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Summer Thermal Thresholds of Fish Community Transitions in Connecticut Streams

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ARTICLE

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Abstract

Thermal tolerances have been studied for individual fish species but few have investigated how stream fish assemblages respond along a temperature gradient and which thermal ranges act as a threshold, triggering discernible community change. The purpose of this study was to define summer temperature thresholds of fish community transitions in Connecticut streams. The program Threshold Indicator Taxa Analysis suggested that the coldwater class had a June–August mean water temperature < 18.29°C, the coolwater class 18.29–21.70°C, and a warmwater class > 21.70°C. Significant indicator species of coldwater streams were Slimy Sculpin *Cottus cognatus* and Brook Trout *Salvelinus fontinalis*. Significant indicator species of warmwater streams were Cutlip Minnow *Exoglossum maxillingua*, Smallmouth Bass *Micropterus dolomieu*, Rock Bass *Ambloplites rupestris*, Brown Bullhead *Ameiurus nebulosus*, Redbreast Sunfish *Lepomis auritus* and Yellow Bullhead *A. natalis*. The narrow 3.41°C temperature range between the coldwater and warmwater thresholds was designated as a coolwater transition zone, with potential for the presence of both coldwater and warmwater species and lack of species uniquely associated with this thermal range. Our approach based on a robust set of water temperature and fish community data should be applicable to other temperate regions and will be useful for informing development of thermal criteria, application of multimetric indices, and planning for anticipated effects of climate change.

Stream temperature is an important environmental variable for aquatic ectotherms. Stream temperature affects survival (Xu et al. 2010), growth (Sloat et al. 2005), spawning timing (Warren et al. 2012), abundance (Merten et al. 2010), and geographic distributions (Buisson et al. 2008) of fish. Thermal requirements and preferences have been studied for many freshwater fishes (Coutant 1977; Carveth et al. 2006; Hartman and Cox 2008; Underwood et al. 2012), and fisheries managers have

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traditionally classified their inland fishes as coldwater, coolwater, or warmwater species (Eaton et al. 1995; Stoneman and Jones 1996). Biological monitoring using stream fish communities has applied different sets of indicators for coldwater (Lyons et al. 1996; Kanno et al. 2010), coolwater (Leonard and Orth 1986; Lyons 2012), and warmwater (Karr 1981; Smogor and Angermeier 2001) streams.

Understanding thermal thresholds at the community level is critical for sound fisheries resources management. Stream temperature is influenced by a number of anthropogenic factors including construction of dams (Sinokrot et al. 1995), riparian zone modification (Gaffield et al. 2005; Isaak et al. 2010), groundwater extraction (Markle and Schincariol 2007), and urbanization (Nelson and Palmer 2007). Climate change is potentially a major threat to stream biota (Ficke et al. 2007). In particular, the impact of climate change on coldwater streams is of great interest to natural resources managers, but the magnitude of such an impact is uncertain and will vary spatially (Chu et al. 2008; Isaak et al. 2010; Velasco-Cruz et al. 2012). Protective measures of fisheries resources will depend upon identifying thermal thresholds at which discernible changes in biological communities occur, as well as improving our abilities to predict changes in stream temperatures in response to anthropogenic activities.

Although simple in concept and potentially useful in fisheries resources management, it is challenging to quantify thresholds associated with noticeable fish community changes along a thermal gradient. Lyons et al. (2009) defined coolwater streams in Michigan and Wisconsin as those having June–August mean temperatures of 17.0–20.5°C, but two subgroups were identifiable within their coolwater streams: "cold transition" (17.0–18.7°C) and "warm transition" (18.7–20.5°C). Thus, our abilities to classify streams thermally rely upon precise measurements of stream temperatures and analytical techniques that can identify subtle changes in taxonomic composition. However, a robust stream temperature data set has not been used in thermal classifications of fish communities. Thermal classifications have been attempted based on single measurements of daily maximum air and water temperatures (Stoneman and Jones 1996; Chu et al. 2009) or model-predicted stream temperatures (Lyons et al. 2009; McKenna et al. 2010). Continuous monitoring of stream temperatures temporally over a spatially dispersed area is now feasible due to technical developments in temperature-measurement devices. In addition, analyses of fish community patterns have nearly always used certain multivariate approaches, particularly ordination and cluster analyses (Maret et al. 1997; Kanno and Vokoun 2008; Lyons et al. 2009). These approaches may not identify community thresholds with precision and mask taxonomic contributions to the community shift patterns (Baker and King 2010).

Identifying thermal thresholds and characterizing fish community types has met challenges in Connecticut. The state harbors coldwater streams dominated by the families Salmonidae and Cottidae, and warmwater streams occupied by a greater diversity of species (e.g., families Cyprinidae and Centrarchidae). Yet, a good portion of wadeable streams in Connecticut appear to be inhabited by both coldwater and warmwater species (i.e., coolwater streams). Kanno et al. (2010) developed two indices of biotic integrity in the region, the first for coldwater streams and the second for all other wadeable streams ("mixed-water" streams). However, the lack of an objective assessment of thermal classifications is an obstacle in their practical applications. Co-occurrence of coldwater, coolwater, and warmwater streams is a common feature in many temperate regions of North America (Vannote et al. 1980; Chu et al. 2008; Lyons et al. 2009). Still, characterization of how fish communities respond along the thermal gradient, especially the transition between cold water and warm water is poorly understood.

This study was initiated to describe summer thermal thresholds and fish community transitions for Connecticut streams. Our objectives were to (1) identify thermal thresholds that trigger fish community changes using three summer temperature metrics (Lyons et al. 2009), and (2) describe taxonomic composition and indicator species of each fish community.

METHODS

Fieldwork.—This study was based on stream fish survey and water temperature data collected at 160 sites located on primarily wadeable, perennial, first- to fourth-order streams that contained a mix of riffle, run, and pool habitat types across Connecticut (Figure 1). We omitted sites with substantial habitat alterations (e.g., immediately downstream from a dam, adjacent to significant stream diversion, or contained within flood control channels), or ones that were low gradient (dominated by pool–glide habitat and having fine silt–sand substrate).

Our analysis included 212 paired fish community and water temperature samples collected between 2002 and 2011. The majority of the 160 sites had one fish community sample and one temperature data set during the same year, although 36 sites had more than one pair collected during multiple years. Fish were collected primarily during base flow conditions, the months of June and July, to maximize capture efficiency. In addition, these months correspond to the time of the year when temperature differences between coldwater, coolwater, and warmwater streams are greatest in Connecticut (see Results). Fish were collected by a crew of 4–8 people using pulsed-DC electrofishing (Smith-Root model L-24 backpack electrofisher, Smith-Root, Vancouver, Washington; or Coffelt model BP-4 backpack electrofisher, Coffelt Manufacturing, Flagstaff, Arizona, or a tote-barge with a Coffelt model VVP-2 electrofisher, powered by a generator). In general, the sampled reach lengths were between 100 and 150 m and total electrofishing time per reach ranged from 15 to 35 min. Reach lengths were determined by trying to target a length of 15–30 times the stream width to characterize fish community composition (Dauwalter and Pert 2003; Reynolds et al. 2003). After a single pass in a stream reach, all fish were identified

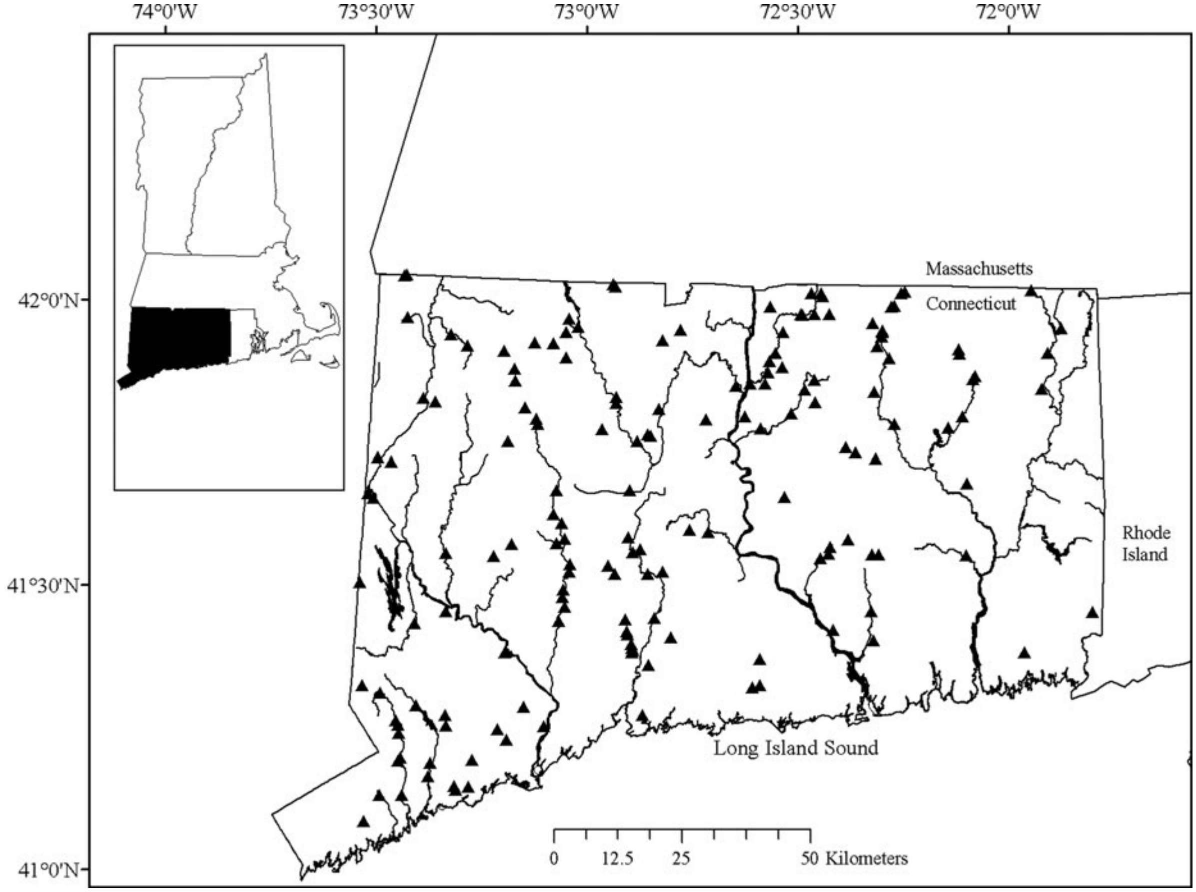

FIGURE 1. Site locations (solid triangles) in Connecticut where fish community and water temperature data were collected.

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to species, measured to nearest centimeter, and returned to the stream.

Stream water temperatures were collected hourly using data loggers (TidBit v2 Data Logger and Pro v2 Data Logger, ONSET Computer Corporation, Bourne, Massachusetts) deployed in the thalweg of the same stream reach where we sampled the fish community. Prior to deployment, all data loggers went through a quality control procedure using an ice bath to ensure that accuracy was within the manufacturer's specifications (CT DEEP 2012). Once the data loggers passed the quality control procedures, they were placed in PVC pipe, secured to weighted angle iron, placed in the stream location with adequate depth to keep the probe submerged throughout the duration of the deployment period, and covered with large rocks to secure from high stream flows and prevent discovery and reduce vandalism. The data loggers were deployed year round, but were visually inspected approximately every 6 months, and data were downloaded during site visits. After each deployment, water temperature values were reviewed for anomalies and quality-controlled values were stored in a relational database.

Statistical analysis.—Our analyses were based on commonly distributed fish species in Connecticut. Stocked salmonids (Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutta*, Rainbow Trout *Oncorhynchus mykiss*, and Atlantic Salmon *S. salar*), defined as adults or fry and fingerlings of hatchery origin, were removed from the data set and not included in analysis. Adult stocked salmonids are easily distinguished by the presence of multiple regenerated fins, damaged opercula, and bland coloration. Liberation records were used to identify sites where Brown Trout or Atlantic Salmon fry and fingerling stocking had occurred. At these sites all individuals were considered to be of hatchery origin as holdover individuals of these species are virtually impossible to distinguish from fish of similar size that were hatched within the stream. Species that occurred in less than 5% of the samples were removed because ecological thresholds cannot be reliably inferred for these rare species (Baker and King 2010). We calculated fish abundance per 100 m of stream to standardize count data among samples.

We calculated three water temperature metrics: June–August mean, July mean, and maximum daily mean (Lyons et al. 2009). We then used the program Threshold Indicator Taxa Analysis (TITAN) (Baker and King 2010) to identify change points in fish species response to thermal gradients and community-level temperature thresholds by considering aggregate changes across species. We ran TITAN to identify thermal thresholds for each of the three water temperature metrics. The TITAN method

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integrates information on the occurrence, abundance, and directionality of taxa responses (Baker and King 2010) using indicator value (IndVal) scores (Dufrêne and Legendre 1997). The IndVal scores are calculated and used to associate individual taxa with either a positive or negative response across the observed continuous gradient, in our case a thermal gradient. The TITAN method identifies the point at which the maximum IndVal of the taxon occurs across the observed gradient as the observed change point and assigns the taxa to either a positive or negative partition. Evidence for community thresholds is identified by synchronous taxa response. The TITAN method standardizes the observed IndVal as z-scores and sums the z-scores of each individual taxon within each partition for every candidate change point across the observed thermal gradient. This standardization ensures that both common and uncommon species contribute equally to the community change analysis (Baker and King 2010). The largest sums for each positive and negative partition are identified as observed community-level change points. The TITAN program was written in Program R and the code is included in Baker and King (2010).

Bootstrap resampling was used to estimate uncertainty and identify significant indicator taxa by providing measures of indicator purity and reliability. Indicator purity provides information on the proportion of agreement between the observed change-point response direction (negative or positive) and the bootstrap replicates. Indicator reliability provides an estimate of how significantly different the data set is from a random distribution. Individual taxa were considered significant if at least 95% of the bootstrap runs indicated the same response direction as the observed response (i.e., high purity) and at least 95% of the bootstrap runs were significantly different from a random distribution at $P \leq 0.05$ (i.e., high reliability). Bootstrap replicates were also used to develop empirical confidence limits around the community level change points. Bootstrap replicates were run 500 times and used to define thermal classes for Connecticut streams. We used the 5% sum $z-$ from 500 bootstrap replicates to define the change point for cold water to cool water, and we used the 95% sum $z+$ from the 500 bootstrap replicates to define the temperature change point for cool water to warm water. This approach would result in a more liberal range of coolwater streams, compared with using the median values of sum $z+$ and sum $z-$. We chose our approach because coolwater streams are, by definition, a transitional zone where both coldwater and warmwater species co-occur (Lyons et al. 2009), and thus there is an inherent difficulty when characterizing the thermal range of the coolwater community precisely.

To further assess the temperature preferences of fish species and identify indicator species of cold, cool, and warm waters, we used an extension of the original indicator species analysis proposed by Dufrêne and Legendre (1997) that considers an association between indicator species of both individual site groups and combinations of site groups (De Cáceres et al. 2010). For example, one particular species may be associated with only cold waters, while another may be associated with both cold and cool waters. We assigned sites to one of the temperature groups based upon the TITAN cutoffs described above. The method looks at each possible combination of site groups and retains the strongest group association with the target species. We choose the square-root indicator value index (Sqrt IndVal) as the measure of association (De Cáceres et al. 2010). The indicator value index is composed of two metrics: the probability of a site belonging to a site-group combination when the species has been found at that site and how frequently the species is found at sites belonging to the site-group. The indicator value measure ranges from 0 to 1 with higher values representing a greater association with a particular site-group. Statistical significance of the association was evaluated with a permutation test that uses the maximum Sqrt IndVal for the test value. We ran 999 random permutations. Species with P-values < 0.05 were considered significant indicators of a particular site-group. Indicator species analysis was implemented using the "indicspecies" package version 1.6.7. in R (De Cáceres and Legendre 2009).

We also used the sum $z+$ and sum $z-$ scores from the TITAN runs as an additional measure of thermal preferences for stream fish. Each species was categorized as either an increaser ($z+$) or a decreaser ($z-$) through TITAN analysis of each of the three temperature metrics and the final response to temperature category was determined by simple majority of two out of the three metrics.

RESULTS

A total of 26 fish species were used in our analysis (Table 1). Blacknose Dace and White Sucker were the most common species and were present in 84.4% and 79.6% of the stream samples, respectively. Slimy Sculpin, Brook Trout, Brown Trout, and Redfin Pickerel were categorized as "decreasers" in response to increasing stream temperature (Table 1; Tables A.1–A.3 in the Appendix), although Redfin Pickerel was not a statistically significant species (purity ≤ 0.95, reliability ≤ 0.95, $P > 0.05$ in response to any of the temperature metrics). All of the other species (22) were categorized as "increasers."

The 5th–95th percentiles of fish community change points overlapped between decreasers (sum $z-$) and increasers (sum $z+$) in all three temperature metrics (Table 2). Fish community change points for decreasers (sum $z-$) were 19.40°C for the June–August mean temperature, 21.00°C for the July mean, and 23.35°C for the maximum daily mean. The fish community change points for increasers (sum $z+$) were 20.50°C for the June–August mean temperature, 21.90°C for the July mean, and 23.30°C for the maximum daily mean.

As all of the species were consistently increasers or decreasers across three temperature metrics tested, except for Creek Chub (Tables 1, A.1–A.3); hence, we focused on the results for the June–August mean in the subsequent sections. Thermal classes for Connecticut streams using the June–August mean were defined as cold water, <18.29°C; cool water,

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TABLE 1. The 26 fish species in order of decreasing percent occurrence among the 212 stream samples. Species response as an increaser or decreaser to increasing water temperature is based on the TITAN analysis.

Family	Species	Percent occurrence	Response to temperature
Cyprinidae	Blacknose Dace *Rhinichthys atratulus*	84.4	Increaser
Catostomidae	White Sucker *Catostomus commersonii*	79.6	Increaser
Anguillidae	American Eel *Anguilla rostrata*	64.0	Increaser
Percidae	Tessellated Darter *Etheostoma olmstedi*	63.0	Increaser
Cyprinidae	Longnose Dace *Rhinichthys cataractae*	58.3	Increaser
Centrarchidae	Bluegill *Lepomis macrochirus*	40.8	Increaser
Salmonidae	Brook Trout *Salvelinus fontinalis*	38.9	Decreaser
Cyprinidae	Common Shiner *Luxilus cornutus*	38.4	Increaser
Salmonidae	Brown Trout *Salmo trutta*	36.0	Decreaser
Cyprinidae	Fallfish *Semotilus corporalis*	35.5	Increaser
Centrarchidae	Pumpkinseed *Lepomis gibbosus*	35.1	Increaser
Centrarchidae	Largemouth Bass *Micropterus salmoides*	33.6	Increaser
Centrarchidae	Redbreast Sunfish *Lepomis auritus*	31.8	Increaser
Cyprinidae	Creek Chub *Semotilus atromaculatus*	21.8	Increaser
Centrarchidae	Smallmouth Bass *Micropterus dolomieu*	19.0	Increaser
Cyprinidae	Cutlip Minnow *Exoglossum maxillingua*	17.1	Increaser
Centrarchidae	Rock Bass *Ambloplites rupestris*	14.2	Increaser
Ictaluridae	Brown Bullhead *Ameiurus nebulosus*	11.4	Increaser
Cottidae	Slimy Sculpin *Cottus cognatus*	10.9	Decreaser
Esocidae	Redfin Pickerel *Esox americanus*	10.4	Decreaser
Ictaluridae	Yellow Bullhead *Ameiurus natalis*	10.4	Increaser
Cyprinidae	Golden Shiner *Notemigonus crysoleucas*	10.0	Increaser
Centrarchidae	Green Sunfish *Lepomis cyanellus*	9.0	Increaser
Percidae	Yellow Perch *Perca flavescens*	9.0	Increaser
Esocidae	Chain Pickerel *Esox niger*	7.6	Increaser
Petromyzontidae	Sea Lamprey *Petromyzon marinus*	5.2	Increaser

18.29–21.70°C; and warm water, >21.70°C (Table 3). Frequency and abundance of decreaser species sharply declined above the coolwater thermal range, while increaser species became more prevalent, suggesting a community shift across the thermal gradient for the July–August mean (Figure 2A, B). Similar patterns were observed for the other two metrics. The coolwater thermal range was 3.41°C for the June–August mean and less than 4°C for all three metrics.

Fourteen species were considered significant indicators (*P*-value $>$ 0.05) of one or more temperature groups using indicator species analysis (Table 4; Figure 3). Two species were significant indicators of coldwater only (Slimy Sculpin and Brook Trout); six species were significant indicators of warm water only (Redbreast Sunfish, Cutlip Minnow, Smallmouth Bass, Rock Bass, Brown Bullhead, and Yellow Bullhead). No species were considered to be significant indicators for the coolwater range, 18.29–21.70°C. One species (Brown Trout) was a significant indicator for the combination of cold and cool waters and five species (American Eel, Tessellated Darter, Common Shiner, Bluegill, and Fallfish) were

TABLE 2. Threshold Indicator Taxa ANalysis (TITAN) community-level thresholds estimated from fish species responses to water temperature metrics (°C). The observed change point (CP) corresponds to the value of the x resulting in the largest sum of indicator value (IndVal) z-scores among all negative ($z-$) and positive ($z+$) taxa, respectively. Percentages (5%, 50%, 95%) correspond to change points from 500 bootstrap replicates and represent uncertainty around the CP.

	June–August mean				July mean				Maximum daily mean			
Method	CP	5%	50%	95%	CP	5%	50%	95%	CP	5%	50%	95%
TITAN sum ($z-$)	19.40	18.29	19.70	20.20	21.00	18.45	20.65	21.70	23.35	22.40	23.20	24.00
TITAN sum ($z+$)	20.50	20.00	20.35	21.70	21.90	21.50	21.90	22.30	23.20	23.00	24.23	26.30

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TABLE 3. The three stream temperature metrics (°C) for classifying streams in Connecticut into thermal classes.

	Water temperature (°C)		
Thermal Class	June–August mean	July mean	Maximum daily mean
Cold	<18.29	<18.45	<22.40
Cool	18.29–21.70	18.45–22.30	22.40–26.30
Warm	>21.70	>22.30	>26.30

significant indicators of the combination of cool and warm waters.

We used water temperature change points from the TITAN analysis for the June–August mean metric to evaluate annual stream temperature distribution among the thermal classes for the 160 study sites. Mean daily stream water temperatures were warmest in July (Figure 4). The maximum June–August mean temperature values for cold water was (22.9°C, $N = 25$), cool water (27.6°C, $N = 109$), and warm water (29.0°C, $N = 26$) with thermal differences between temperature groups greatest during June–September. Mean daily stream temperatures were similar between coldwater, coolwater, and warmwater streams in November–March.

TABLE 4. Species identified as significant indicators (P-value < 0.05) of a particular temperature group or combination of groups using indicator species analysis. We indicate the temperature site-group or group combination that obtained the highest indicator index value (Sqrt IndVal) and the statistical significance of the association (P-value). Larger Sqrt IndVals indicate a greater association with a particular temperature group.

Species	Group	Sqrt IndVal	P-value
Brook Trout	Cold	0.890	0.001
Slimy Sculpin	Cold	0.608	0.001
Brown Trout	Cold + cool	0.606	0.019
American Eel	Cool + warm	0.812	0.002
Tessellated Darter	Cool + warm	0.807	0.002
Common Shiner	Cool + warm	0.662	0.003
Bluegill	Cool + warm	0.653	0.009
Fallfish	Cool + warm	0.629	0.003
Redbreast Sunfish	Warm	0.759	0.001
Smallmouth Bass	Warm	0.652	0.001
Rock Bass	Warm	0.535	0.001
Cutlip Minnow	Warm	0.495	0.007
Brown Bullhead	Warm	0.489	0.002
Yellow Bullhead	Warm	0.403	0.016

DISCUSSION

Applying the TITAN method to a robust fish community and temperature data set, we defined stream temperature ranges

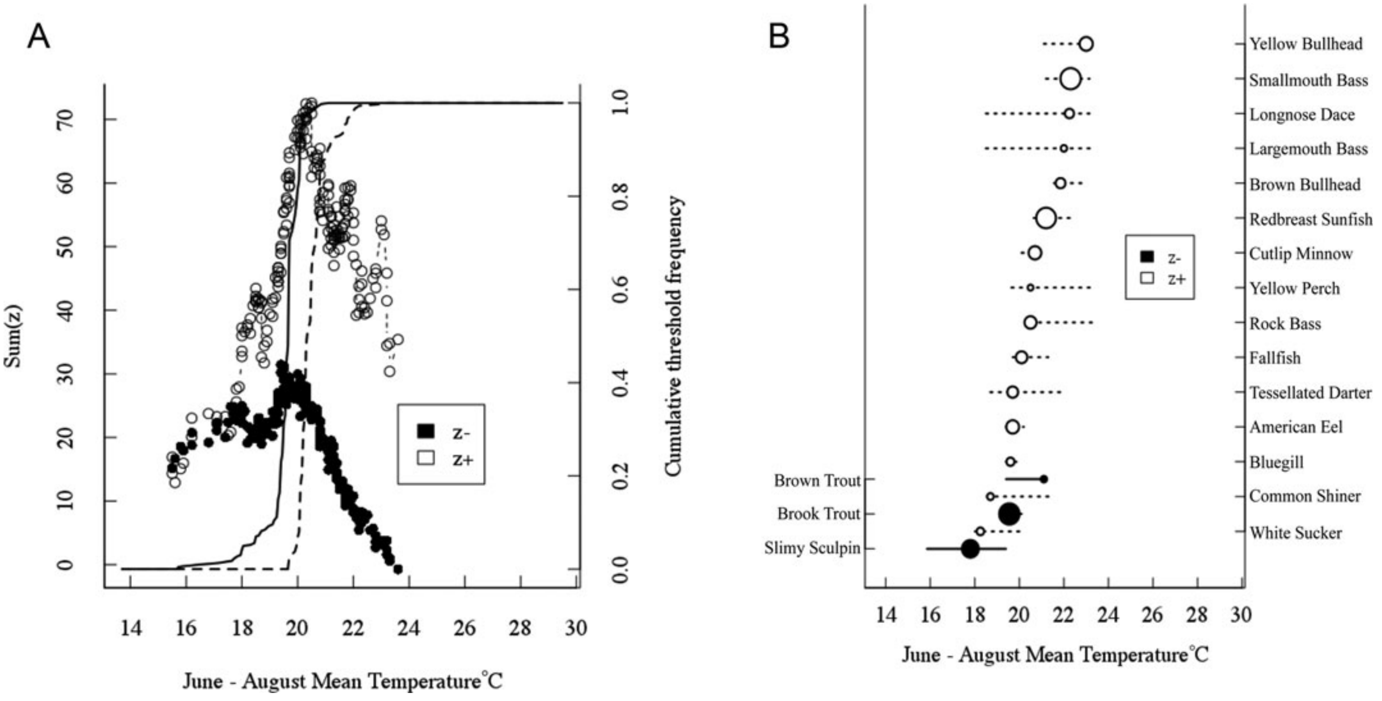

FIGURE 2. Threshold Indicator Taxa ANalysis (TITAN) outputs. (**A**) sum (z) scores for decreasers (filled circles) and increasers (open circles) across the summer temperature gradient. Vertical lines are cumulative frequency distributions of change points for negative (solid) and positive (dashed) indicator species across 500 replicate runs. (**B**) Significant species (purity ≥ 0.95, reliability ≥ 0.95, $P < 0.05$) in response to increasing ($z+$) or decreasing ($z-$) June–August mean water temperature. The circle size represents z-scores and horizontal lines overlapping each circle cover the 5th and 95th percentiles among 500 replicate runs.

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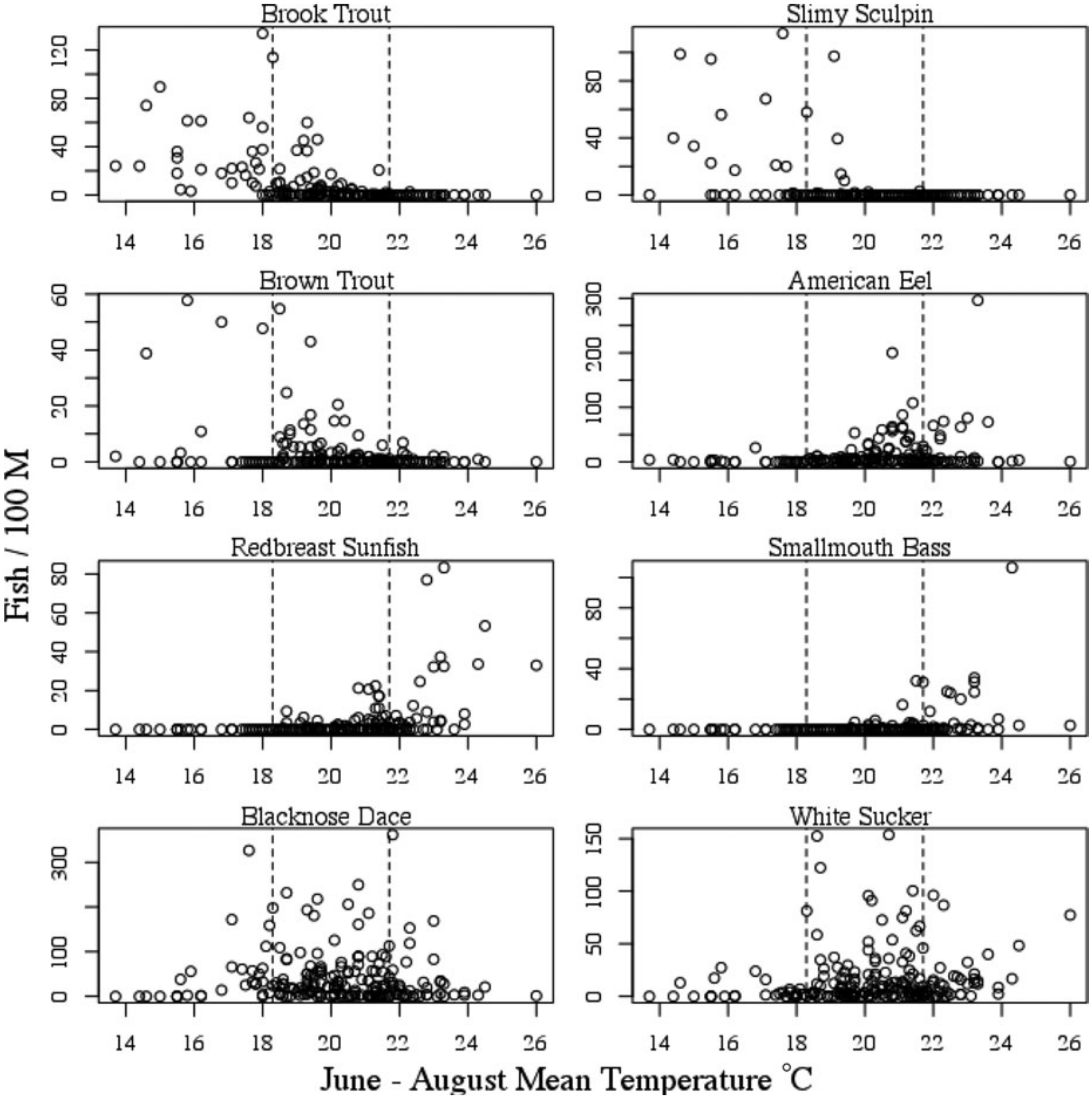

FIGURE 3. Scatter plots of select species displaying standardized abundance (fish count per 100 m) in response to June–August mean water temperature. Shown are representative coldwater species (Brook Trout, Slimy Sculpin), coldwater + coolwater species (Brown Trout), coolwater + warmwater species (American Eel), and warmwater species (Redbreast Sunfish, Smallmouth Bass), as well as cosmopolitan species (Blacknose Dace, White Sucker). Vertical lines show temperature cutoffs (cold, <18.29°C; cool, 18.29–21.70°C; warm, >21.70°C) from TITAN analysis.

for coldwater, coolwater, and warmwater streams in Connecticut. Thermal ranges have been defined in previous studies using various approaches, and the ranges have differed slightly among studies (Lyons et al. 1996, 2009; Stoneman and Jones 1996; Wehrly et al. 2003; McKenna et al. 2010). The ranges of June–August mean temperatures were <18.29°C for coldwater, 18.29–21.70°C for coolwater, and >21.70°C for warmwater streams in Connecticut. Thermal ranges of June–August mean temperatures were lower for coldwater (<17.0°C), coolwater (17.0–20.5°C), and warmwater (>20.5°C) streams in Michigan and Wisconsin (Lyons et al. 2009). As another example, McKenna et al. (2010) used daytime summer stream temperature records to define cold water (<18°C), cool water (18–24°C), and warm water (>24°C) in New York. The inconsistency may reflect true biological patterns among regions, differences among analytical approaches among studies, or a combination of both. Given that many temperate regions of North America harbor cold-, cool-, and warmwater habitats, a continental-scale analysis using a standard approach could advance our understanding of this important topic in fisheries management.

Some previous studies divided the coolwater community into two subclasses: “cold transition” and “warm transition” (Lyons

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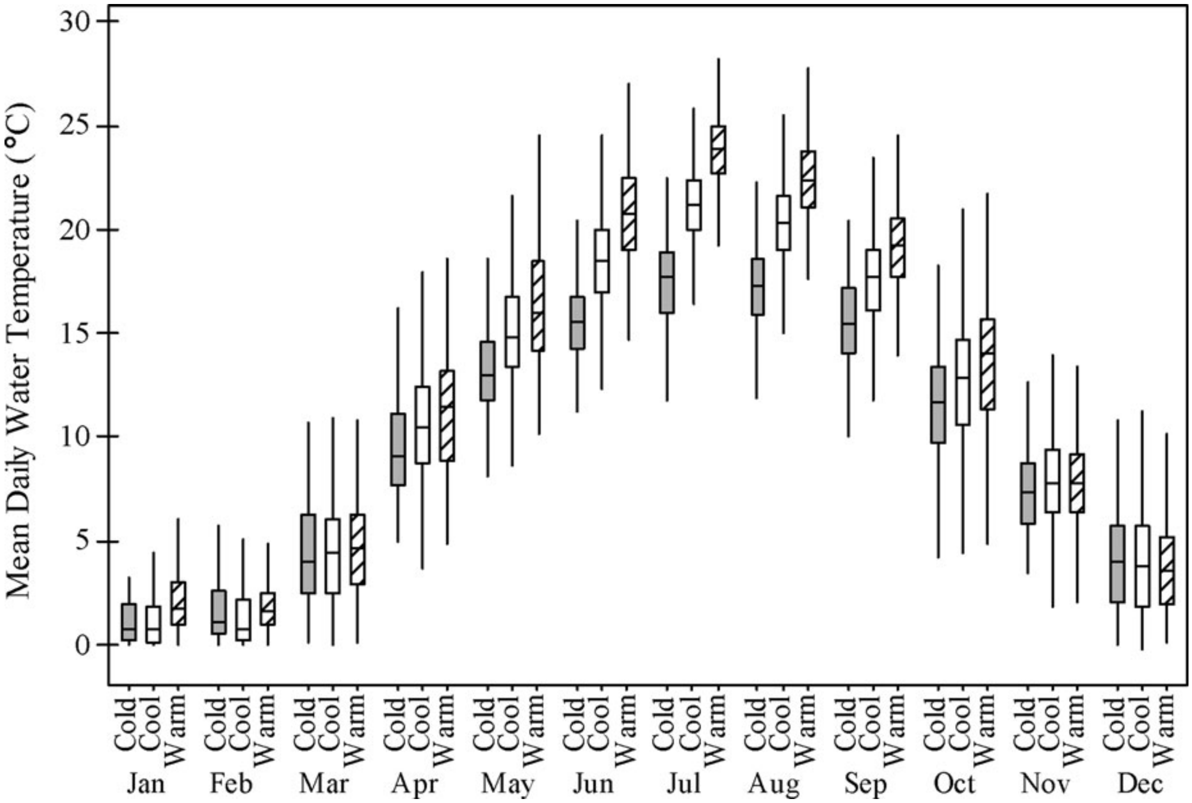

FIGURE 4. Box and whisker plots of mean daily water temperature (°C) by month and thermal class: cold (solid grey), cool (solid white), and warm (striped). The box represents the 25th percentile, median (horizontal line), and 75th percentile, and whiskers indicate the range of temperatures excluding outlier values.

et al. 2009; McKenna et al. 2010), but we did not attempt the finer classification within the coolwater community. Our inability to make a finer classification is attributable to low species richness (e.g., 26 species in this study versus 99 species in Lyons et al. 2009) and the absence of characteristic species (i.e., indicator species) for the coolwater community in Connecticut streams. Blacknose Dace and White Sucker, which are typically considered coolwater species, had cosmopolitan distributions across the thermal range observed (Figure 3). Also, the coolwater range was liberally defined by including 5th and 95th percentiles of change points for decreasers and increasers. As a result, the coolwater community could be best viewed as the transition zone where coldwater ("decreasers") and warmwater ("increasers") species co-occur, rather than as a distinct community composed of obligate coolwater species (Lyons et al. 2009). We believe the differences between the two studies can be attributed to the natural variation in ecological preferences of fish species throughout their ranges and methodological differences in how thresholds were defined including in situ measurement versus modeled values, use of TITAN, and paired fish community and water temperature data.

The coolwater class had a 3.41°C range for the June–August metric and <4°C for all three metrics. Despite this narrow range, 68.1% of the 160 streams were classified as coolwater streams. As such, the coolwater class represents the majority habitat class as represented by total stream miles and this is similar to findings in Lyons et al. (2009). The similarity illustrates that coolwater streams are more common than previously recognized, and identifying the distribution and function of coolwater habitat is an important area of research for many regions experiencing increasing trends in air and water temperature regimes.

The coldwater–coolwater transition was characterized by discernible changes in the presence and abundance of Slimy Sculpin, Brook Trout, and Brown Trout. Identifying this threshold is of particular interest in understanding the potential impact of climate change and other anthropogenic factors on coldwater resources. Slimy Sculpin was associated with the coldest streams among the three species (July–August mean temperature threshold, 17.80°C [90% CI: 15.7–19.5°C]). The distribution of this species in Connecticut is geographically limited (Kanno and Vokoun 2008), yet its high thermal sensitivity would make it a suitable candidate species for monitoring thermal changes caused by anthropogenic factors in a region where the species is distributed more commonly (e.g., northern New England). Brook Trout was the other indicator species of coldwater communities, while Brown Trout was an indicator of coldwater–coolwater communities. Preference of Brook Trout for colder temperatures has been known from laboratory behavioral observations (Taniguchi et al. 1998) and broad-scale spatial distributions of the two trout species in the field (Eaton et al. 1995; Wehrly et al. 2003). We had considered removing naturalized nonnative species (including Brown Trout) from

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our analyses as it would have lowered the coldwater–coolwater transition threshold. However, we retained naturalized nonnative species in our analyses because they are actively managed for recreational fishing and comprise a nontrivial part of fish communities in our landscape.

The coolwater–warmwater transition represented a thermal range in which a number of species became more common and abundant (i.e., members of the families Anguillidae, Cyprinidae, Centrarchidae, Ictaluridae, and Percidae). This pattern was to be expected because stream temperature is positively associated with species richness in Connecticut (Kanno and Vokoun 2008) and other temperate regions (Rathert et al. 1999; Buisson et al. 2008). Thermal associations of a couple of species found in this study differed slightly from those reported in the literature. Smallmouth Bass was an indicator species of warmwater streams in Connecticut but it is often regarded as a coolwater species (Halliwell et al. 1999); similarly, Bluegill was indicative of coolwater–warmwater streams in this study although it is considered a warmwater species (Halliwell et al. 1999). We do not necessarily suggest changes in thermal preference classification for these species, because this study was limited primarily to wadeable streams. Inclusion of nonwadeable streams and rivers would be required for an improved understanding of thermal preferences for warmwater species in the region. Restricting the scope of the current study to wadeable streams allowed us to understand the summer temperature effect on fish community changes without introducing the confounding effect of stream size.

Continuous temperature monitoring throughout the year revealed an interesting seasonal pattern; thermal differences among coldwater, coolwater, and warmwater streams were noticeable only during summer but not during the rest of the year (Figure 4). Air temperature alone cannot explain stream temperature variation within a watershed or among neighboring watersheds (Velasco-Cruz et al. 2012; Kanno et al. 2013). An important factor contributing to heightened thermal differences during the summer base flow period is probably groundwater discharge (Wehrly et al. 2003). Understanding how groundwater mediates stream temperature is a much-needed area of research that would improve our ability to classify stream fish communities, as well as our assessment of climate change effects on fisheries resources.

In addition to benefiting fisheries management, our findings will help state environmental regulatory agencies in their efforts to develop biology-based water temperature criteria (Todd et al. 2008), and to augment biological assessments (Barbour et al. 1999) as required under the U.S. Clean Water Act (CWA). Our ability to develop biology-based water temperature criteria to protect fish and other aquatic species has been hindered by our incomplete understanding of species' thermal thresholds. Historically, temperature criteria have been developed primarily based on lethal and sublethal thresholds for fish derived from laboratory studies (e.g., Brungs and Jones 1977). More recently, there is recognition that maintaining a distribution of natural temperature regimes, spatially and temporally, is perhaps a better approach to protect aquatic species (Poole et al. 2004).

In summary, we have identified a coldwater and warmwater summer temperature threshold with statistically significant indicator fish species. In addition we have defined coolwater habitat between the thresholds, but this temperature range did not have any statistically significant indicator species. When the coolwater range was viewed as a transition, combining the coldwater–coolwater sites or coolwater–warmwater sites, at least one significant indicator was present. The 3.41°C coolwater transition zone, encompassing the majority of river miles in Connecticut, is an important habitat harboring many of our native species. The definition of these summer temperature thresholds and resulting fish community structure will help to inform future fish community and water resource management in the context of changing climatic conditions and other direct and indirect human-related impacts to stream water temperatures.

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Appendix: Temperature–Fish Species Relationships Based on TITAN

TABLE A.1. Threshold Indicator Taxa ANalysis (TITAN) change points of fish species in response to June–August mean water temperature (°C). The observed change points (CP) corresponds to the value resulting in the largest indicator value (IndVal) z-scores for each taxon either as an increase (+) or decrease (−) to the temperature gradient. Percentiles (5%, 50%, 95%) correspond to change points from 500 bootstrap replicates. Purity is the mean proportion of correct response direction ($z-$ or $z+$) assignments; reliability (Rel) is the mean proportion of P-values < 0.05 among 500 bootstrap iterations.

		June–August mean temperature (°C)								
Species	±	CP	5%	50%	95%	IndVal	P-value	z-score	Purity	Rel
Blacknose Dace	$z+$	15.50	15.50	16.50	22.80					
White Sucker	$z+$	18.25	17.95	18.50	20.50	66.42	<0.01	4.54	1.00	1.00
American Eel	$z+$	19.70	19.40	19.70	20.45	65.93	<0.01	7.89	1.00	1.00
Longnose Dace	$z+$	22.25	18.25	22.10	23.20	62.88	<0.01	5.55	1.00	1.00
Smallmouth Bass	$z+$	22.30	20.90	22.30	23.25	62.74	<0.01	12.52	1.00	1.00
Tessellated Darter	$z+$	19.70	18.50	20.10	22.15	57.03	<0.01	6.61	1.00	1.00
Redbreast Sunfish	$z+$	21.20	20.45	21.30	22.80	53.68	<0.01	12.15	1.00	1.00
Fallfish	$z+$	20.10	19.65	20.10	22.45	44.59	<0.01	7.06	1.00	1.00
Common Shiner	$z+$	18.70	18.50	20.20	21.75	44.46	<0.01	4.09	1.00	1.00
Bluegill	$z+$	19.60	19.30	19.70	20.20	42.47	<0.01	4.87	1.00	1.00
Largemouth Bass	$z+$	22.00	18.00	22.00	23.45	37.23	<0.01	3.84	0.98	0.93
Yellow Bullhead	$z+$	23.00	20.85	21.50	23.45	32.53	<0.01	8.10	1.00	1.00
Pumpkinseed	$z+$	19.40	17.55	20.30	23.25	27.94	0.06	1.93	0.88	0.82
Rock Bass	$z+$	20.50	20.45	21.75	23.47	27.33	<0.01	7.38	1.00	1.00
Cutlip Minnow	$z+$	20.70	19.80	20.45	21.30	27.00	<0.01	7.84	1.00	1.00
Brown Bullhead	$z+$	21.85	20.65	21.80	23.20	24.20	0.01	5.99	1.00	1.00
Yellow Perch	$z+$	20.50	19.40	21.70	23.45	12.34	0.01	3.48	1.00	0.99
Green Sunfish	$z+$	18.50	18.50	20.30	21.70	10.80	0.06	1.48	0.56	0.32
Golden Shiner	$z+$	20.20	19.30	20.30	23.15	10.95	0.03	2.37	0.83	0.72
Chain Pickerel	$z+$	22.00	18.70	21.20	23.20	9.37	0.06	1.55	0.90	0.69
Sea Lamprey	$z+$	19.30	19.10	20.15	22.20	7.24	0.06	2.11	0.96	0.79
Brook Trout	$z-$	19.55	18.75	19.70	20.30	69.09	<0.01	16.49	1.00	1.00
Slimy Sculpin	$z-$	17.80	15.55	17.80	19.50	50.21	<0.01	13.68	1.00	1.00
Brown Trout	$z-$	21.10	17.55	20.80	21.30	36.99	<0.01	5.02	0.99	0.99
Creek Chub	$z-$	20.50	18.35	20.30	22.00	17.79	0.07	1.71	0.70	0.53
Redfin Pickerel	$z-$	21.30	17.25	20.55	21.70	11.22	0.06	1.93	0.88	0.68

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TABLE A.2. Threshold Indicator Taxa ANalysis (TITAN) change points of fish species in response to July mean stream temperature (°C). The observed change points (CP) corresponds to the value resulting in the largest indicator value (IndVal) z-scores for each taxon either as an increase $(+)$ or decrease $(-)$ to the temperature gradient. Percentiles (5%, 50%, 95%) correspond to change points from 500 bootstrap replicates. Purity is the mean proportion of correct response direction ($z-$ or $z+$) assignments; reliability (Rel) is the mean proportion of P-values < 0.05 among 500 bootstrap iterations.

		July mean temperature								
Species	±	CP	5%	50%	95%	IndVal	P-value	z-score	Purity	Rel
Blacknose Dace	$z+$	16.75	15.80	18.35	24.45	72.42	<0.01	3.56	0.69	0.69
Yellow Bullhead	$z+$	24.55	21.95	24.50	24.95	67.87	<0.01	10.88	1.00	1.00
Smallmouth Bass	$z+$	24.30	22.05	23.43	24.40	67.08	<0.01	11.48	1.00	1.00
White Sucker	$z+$	18.60	16.73	19.05	23.30	62.81	0.01	3.38	0.99	0.97
American Eel	$z+$	21.20	20.60	21.10	22.10	61.66	<0.01	7.00	1.00	1.00
Tessellated Darter	$z+$	22.10	20.90	21.80	23.30	58.31	<0.01	6.49	1.00	1.00
Longnose Dace	$z+$	22.85	19.30	22.90	23.85	54.57	<0.01	6.04	1.00	1.00
Redbreast Sunfish	$z+$	22.50	21.50	22.35	24.00	52.06	<0.01	10.83	1.00	1.00
Common Shiner	$z+$	19.20	19.05	20.85	24.65	43.92	<0.01	4.05	1.00	1.00
Bluegill	$z+$	20.35	19.10	20.45	21.65	42.65	<0.01	4.35	1.00	1.00
Fallfish	$z+$	21.20	20.15	21.60	24.80	39.33	<0.01	5.91	0.99	0.99
Largemouth Bass	$z+$	21.90	18.95	22.20	24.00	29.26	0.01	2.92	0.94	0.86
Rock Bass	$z+$	22.20	21.70	22.15	22.65	28.98	<0.01	8.37	1.00	1.00
Pumpkinseed	$z+$	21.15	18.18	21.10	23.35	27.68	0.02	2.31	0.87	0.83
Creek Chub	$z+$	18.60	18.60	21.18	23.70	22.47	0.11	1.69	0.47	0.31
Cutlip Minnow	$z+$	20.80	20.75	21.95	22.80	25.34	<0.01	8.01	1.00	1.00
Brown Bullhead	$z+$	22.30	20.60	22.70	24.80	19.04	<0.01	4.00	1.00	0.99
Yellow Perch	$z+$	20.50	19.80	21.50	24.80	10.98	0.03	2.58	0.96	0.88
Green Sunfish	$z+$	19.05	19.30	21.03	22.80	10.80	0.05	1.36	0.59	0.43
Golden shiner	$z+$	22.10	19.10	21.90	24.30	9.10	0.19	1.28	0.82	0.57
Chain Pickerel	$z+$	22.80	19.60	22.80	24.50	8.57	0.06	1.71	0.89	0.70
Sea Lamprey	$z+$	20.75	20.60	20.90	23.35	8.40	0.02	3.15	0.99	0.94
Brook Trout	$z-$	21.20	19.60	20.60	21.50	62.39	<0.01	14.94	1.00	1.00
Slimy Sculpin	$z-$	18.55	16.40	18.50	20.90	45.17	<0.01	11.61	1.00	1.00
Brown Trout	$z-$	22.40	20.80	22.25	22.75	40.49	<0.01	5.35	1.00	1.00
Redfin Pickerel	$z-$	15.40	15.40	19.80	22.90	28.82	0.09	2.54	0.88	0.80

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TABLE A.3. Threshold Indicator Taxa ANalysis (TITAN) change points of fish species in response to maximum daily mean stream temperature (°C). The observed change points (CP) corresponds to the value resulting in the largest indicator value (IndVal) z-scores for each taxon either as an increase (+) or decrease (−) to the temperature gradient. Percentiles (5%, 50%, 95%) correspond to change points from 500 bootstrap replicates. Purity is the mean proportion of correct response direction ($z-$ or $z+$) assignments; reliability (Rel) is the mean proportion of P-values < 0.05 among 500 bootstrap iterations.

		Maximum daily mean temperature								
Species	±	CP	5%	50%	95%	IndVal	P-value	z-score	Purity	Rel
Blacknose Dace	$z+$	19.95	19.25	23.00	28.40	70.86	0.01	3.14	0.49	0.49
White Sucker	$z+$	22.30	21.75	22.30	24.75	69.64	<0.01	5.89	1.00	1.00
Longnose Dace	$z+$	27.10	22.30	27.10	27.95	66.13	<0.01	6.43	1.00	1.00
American Eel	$z+$	24.00	22.90	23.90	24.60	61.26	<0.01	6.67	1.00	1.00
Tessellated Darter	$z+$	24.30	22.30	24.30	26.66	60.36	<0.01	7.05	1.00	1.00
Cutlip Minnow	$z+$	28.15	23.70	27.10	28.40	59.38	<0.01	9.53	1.00	1.00
Redbreast Sunfish	$z+$	25.50	25.10	25.80	27.15	54.85	<0.01	11.78	1.00	1.00
Rock Bass	$z+$	28.25	24.65	27.10	28.55	51.61	0.01	7.22	1.00	1.00
Common Shiner	$z+$	27.15	22.30	25.10	27.60	50.63	<0.01	4.57	1.00	1.00
Bluegill	$z+$	23.20	22.40	23.25	24.16	47.22	<0.01	5.36	1.00	1.00
Fallfish	$z+$	24.50	23.65	24.50	25.90	46.27	<0.01	8.28	1.00	1.00
Smallmouth Bass	$z+$	26.05	25.30	26.00	28.25	45.01	<0.01	11.84	1.00	1.00
Largemouth Bass	$z+$	24.65	22.75	24.85	27.80	34.38	<0.01	4.74	0.99	0.98
Pumpkinseed	$z+$	23.25	21.50	23.25	26.30	32.96	0.01	3.60	0.94	0.93
Yellow Bullhead	$z+$	25.80	25.40	25.80	27.55	26.66	<0.01	9.13	1.00	1.00
Brown Bullhead	$z+$	26.95	23.55	26.65	27.65	25.35	0.00	5.87	1.00	0.99
Creek Chub	$z+$	20.55	20.95	24.10	28.25	22.10	0.15	0.88	0.71	0.45
Golden Shiner	$z+$	25.00	22.35	25.00	26.10	12.31	0.01	3.06	0.94	0.81
Yellow Perch	$z+$	23.20	23.00	23.55	27.95	12.30	0.01	3.52	0.97	0.95
Green Sunfish	$z+$	23.55	23.10	23.70	25.00	12.22	0.02	3.01	0.85	0.77
Chain Pickerel	$z+$	23.50	22.50	24.10	26.00	9.66	0.03	2.95	0.99	0.93
Sea Lamprey	$z+$	22.80	22.50	24.00	25.61	6.96	0.09	1.63	0.86	0.55
Brook Trout	$z-$	23.00	22.50	23.10	24.00	81.06	<0.01	17.58	1.00	1.00
Slimy Sculpin	$z-$	21.80	19.35	21.50	23.36	44.63	<0.01	12.50	1.00	1.00
Brown Trout	$z-$	25.50	19.25	25.30	26.00	38.38	<0.01	5.08	1.00	1.00
Redfin Pickerel	$z-$	25.30	19.25	24.00	26.10	11.40	0.04	2.08	0.92	0.80

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