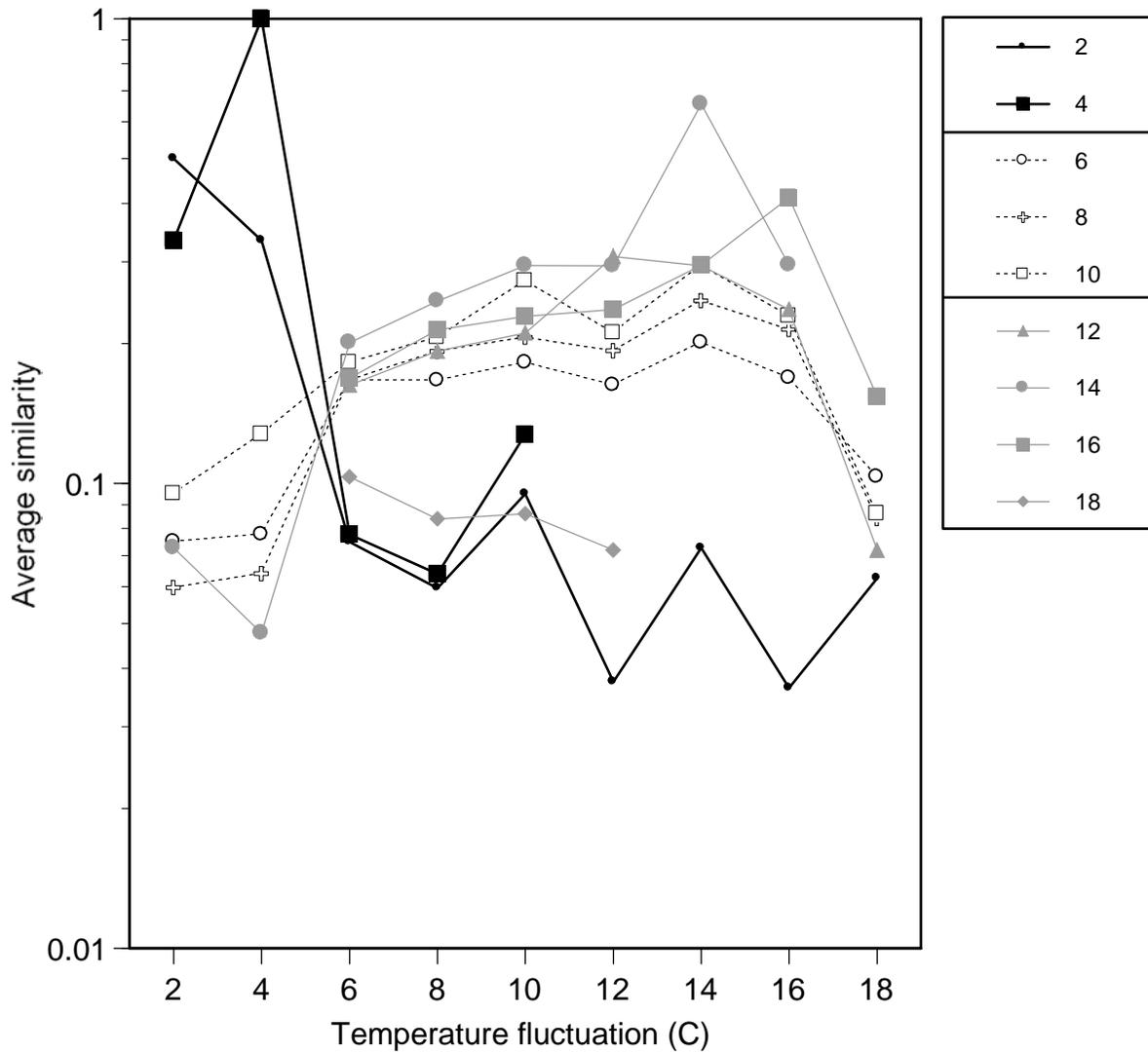
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Figure 5.–Community similarity plots illustrating the extent of similarity in species composition among sites across a gradient of temperature fluctuation. For each line, maximum similarity occurs where species composition at sites having the same temperature fluctuation were compared with one another. Changes in individual lines represent difference in community similarity that are attributable to among site differences in temperature fluctuations.
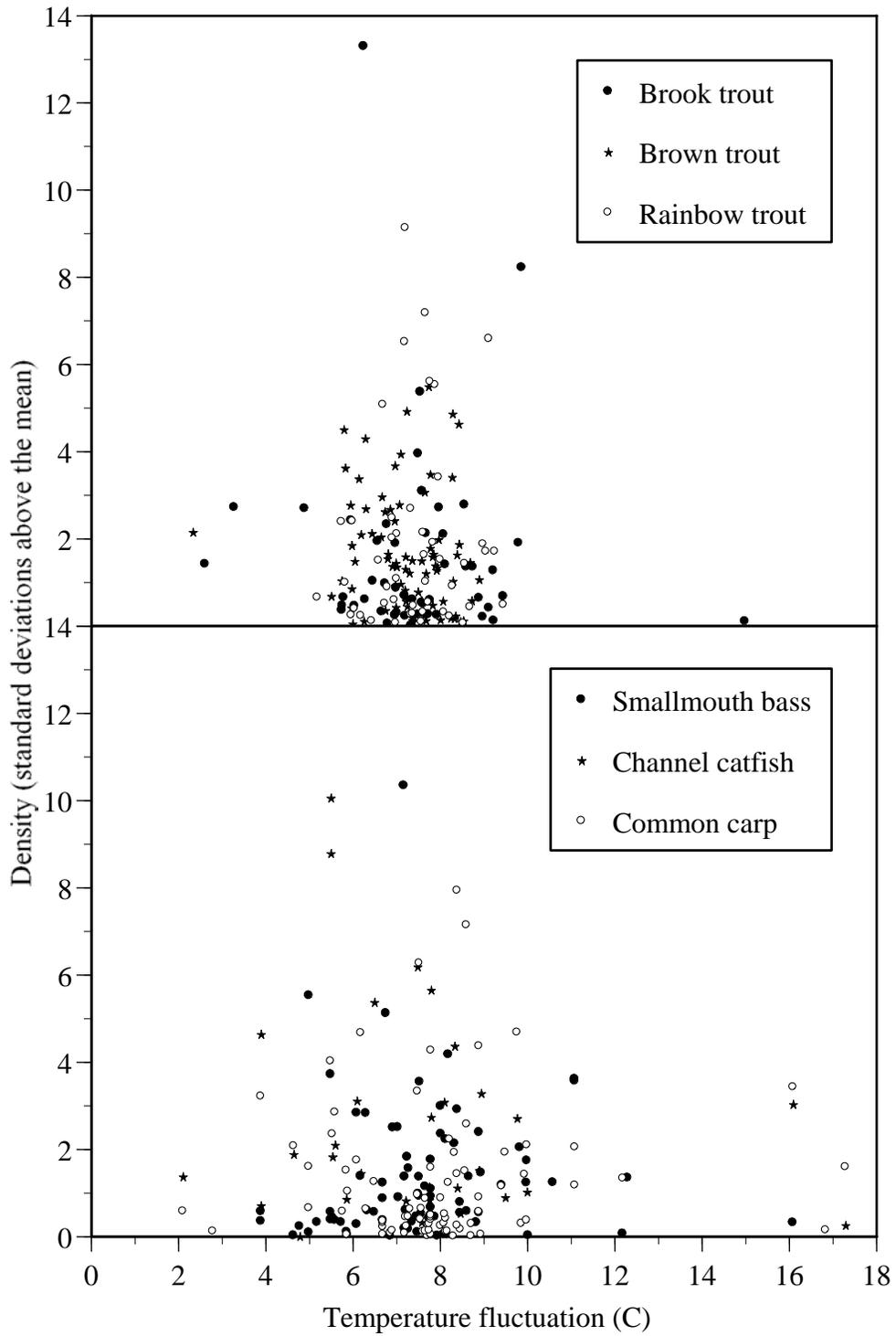
Figure 6.–Relationships between densities (standardized z scores) of selected cold water (upper) and warm water (lower) species and July temperature fluctuations.
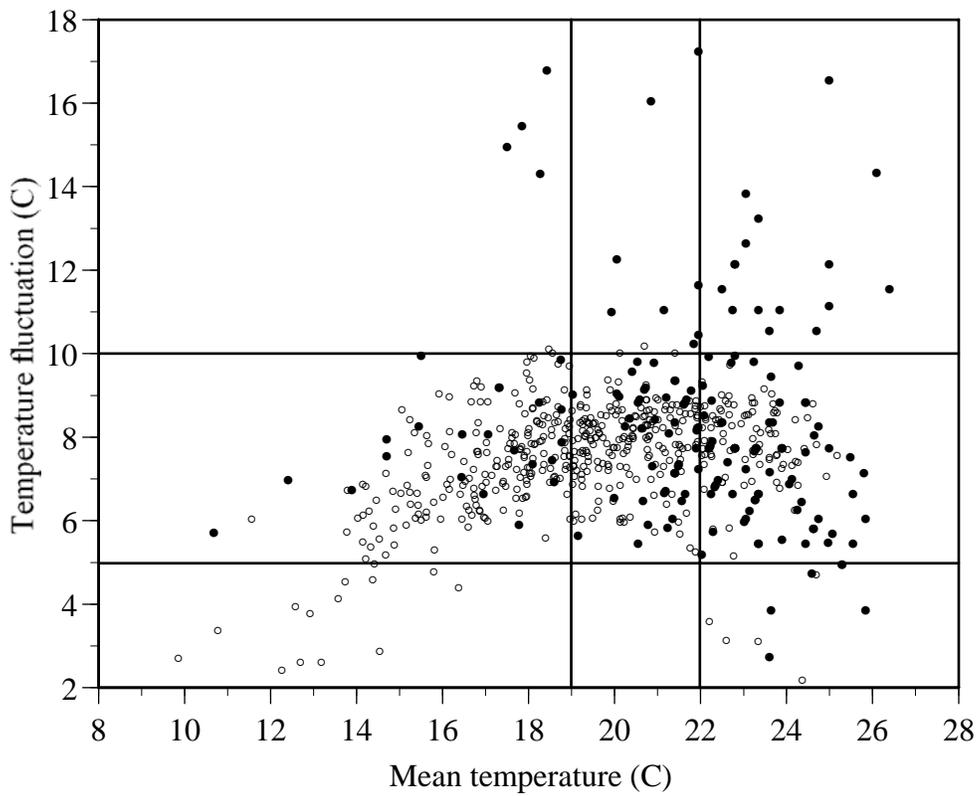
Figure 7.–The distribution of MRI sites (N=667) within each thermal regime. Regimes are defined by the intersection of thermal category boundaries (solid lines) from each axis. Thermal category boundaries for each axis are defined as: cold (<19 °C), cool (19 to <22 °C), and warm (≥22 °C) mean temperatures; and stable (<5 °C), moderate (5 to <10 °C), and extreme (≥10 °C) temperature fluctuations.

Figure 8.–Thermal distribution of brook trout within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 9.–Thermal distribution of rainbow trout within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 10.–Thermal distribution of brown trout within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 11.–Thermal distribution of slimy sculpin within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 12.–Thermal distribution of mottled sculpin within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 13.–Thermal distribution of longnose dace within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 14.–Thermal distribution of creek chub within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 15.–Thermal distribution of blacknose dace within each thermal regime. See Figure 7 for definition of thermal regimes.
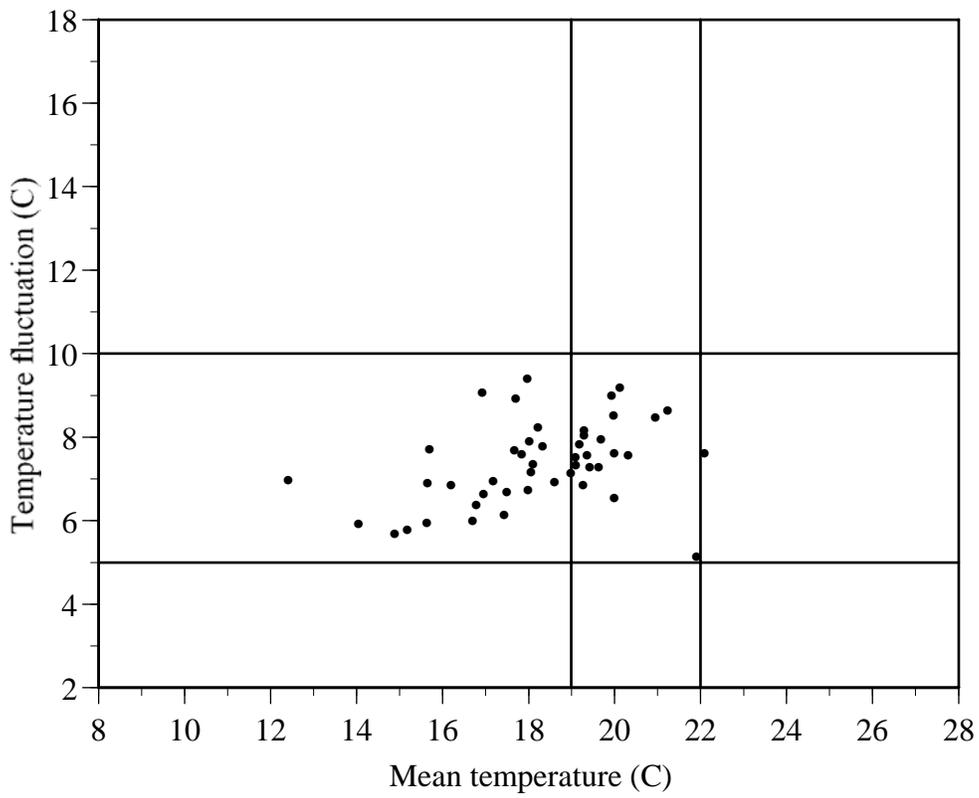
Figure 16.–Thermal distribution of white sucker within each thermal regime. See Figure 7 for definition of thermal regimes.

Figure 17.–Thermal distribution of northern pike within each thermal regime. See Figure 7 for definition of thermal regimes.

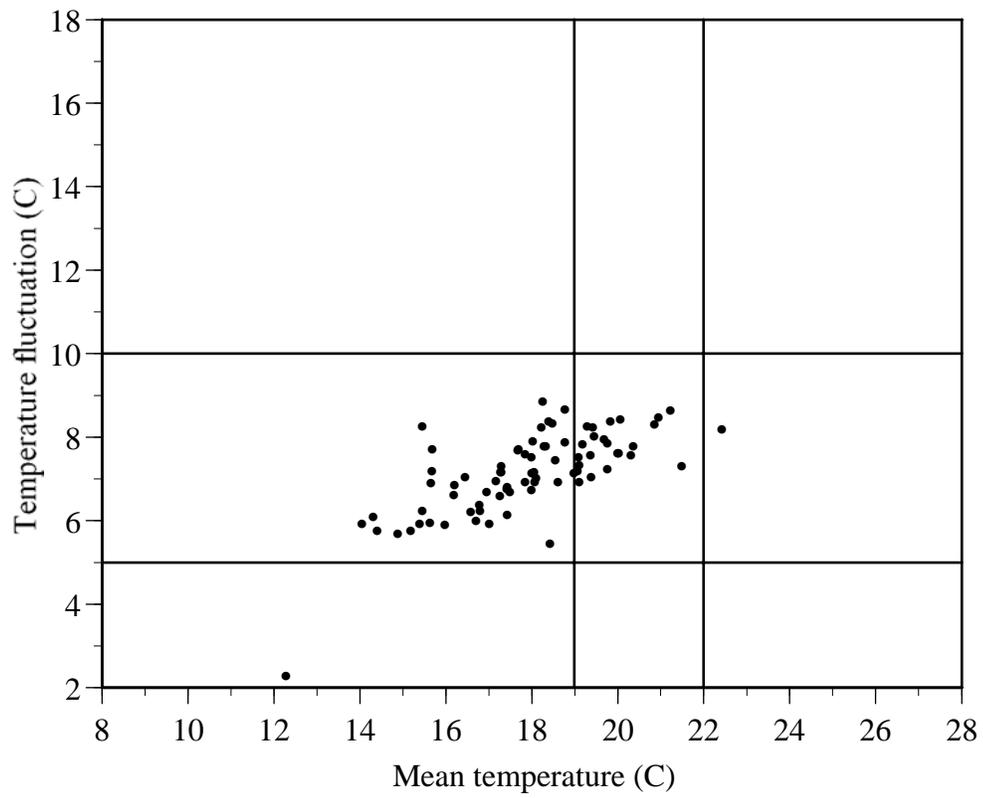Figure 18.–Thermal distribution of mudminnow within each thermal regime. See Figure 7 for definition of thermal regimes.
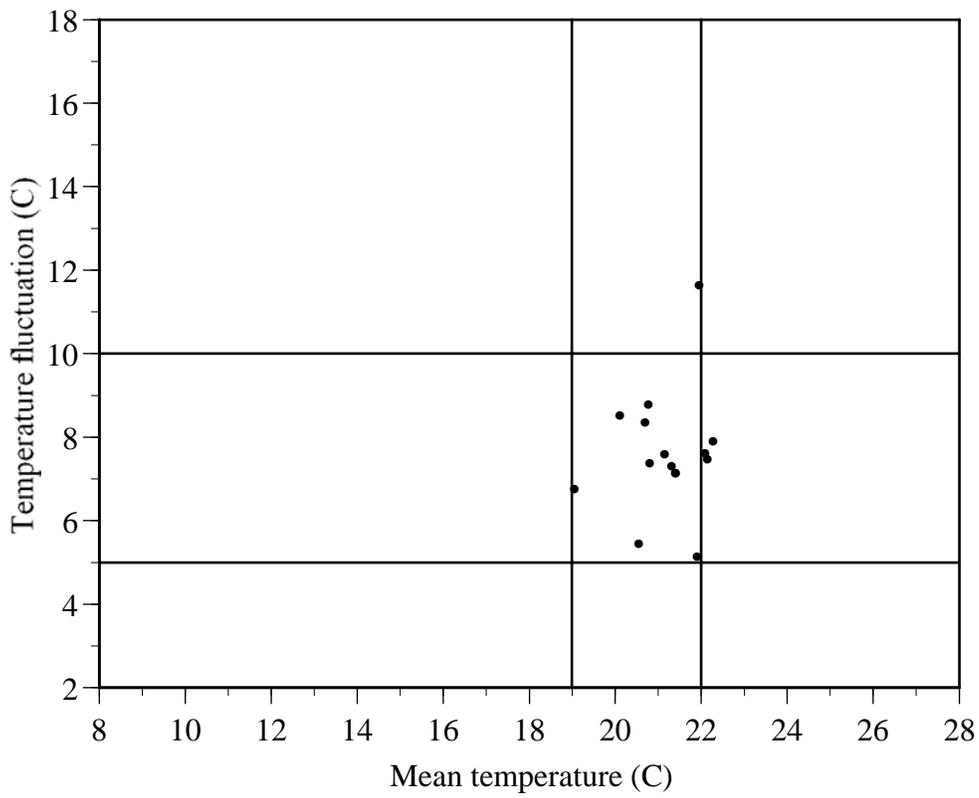
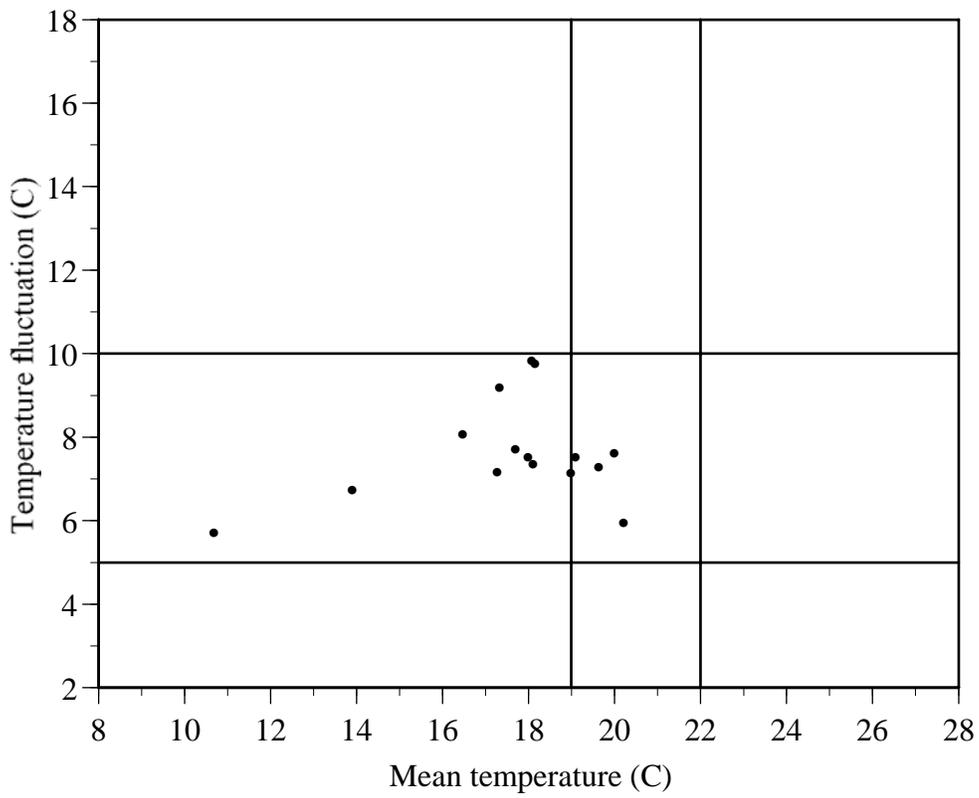Figure 19.–Thermal distribution of burbot within each thermal regime. See Figure 7 for definition of thermal regimes.
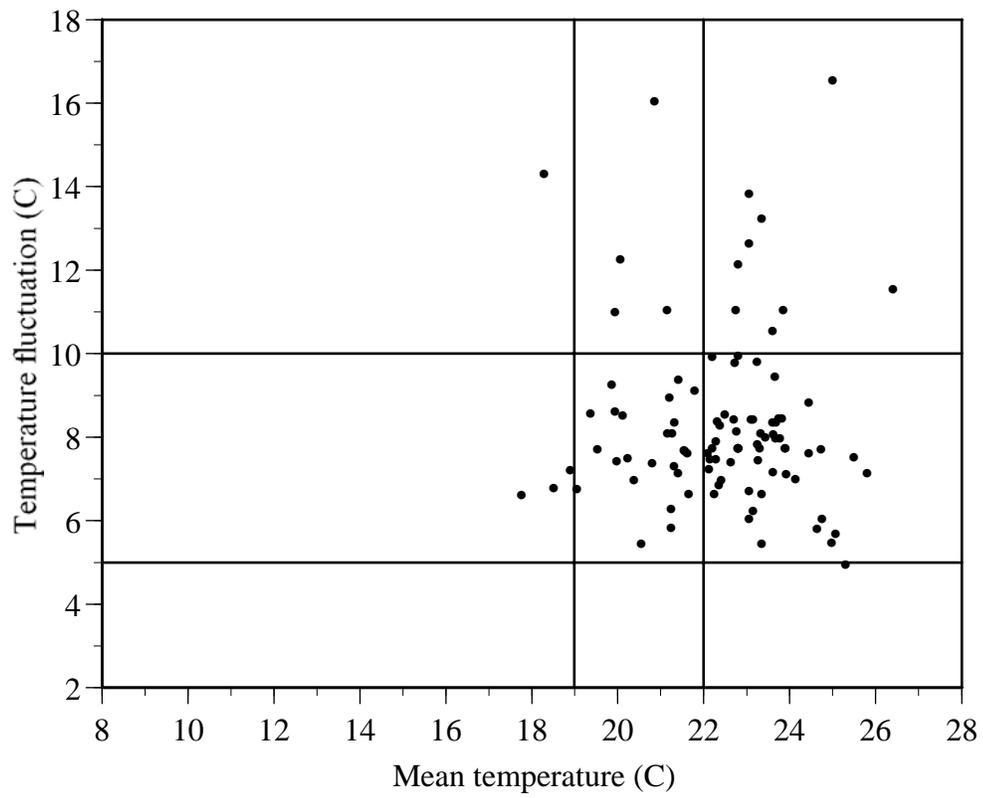
Figure 20.–Thermal distribution of rock bass within each thermal regime. See Figure 7 for definition of thermal regimes.
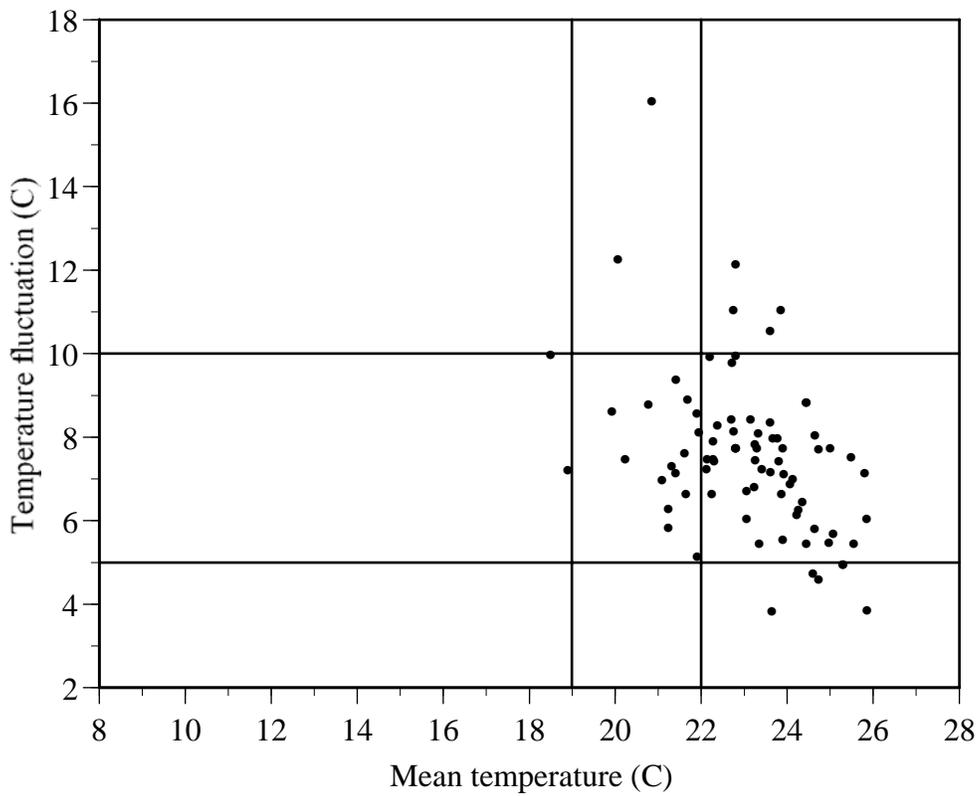
Figure 21.–Thermal distribution of smallmouth bass within each thermal regime. See Figure 7 for definition of thermal regimes.
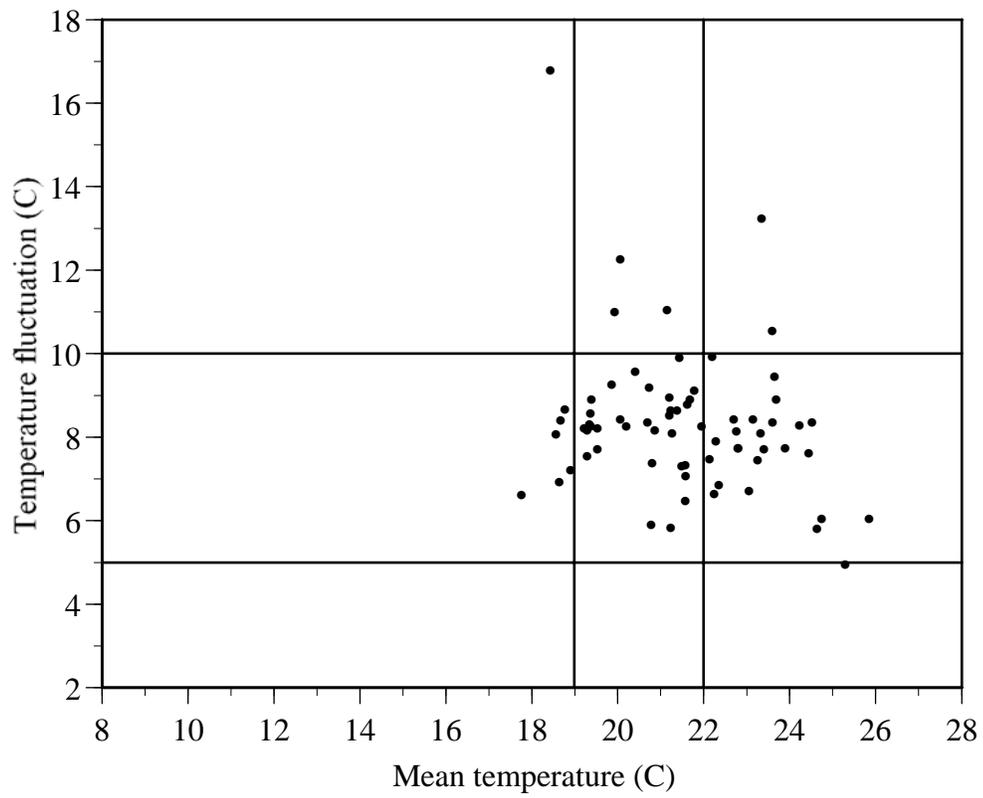
Figure 22.–Thermal distribution of green sunfish within each thermal regime. See Figure 7 for definition of thermal regimes.

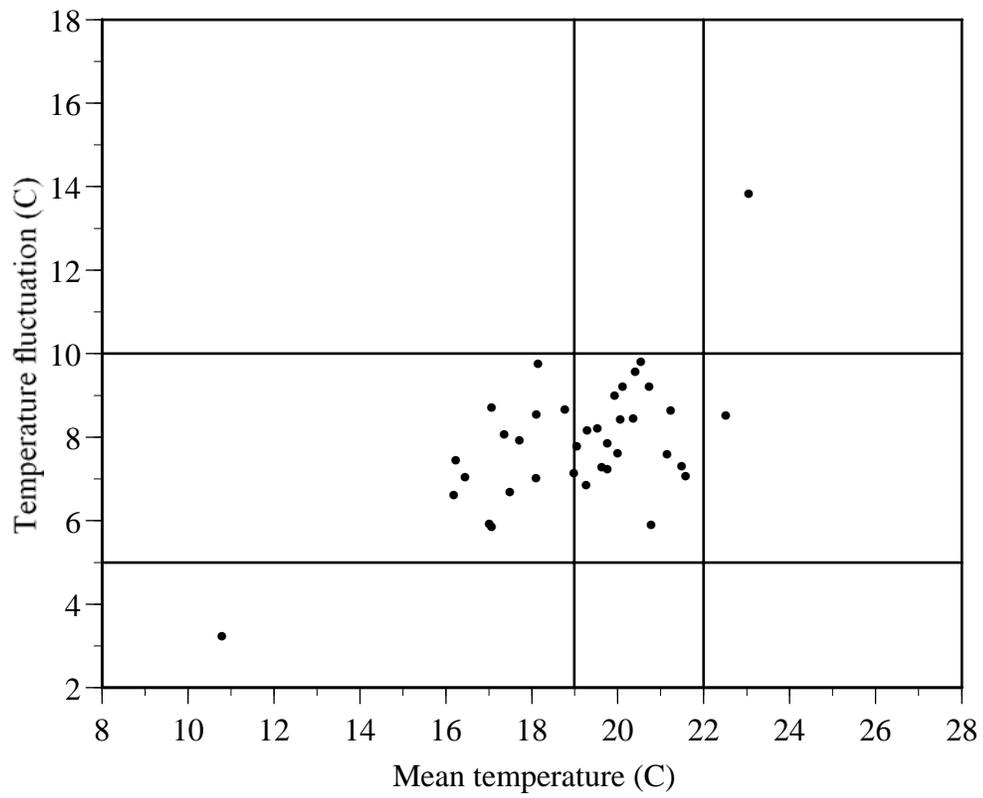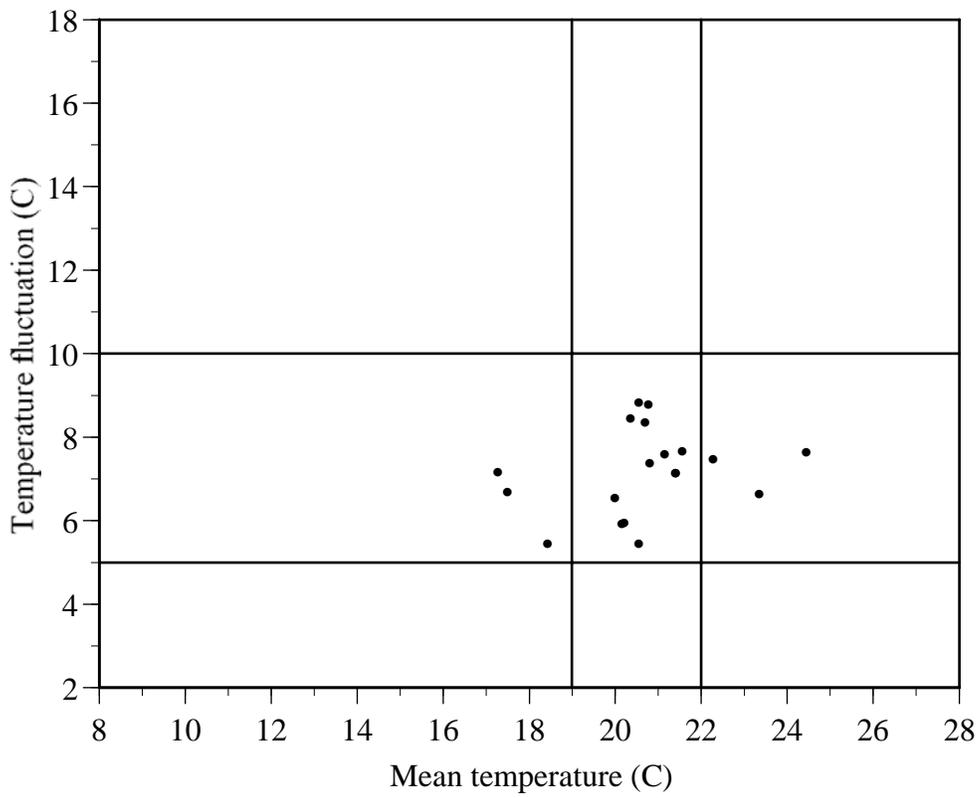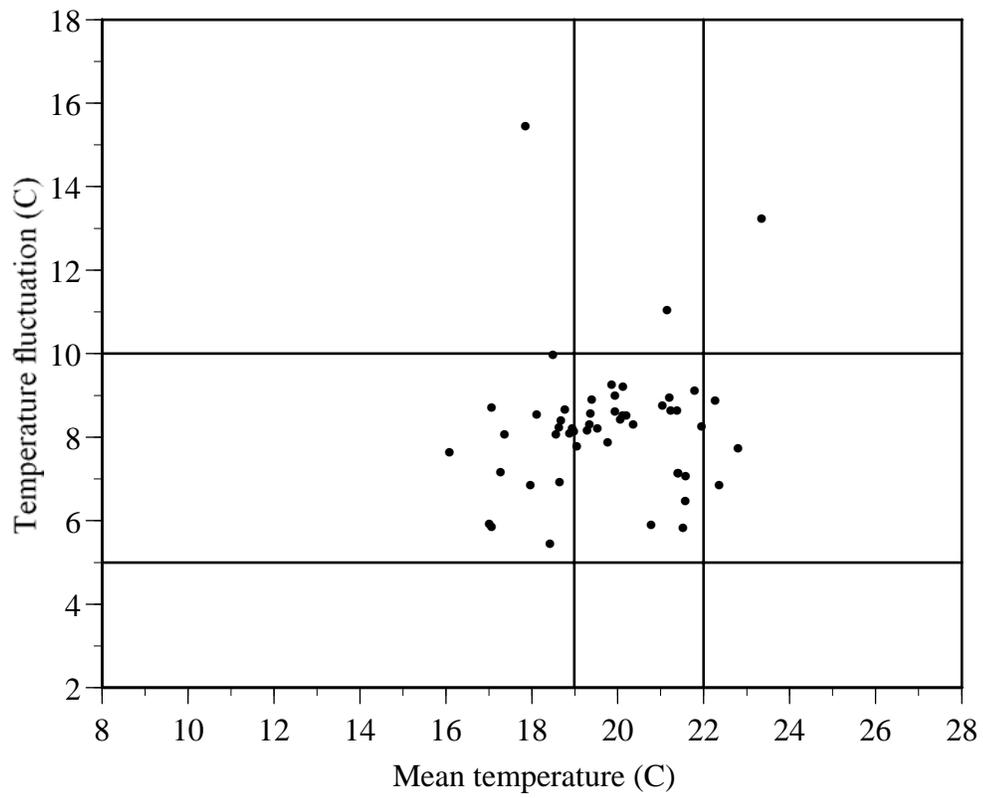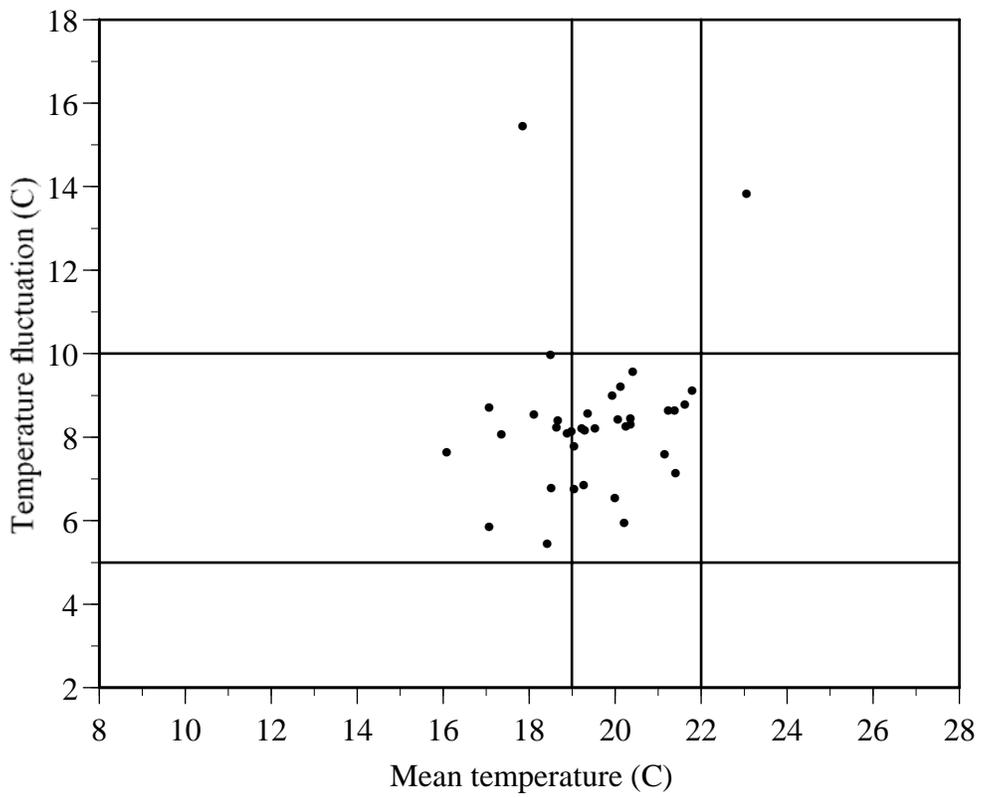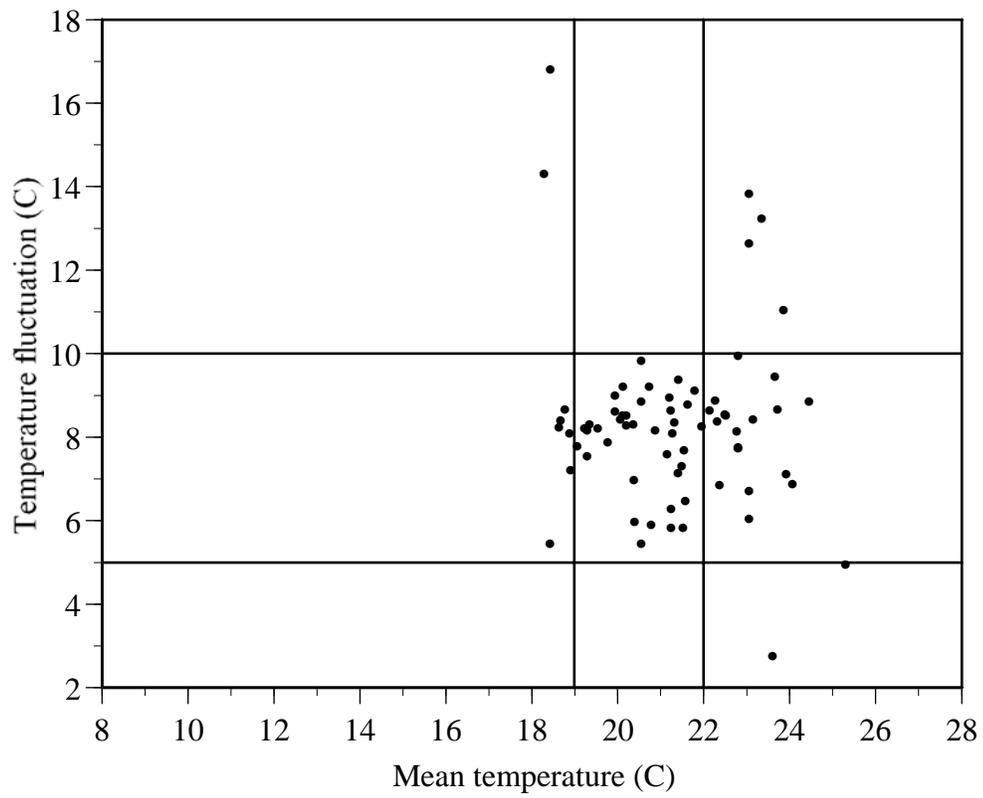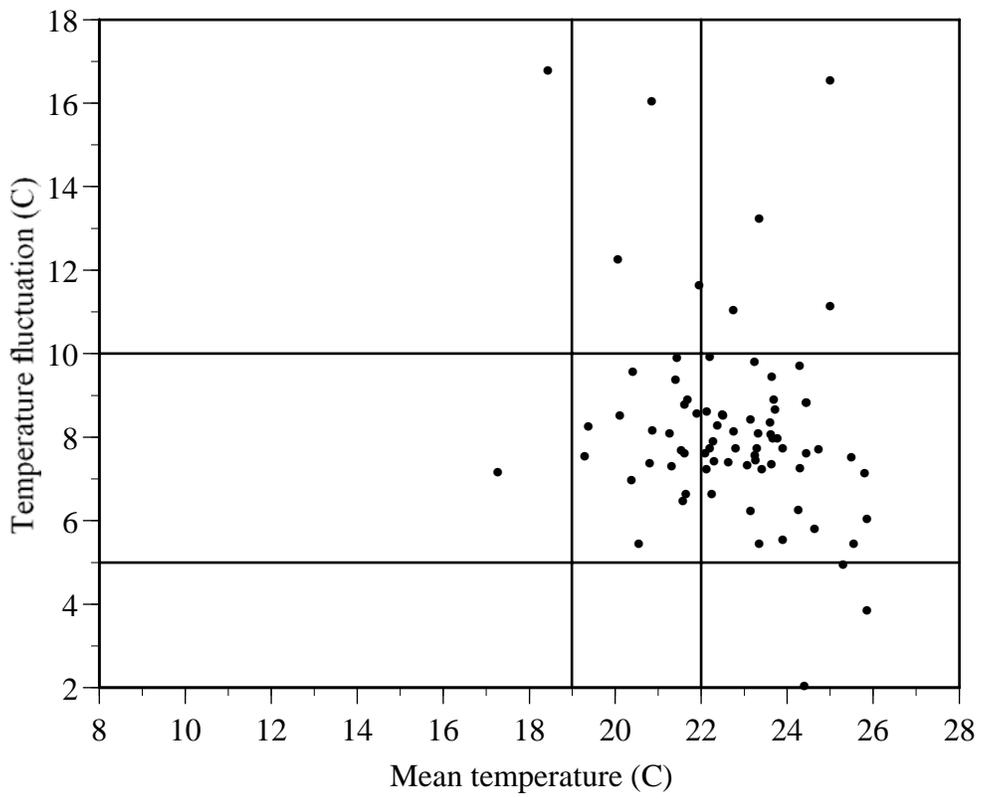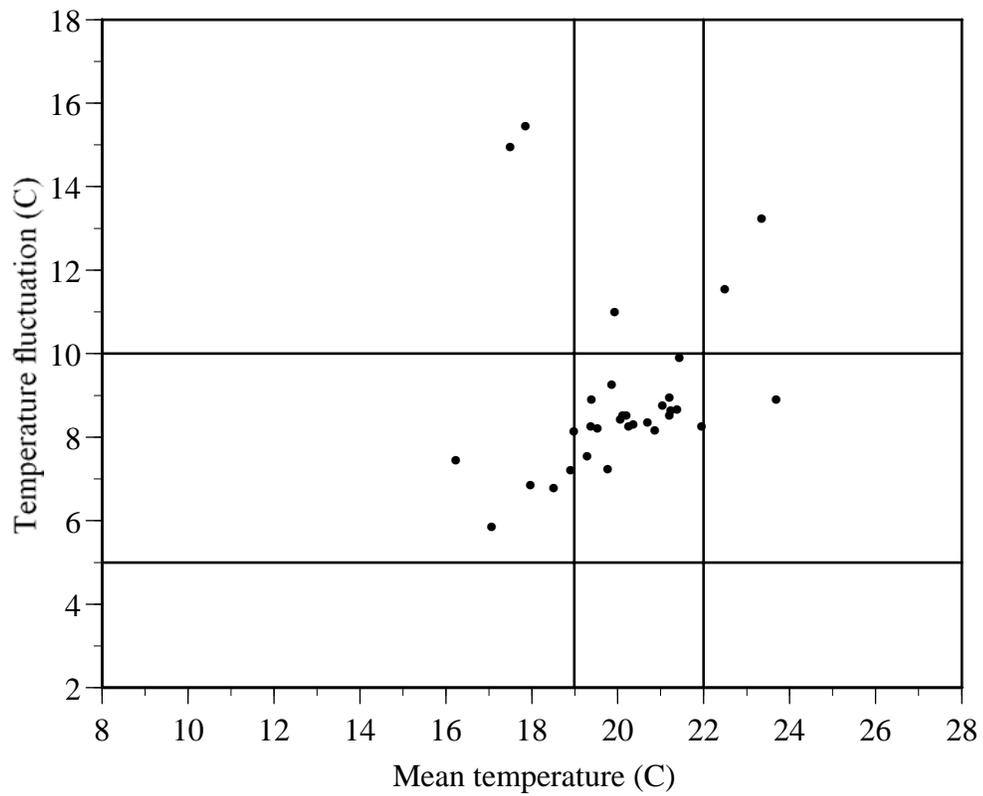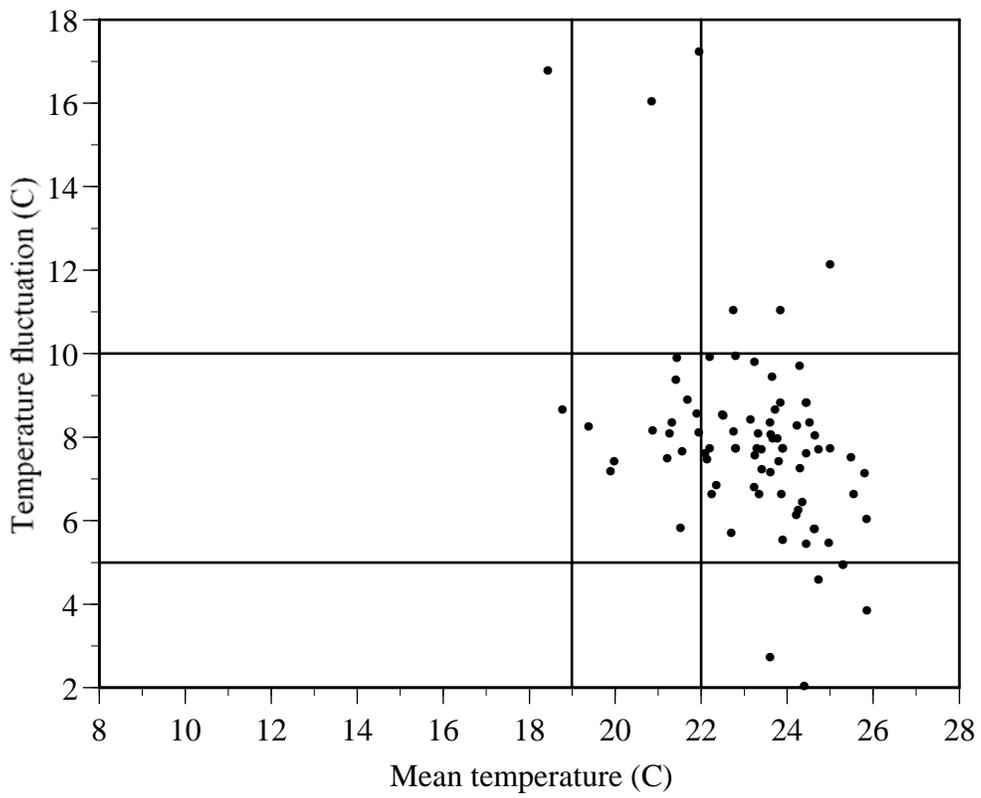Figure 23.–Thermal distribution of carp within each thermal regime. See Figure 7 for definition of thermal regimes.
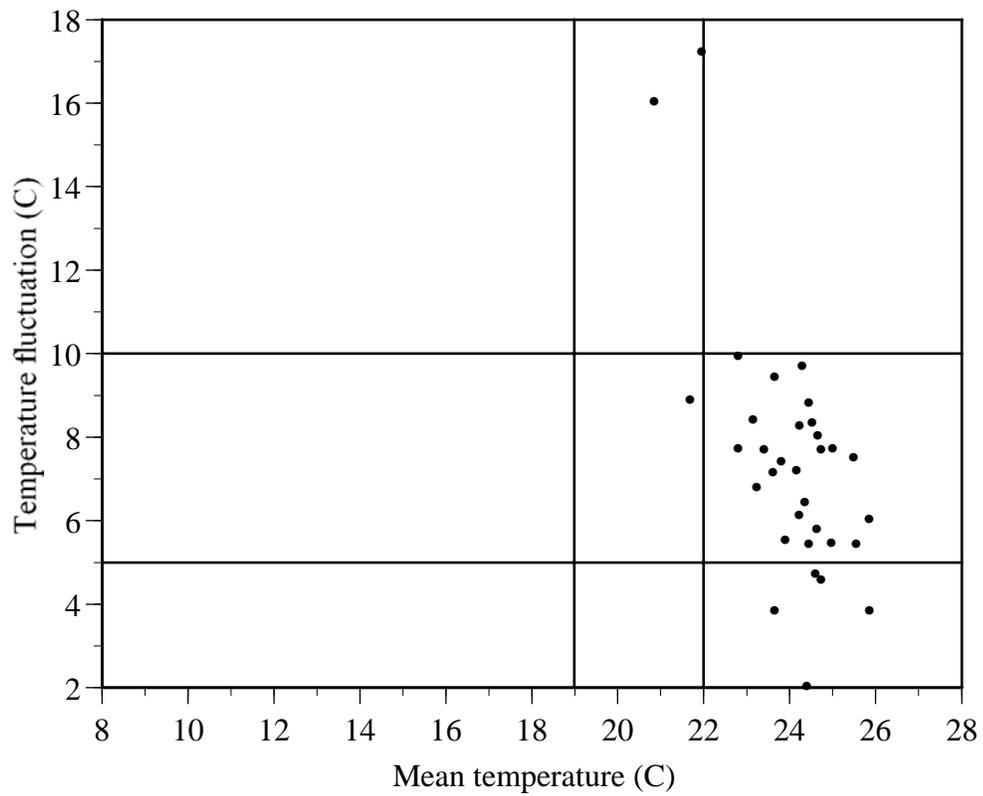
Figure 24.–Thermal distribution of channel catfish within each thermal regime. See Figure 7 for definition of thermal regimes.

Table 1.–Guild membership of fish species used to evaluate thermal classification with the number (N) of sites where each species was present, the maximum weekly average temperature tolerance (data from Eaton et al. 1996), and the optimal thermal category determined in this study.

Guild Common name	Scientific name	N	Maximum tolerance (°C)	Optimal thermal regime
Cold water				
Brook trout	*Salvelinus fontinalis*	78	22.4	cold-stable
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
Cool water				
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
Mudminnow	*Umba limi*	142		cool-moderate
Burbot	*Lota lota*	24		cool-extreme
Warm water				
Rock bass	*Ambloplites rupestris*	176	29.3	warm-extreme
Smallmouth bass	*Micropterus dolimieui*	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

Table 2.–Average species richness (± 2 SE) and average standing stock (in brackets ± 2 SE) within sites (N=402) from each thermal regime.

| Fluctuation | Mean | | | Total |
	Cold	Cool	Warm	
Extreme	17±10.4 [123.6±50.4]	24±5.8 [251.0±218.6]	18±2.0 [203.5±102.4]	20 [192.7]
Moderate	9±0.8 [91.2±14.1]	18±1.2 [130.4±23.4]	25±1.4 [254.8±47.5]	12 [158.8]
Stable	6±2.0 [62.4±18.6]		31±6.6 [271.7±154.1]	19 [167.1]
Total	11 [92.4]	21 [190.7]	25 [243.3]	

Table 3.–Mean standardized density of species within each thermal regime where respective species were present. Only sites having average or above average densities of fish were included in this analysis.

Species	Thermal regime								
	Cold			Cool			Warm		
	Stable	Moderate	Extreme	Stable	Moderate	Extreme	Stable	Moderate	Extreme
Cold water									
Brook trout	2.3	1.6	0.1	1.3					
Rainbow trout		2.1		1.3				7.2	
Brown trout	2.2	2.0		0.9				0.2	
Slimy sculpin		3.8		0.8					
Mottled sculpin	1.2	1.6		1.6				0.1	<0.1
Cool water									
Longnose dace		2.8		3.2				0.9	
Creek chub		1.1	2.0	1.7	0.2			0.7	1.2
Blacknose dace		3.2	0.8	1.6					0.3
White sucker		1.6	0.6	1.2			<0.1	1.2	0.9
Northern pike		0.2	1.2	2.4	1.4		0.1	0.8	0.4
Mudminnow		1.5	0.3	1.6	0.7			0.0	0.8
Burbot				4.2	4.2			2.7	
Warm water									
Rock bass		4.6	0.8	0.5	1.0			1.1	0.9
Smallmouth bass		0.8	0.0	1.0	0.8		0.3	1.5	2.0
Green sunfish		0.7	0.2	1.9	0.3			0.8	0.1
Common carp		0.3	0.1	0.9	2.5		1.5	1.4	1.7
Channel catfish				3.3	1.6		1.7	2.7	1.0

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Table 4.–Proportion of sites within each thermal regime where species were present. Only sites having average or above average densities of fish were included in this analysis.

Species	Thermal regime								
	Cold			Cool			Warm		
	Stable	Moderate	Extreme	Stable	Moderate	Extreme	Stable	Moderate	Extreme
Cold water									
Brook trout	0.75	0.41	0.17		0.03				
Rainbow trout		0.22			0.13			0.01	
Brown trout	0.11	0.43			0.17			0.01	
Slimy sculpin		0.12			0.03				
Mottled sculpin	0.14	0.24			0.18			0.01	0.07
Cool water									
Longnose dace		0.03			0.01			0.03	
Creek chub		0.24	0.33		0.28	0.17		0.03	0.8
Blacknose dace		0.15	0.33		0.19				0.07
White sucker		0.09	0.04		0.42		0.17	0.18	0.38
Northern pike		0.01	0.17		0.15	0.50	0.22	0.47	0.31
Mudminnow		0.07	0.05		0.17	0.17		0.01	0.14
Burbot					0.08	0.17		0.05	
Warm water									
Rock bass		0.03	0.17		0.23	0.67		0.60	0.77
Smallmouth bass		0.01	0.17		0.12	0.33	0.31	0.55	0.31
Green sunfish		0.05	0.17		0.27	0.50		0.27	0.14
Common carp		0.01	0.17		0.10	0.33	0.67	0.56	0.29
Channel catfish					0.01	0.33	0.83	0.23	0.07

Table 5.–Mean density of species (lbs/acre) within each thermal regime where respective species were present. All sites were included in this analysis.

Species	Cold			Cool			Warm		
	Stable	Moderate	Extreme	Stable	Moderate	Extreme	Stable	Moderate	Extreme
Cold water									
Brook trout	54.6	30.5	3.8	8.5					
Rainbow trout		18.1	0.8	9.5				16.5	<0.1
Brown trout	77.8	63.0		22.1		0.7		9.1	0.3
Slimy sculpin		9.3		1.7					
Mottled sculpin	8.3	8.8	0.5	6.4				0.3	1.3
Cool water									
Longnose dace		1.3		1.3				0.5	
Creek chub		27.8	25.9	22.3		4.6		1.9	6.0
Blacknose dace		14.6	5.4	6.8		<0.1		0.2	1.7
White sucker		41.2	21.6	39.1		5.3	7.3	18.6	32.0
Northern pike		2.1	5.0	9.9		9.6	1.5	3.9	2.0
Mudminnow		6.6	1.2	7.3		3.7		0.1	2.4
Burbot				5.3		6.2	0.2	1.6	
Warm water									
Rock bass		28.6	7.4	4.9		9.5	0.9	10.2	11.2
Smallmouth bass		13.9	1.8	5.7		4.0	2.9	8.8	13.0
Green sunfish		2.1	0.9	4.1		1.3		1.5	0.5
Common carp		50.4	33.1	73.4		290.8	127.3	128.1	121.0
Channel catfish				24.2		12.9	13.4	14.2	8.6

Table 6.–Proportion of sites within each thermal regime where species were present. All sites were included in this analysis.

Species	Cold			Cool			Warm		
	Stable	Moderate	Extreme	Stable	Moderate	Extreme	Stable	Moderate	Extreme
Cold water									
Brook trout	0.75	0.54	0.33	0.12					
Rainbow trout		0.25	0.20	0.19				0.04	0.20
Brown trout	0.11	0.51		0.34	0.17			0.02	0.07
Slimy sculpin		0.12		0.03					
Mottled sculpin	0.14	0.29	0.25	0.30				0.10	0.07
Cool water									
Longnose dace		0.03		0.12				0.03	
Creek chub		0.35	0.83	0.74	0.83			0.62	0.77
Blacknose dace		0.25	0.50	0.38	0.17			0.09	0.14
White sucker		0.20	1.00	0.87	0.67		0.67	0.87	0.92
Northern pike		0.02	0.33	0.23	0.50		0.56	0.76	0.77
Mudminnow		0.21	0.83	0.51	0.50			0.45	0.71
Burbot				0.10	0.17		0.22	0.08	
Warm water									
Rock bass		0.04	0.33	0.51	1.00		1.00	0.93	0.92
Smallmouth bass		0.01	0.33	0.20	0.67		0.46	0.74	0.46
Green sunfish		0.09	0.33	0.46	0.83			0.77	0.64
Common carp		0.02	0.33	0.20	0.33		1.00	0.78	0.5
Channel catfish				0.01	0.33		0.83	0.34	0.07

Table 7.–Habitat suitability scores for species within thermal regimes where species were present. Only sites having average or above average densities were included in this analysis.

Species	Cold			Cool			Warm		
	Stable	Moderate	Extreme	Stable	Moderate	Extreme	Stable	Moderate	Extreme
Cold water									
Brook trout	1.00	0.38	0.01	0.02					
Rainbow trout	0.59	0.00		1.00				0.41	0.00
Brown trout	0.28	1.00		0.17	0.00			0.00	0.00
Slimy sculpin		1.00		0.04					
Mottled sculpin	0.45	1.00	0.00	0.76				0.00	0.00
Cool water									
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	0.00			0.00	0.04
White sucker		0.28	0.04	1.00	0.00		0.01	0.44	0.68
Northern pike		0.00	0.29	0.51	1.00		0.03	0.54	0.17
Mudminnow		0.41	0.07	1.00	0.44			0.00	0.41
Burbot				0.48	1.00		0.00	0.20	
Warm water									
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

Table 8.–Habitat suitability scores for species within thermal regimes where species were present. All sites were included in this analysis.

Species	Cold			Cool			Warm		
	Stable	Moderate	Extreme	Stable	Moderate	Extreme	Stable	Moderate	Extreme
Cold water									
Brook trout	1.00	0.40	0.00	0.02					
Rainbow trout		1.00	0.04	0.40				0.15	0.00
Brown trout	0.27	1.00		0.23		0.01		0.02	0.00
Slimy sculpin		1.00		0.04					
Mottled sculpin	0.45	1.00	0.13	0.75				0.01	0.04
Cool water									
Longnose dace		0.25		1.00				0.13	
Creek chub		0.45	1.00	0.77	0.18			0.05	0.21
Blacknose dace		1.00	0.74	0.71	0.00			0.02	0.07
White sucker		0.24	0.63	1.00	0.10		0.14	0.48	0.87
Northern pike		0.01	0.34	0.48	1.00		0.18	0.62	0.32
Mudminnow		0.37	0.27	1.00	0.50			0.01	0.46
Burbot				0.53	1.00		0.04	0.12	
Warm water									
Rock bass		0.11	0.24	0.24	0.92		0.09	0.92	1.00
Smallmouth bass		0.02	0.09	0.18	0.41		0.20	1.00	0.92
Green sunfish		0.10	0.16	1.00	0.57			0.61	0.17
Common carp		0.01	0.09	0.12	0.75		1.00	0.78	0.48
Channel catfish				0.02	0.38		1.00	0.43	0.05

Table 9.–Comparison of proposed temperature ranges for cold, cool, and warm water categories.

Source	Temperature category		
	Cold	Cool	Warm
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.

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