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ARTICLE

Integrating Fish Assemblage Data, Modeled Stream Temperatures, and Thermal Tolerance Metrics to Develop Thermal Guilds for Water Temperature Regulation: Wyoming Case Study

Caitlin P. Mandeville*[1]
Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, 1000 East University Avenue, Department 3166, Laramie, Wyoming 82071, USA

Frank J. Rahel
Department of Zoology and Physiology, University of Wyoming, 1000 East University Avenue, Department 3166, Laramie, Wyoming 82071, USA

Lindsay S. Patterson
Wyoming Department of Environmental Quality, 200 West 17th Street, Cheyenne, Wyoming 82002, USA

Annika W. Walters
U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, 1000 East University Avenue, Department 3166, Laramie, Wyoming 82071, USA

Abstract

Many streams are experiencing increased average temperatures due to anthropogenic activity and climate change. As a result, surface water temperature regulation is critical for preserving a diverse stream fish species assemblage. The development of temperature regulations has generally been based on laboratory measurements of individual species' thermal tolerances rather than community response to temperature in the field, despite multiple limitations of using laboratory data for this purpose. Using field data to develop temperature regulations may avoid some of the limitations of laboratory data, but the use of field data comes with additional challenges that prevent its widespread adoption. We used Wyoming stream fish assemblages as a case study to examine the feasibility of addressing the limitations of field and laboratory data through a hybrid approach that integrates both types of data to classify species into thermal guilds that can potentially inform regulatory standards. We identified coldwater, coolwater, and warmwater classes of sites with modeled mean August temperatures of <15.5, 15.5–19.9, and >19.9°C, respectively. We used species' associations with these temperature classes to place species into site-groups. Finally, we used standardized laboratory measures of species' upper acute and chronic thermal tolerances to identify and reclassify species with unusual thermal distributions. Through this process we classified species into five thermal guilds that may be useful for surface water temperature regulation in Wyoming. Our approach addresses the limitations identified for field and laboratory data and demonstrates a framework that could be used for incorporating multiple types of data to develop temperature standards.

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*Corresponding author: cmpeterson78@gmail.com
[1] Present address: Department of Natural History, Norwegian University of Science and Technology, Erling Skakkes Gate 47B, 7012, Trondheim, Norway.
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Temperature has a major influence on the physiology and behavior of fish (Kingsolver 2009; Buckley et al. 2012). Every fish species has an optimal temperature range, and deviation from this range may result in both individual mortality and reduced population viability (Cherry et al. 1977; Coutant 1977; Hokanson et al. 1977). Because thermal optima, maxima, and minima vary substantially among species, the composition of stream fish assemblages is strongly related to water temperature (Hokanson et al. 1977; Magnuson et al. 1979; Comte and Grenouillet 2013). The preservation of natural thermal regimes is therefore essential to protect distinct stream fish species assemblages (Rahel and Hubert 1991; Wehrly et al. 2003; Poole et al. 2004).

Stream thermal regimes are driven by natural and anthropogenic factors. Natural factors include solar radiation, air temperature, elevation, groundwater input, channel morphology and shading, and stream flows (Caissie 2006; Webb et al. 2008). Anthropogenic influences such as riparian zone alteration, dams and diversions, land use change, and the direct input of thermal effluent often increase water temperatures (Walsh et al. 2005; Hester and Doyle 2011; Firkus et al. 2018). Models predict that climate change is likely to further increase stream temperatures (Isaak et al. 2010; Paukert et al. 2016). Because of these anthropogenic influences, preventing increases in stream temperature that may be detrimental to fish and other aquatic life is a major focus of stream water quality regulation.

Thermal regulatory approaches vary among regulatory agencies along with regional differences in stream fish assemblages and stream thermal regimes, but a common objective is that regulations should be protective while also remaining attainable (Poole et al. 2004; CWQCC 2011). In other words, maximum allowable temperatures must be low enough to protect species from harmful thermal change but should not be exceeded by naturally occurring thermal regimes.

The identification of thermally distinct species assemblages, or guilds, is a common approach used to balance protection and attainability (Todd et al. 2008; McCullough et al. 2009; McCullough 2010). Species associated with a thermally distinct species assemblage are classified into a thermal guild, and regulatory criteria are developed for each guild. Streams are tested for compliance with the criteria associated with the guild expected to be present. The number of recognized guilds, as well as their taxonomic composition and regulatory criteria, are expected to vary regionally. The lowest resolution approach would involve two guilds (for example, coldwater and warmwater guilds); the highest resolution approach would entail a unique regulatory criterion for each species expected to be present in a management area. The high-resolution scenario could in theory achieve perfect protection and attainability but would be infeasible to implement. Therefore, a general maxim is that species should be divided into the maximum number of guilds for which regulations can be feasibly implemented.

Although the division of species into guilds of similar thermal requirements is a simple concept, it is difficult in practice to detect thermal thresholds between distinct species assemblages (Beauchene et al. 2014). Historically, thresholds were established by ranking species-specific metrics, most commonly laboratory-derived thermal optima or maxima, and subjectively drawing “break points” along the gradient of species’ responses (Magnuson et al. 1979; Eaton et al. 1995). Ranked species-specific laboratory values remain the basis of many thermal regulations today. Laboratory-derived thermal tolerance provides a good measure of species’ physiological sensitivities to thermal stress under otherwise ideal conditions but may not represent upper thermal limits in natural settings where other abiotic or biotic stresses may be present (Magnuson et al. 1979; Meeuwig et al. 2004; Wehrly et al. 2007). Furthermore, the quantity and quality of thermal stress test results vary widely by species, so regulations derived from these results may favor species with an extensive history of stress testing and disadvantage less-studied species (Isaak et al. 2017b; Peterson 2017) (Table 1).

Recently, there has been increased interest in studying species’ thermal requirements in the context of their natural thermal regimes (Eaton et al. 1995; Poole et al. 2004; McCullough 2010). Newer approaches for thermal threshold detection involve collecting paired field data on species assemblages and stream temperatures at a large number of stream sites (Eaton et al. 1995; Beauchene et al. 2014; Parkinson et al. 2016). Threshold detection approaches include multivariate methods, such as ordination, cluster, and similarity index analyses, or threshold indicator methods (Wehrly et al. 2003; Lyons et al. 2009; Beauchene et al. 2014). After thresholds are identified, fish species’ associations with the assemblages on either side of the thresholds are used to inform the development of regulatory thermal guilds. The advantage of field data is its ability to capture the impact of factors that alter species’ thermal niches. These factors include thermally mediated species interactions (Fausch et al. 1994; Taniguchi et al. 1998; Carmona-Catot et al. 2013), food availability and metabolic rate at various temperatures (Sullivan et al. 2000; Larsson 2005), and access to thermal refugia (Westhoff et al. 2016; Ouellet et al. 2017). Additionally, species assemblage data offer an objective method for classifying species with limited or no thermal stress test data from laboratory studies.

Despite the development of threshold detection approaches, regulatory agencies have generally not begun to use field-based data for developing stream temperature regulations. One barrier to the application of field data to

TABLE 1. Challenges in thermal guild development using laboratory-derived data (cases A through C) and field-derived data (cases D through G).

Case	Limitation	Example
A	*Thermal niche constraints.* Laboratory data often fail to capture species' realized thermal niches because factors that alter species' thermal distribution in the field are difficult to measure in the lab. If a species' thermal tolerance is lower under field conditions than lab conditions, regulations derived from laboratory data will not be protective; if higher, they may be unattainable.	In some streams with both Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta*, the Brown Trout thermal niche is constricted by competitive interactions (Taniguchi et al. 1998).
B	*Variable data quality.* Studies measure species' stress responses using a variety of metrics that are not easily standardized and compared so species' standardized upper temperature tolerance depends to some extent on the type of stress testing implemented (Peterson 2017). Therefore, thermal tolerance values may not be comparable between species.	Two common stress test metrics, UUILT[a] and CTM[b], produce standardized acute thermal tolerance values for the same species that differ by an average of 1.7°C (Peterson 2017).
C	*Variable data quantity.* Some species have many available thermal stress test studies and others have little to no thermal tolerance data available (Isaak et al. 2017b; Peterson 2017). There is no objective lab-based method to classify species into guilds when they have no available thermal stress test data.	In Wyoming, 19 species had insufficient data to calculate an acute thermal tolerance (Table 3).
D	*Thermal generalist species.* Thermal generalists have a wide thermal niche and occur frequently along the thermal spectrum. Their frequent co-occurrence with warmwater species in waters at the lower end of the warmwater species' ranges may cause them to be classified into a warmwater guild, leaving them vulnerable to thermal increases. Note, however, that if generalists are classified into too cold a guild, their presence in warmer streams may trigger the application of unattainable regulations under some methods of stream classification.	White Sucker *Catostomus commersonii* occurs at sites with modeled temperatures ranging from 12.7°C to 22.9°C. Its thermal niche width is 10.2°C, wider than the average of 5.3°C (Figure 3).
E	*Species with truncated distributions.* A species' statewide thermal distribution may not be representative of its overall distribution. Because stream temperature regulation in the USA is applied at the state level, a species with a limited statewide range may be classified inappropriately.	Utah Sucker *Catostomus ardens* occupies warmer habitat in most of its range, but in Wyoming is restricted to a part of the state with mostly coldwater streams (Baxter et al. 1995).
F	*Rare species.* Common threshold detection methods require a minimum number of observations so it may not be possible to classify rare species or those with a low probability of detection.	Orangethroat Darter *Etheostoma spectabile*, whose range in Wyoming is small, was observed at only two sites in the 1,763-site database.
G	*Species that coexist on the landscape but have different levels of sensitivity to thermal change.* If two species coexist at the high end of one's thermal range and the low end of the other's, the former will be more sensitive to thermal change. Regulations designed to protect one species may not be appropriate for the other.	Fathead Minnow *Pimephales promelas* and Channel Catfish *Ictalurus punctatus* frequently occur together, but their thermal tolerance values suggest that Fathead Minnow is less tolerant of stream warming than Channel Catfish (Figure 3).

[a] UUILT = ultimate upper incipient lethal temperature.

[b] CTM = critical thermal maximum.

thermal regulation is that species with unusual thermal distributions may be classified into inappropriate guilds. We identify four general cases in which a species might be inappropriately classified based on field data (Table 1). Such species may not be adequately protected by classification into a guild with commonly co-occurring species, so additional types of data may be required to classify them into thermal guilds that will be useful for developing thermal standards.

We propose integrating field data with laboratory-derived thermal tolerance data to address some of the limitations inherent in guild development methods that use just one type of data (Figure 1). We used the streams and rivers in the state of Wyoming as a case study to explore the feasibility of integrating thresholds detected using paired species assemblage and temperature field data with laboratory data on species' thermal tolerances to develop thermal guilds that could be used in a regulatory context.

METHODS

Our analyses included two distinct approaches, one based on field data and the other on laboratory data, which were merged to produce a set of thermal guilds that may be suitable for stream temperature regulation in Wyoming. In the first approach, we paired field-derived data on fish assemblages with modeled water temperature at stream sites throughout Wyoming to determine species' associations with thermally distinct assemblages. We considered these thermally distinct species assemblages to be candidate regulatory thermal guilds. In the second approach, we used laboratory-derived data on species' responses to thermal stress testing to derive an acute and chronic upper thermal tolerance value for Wyoming fish species. Finally, we used a four-step process to integrate laboratory and field data to determine the taxonomic composition of a set of thermal guilds that may be useful for regulation (Figure 1). Each step of this process addressed one or more of the concerns noted in Table 1.

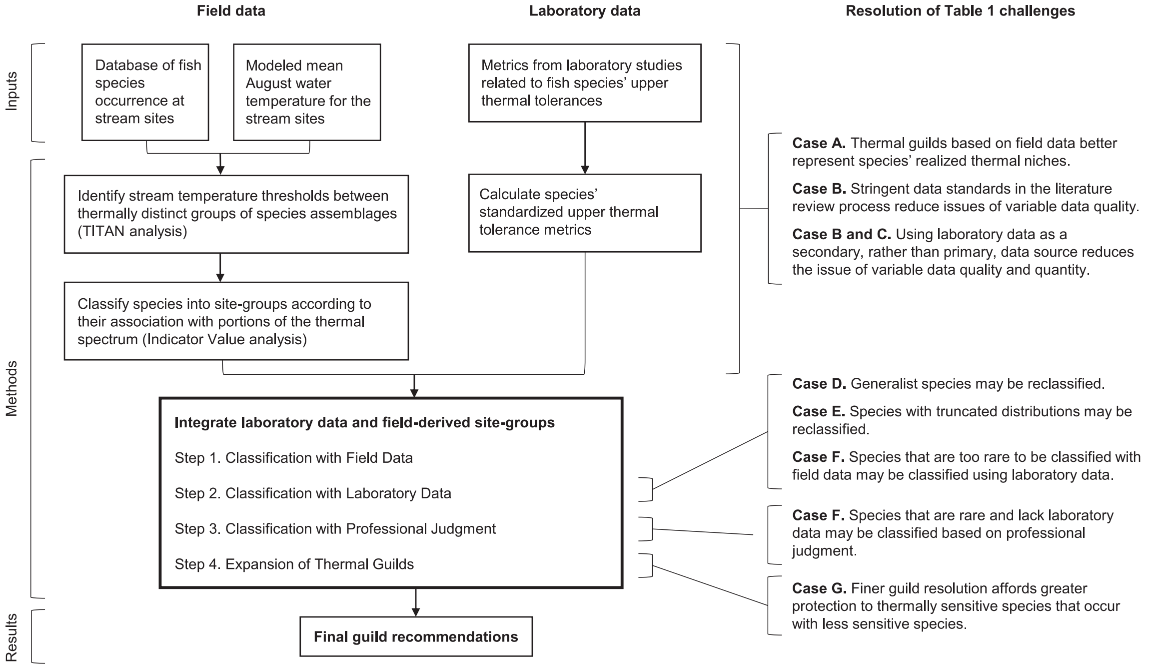
Field-Derived Thermal Distributions

We used the program Threshold Indicator Taxa Analysis (TITAN) (Baker and King 2010) to identify thermal thresholds that separate distinct species assemblages. A thermal threshold is defined here as a small temperature gradient over which a relatively large change in the species assemblage occurs.

Our species assemblage database consisted of stream fish occurrence data collected by the Wyoming Game and Fish Department from distinct sites in summer surveys (defined here as between May and October) from 1989 through 2016. We excluded surveys that did not sample comprehensively for all species present. After removing 21 species with three or fewer observations, the final species assemblage database consisted of 1,763 sites with presence or absence data for 52 stream fish species (Figure 2; see the Supplement in the online verion of this manuscript). We paired each of the 1,763 species assemblage sites with a modeled historical (1993–2011) mean August stream temperature for the 1-km stream reach in which it was located. Modeled temperatures were produced by the Air, Water, and Aquatic Environments Program of the United States Forest Service Rocky Mountain Research Station as part of their series of publicly available modeled historical (1993–2011) stream temperatures for much of the western United States at a 1-km resolution (Isaak et al. 2016).

Threshold identification.— The program TITAN iteratively tests along an environmental gradient for change points in the distribution of individual species and uses synchronous responses among these species to infer community-level thresholds (Baker and King 2010). It first uses indicator species analysis (Dufrêne and Legendre 1997) to calculate species' strengths of association with each side of a binary partition at x – 2 candidate change points along the environmental gradient (here, modeled stream temperature), where x is the number of unique modeled mean August temperatures (n = 724), modeled to the hundredth of a degree, present among the 1,763 study sites. A species' strength of association with the group of sites on each side of the partition (group i) is expressed as an indicator value (IndVal) score, which is a product of two characteristics: the proportion of occurrences among sites in group i relative to occurrences at all sites and the proportion of occurrences at sites within group i (Baker and King 2010). Each species has two IndVal scores at each candidate change point; its association with the group of sites on the colder side of the partition is expressed as a negative IndVal score and its association with the group of sites on the warmer side of the partition is expressed as a positive score. At each candidate change point, the IndVal score with the greatest absolute value is retained, along with the side of the partition with which it is associated (colder or warmer). The program TITAN then identifies and retains the candidate change point that maximizes the absolute value of each species' IndVal score and also retains the IndVal score and side of the partition at the retained change point for each species. Significance of each species' IndVal score is determined by conducting IndVal analysis on 250 random permutations of the thermal gradient data to establish the mean and standard deviation of IndVal scores for each species (Baker and King 2010).

Community-level thresholds are indicated by a synchronous response among species. The program TITAN standardizes all species' IndVal scores to z-scores using the mean and standard deviation obtained with permutation analysis, then sums all positive (z+) and negative (z–)



Steps 1-3 are concerned with defining classification mechanisms that are sufficient to classify all species using as many lines of evidence (i.e., field data, laboratory data, and professional judgment) as possible for each species.

Step 1. Classification with Field Data

1) Species' association with the final site-group combinations are applied as the initial candidate guilds.
2) Any candidate guild with fewer than four species is eliminated, and its species are reclassified into the least sensitive (i.e., warmer) adjacent site-group.

Step 2. Classification with Laboratory Data

Step 2A. Lab data are used to reclassify species classified in Step 1.

1) Calculate the mean MWAT and mean DM for each candidate guild.
2) If a species' metrics are more than halfway between the mean of its own thermal guild and an adjacent thermal guild, then that species is reclassified into the adjacent guild[1].
3) If a species' metrics are colder than the average of the guild two guilds colder, or warmer than that of the guild two guilds warmer, then that species is reclassified into this guild[1].

Step 2B. Lab data are used to classify species not yet classified.

1) Recalculate the mean MWAT and mean DM for each candidate guild.
2) Classify all remaining species with lab values into the candidate guild with the closest MWAT and DM values[1].

Step 3. Classification with Professional Judgment

Step 3A. Professional judgment is used to classify species with no field or lab data.

1) Classify species into the candidate guild that contains other species of the same genus, if possible.
2) If there are no other species of the same genus, classify species into the candidate guild containing the most ecologically similar species, according to local experts.

Step 3B. Professional judgment may be used to reclassify species classified in Step 1 that have no lab data.

1) Species that were classified by field data, but which have no available lab data to be considered for potential reclassification, may be reclassified by professional judgment if deemed necessary by local fisheries experts.

Step 4 is concerned with altering the resolution of the taxonomic classifications achieved in Steps 1-3 to produce the greatest number of guilds that is subjectively considered feasible to implement in a regulatory context. As such, Steps 1-3 could be considered necessary for guild development, while Step 4 could be considered supplemental.

Step 4. Expansion of Thermal Guilds

Step 4A. Increase guild resolution: subdivide candidate guilds.

1) Recalculate the mean MWAT and mean DM for each candidate guild.
2) Divide each candidate guild that contains four or more species into two sub-guilds, one composed of all the guilds' species with MWAT/DM values that are lower than the guild mean, and one composed of those with MWAT/DM values that are greater than the guild mean[1].
3) Species with no lab values should be classified into the sub-guild that contains the most ecologically similar species, according to local fisheries experts.

Step 4B. Decrease guild resolution: merge candidate guilds.

1) Calculate the mean and minimum MWAT and DM for each candidate guild. Any two adjacent guilds for which two or more of these four metrics are less than 1°C apart should be merged into one guild.
2) Repeat Step 4B1 for the newly consolidated set of thermal guilds. If there are no adjacent guilds with two or more of the four metrics less than 1°C apart, then the existing set of guilds is considered the final proposed guild system.

[1] If a species' MWAT and DM values do not prompt the same action on these steps, then MWAT is prioritized.

FIGURE 1. The first panel shows a flow diagram illustrating the process for combining field data on fish species distributions and modeled mean August stream temperatures with laboratory thermal tolerance data to identify fish thermal guilds. The challenges outlined in Table 1 can be resolved at various steps throughout the process. The second panel shows the specific methods for each step in the bolded "Integrate laboratory data and field-derived site-groups" box of the first panel.

standardized scores at each candidate change point. The candidate change points associated with the largest sum $z+$ score and largest sum $z-$ score are identified as the two potential community-level thresholds. We used 500 bootstrap resamples to develop confidence limits for the two potential community-level thresholds. All TITAN analyses were conducted using the TITAN2 package in R (Baker et al. 2015).

Species assemblage classification.— Because TITAN's output consisted of two thresholds between thermally distinct species assemblages, we defined three distinct groups of sites: sites with modeled mean August temperatures colder than the first threshold (referred to as the coldwater site-group), sites with temperature values between the first and second thresholds (referred to as the coolwater site-group), and sites with temperature values warmer than the second threshold (referred to as the warmwater site-group).

We used the 5% confidence limit of the first community-level threshold as the threshold between the coldwater and coolwater site-groups and used the 95% confidence limit of the second community-level threshold as the threshold between the coolwater and warmwater site-groups. This choice of confidence limits, first implemented by Beauchene et al. (2014), resulted in a broader coolwater site-group. We preferred the broader site-group because it allowed for the potential emergence of distinct subdivisions within the coolwater guild.

Each site-group contained a species assemblage that was more similar within the site-group than among the other site-groups. To characterize the taxonomic composition of the distinct species assemblages associated with each site-group, we applied indicator value analysis to determine species' strengths of association with each site-group or combination of site-groups. Because species could be associated with either a single site-group (coldwater, coolwater, or warmwater groups) or a combination of site-groups (cold–cool, cool–warm, cold–warm, cold–cool–warm), there were seven potential associations for each species. We evaluated the strength of association between species and combinations of site-groups using the phi coefficient of association, which measures a species' association with a given site-group relative to its association with other site-groups, corrected to account for the differing size of site-groups (Chytrý et al. 2002; De Cáceres and Legendre 2009).

The statistical significance of species' strengths of association was determined by conducting indicator value analysis on 999 random permutations. All species were classified according to the site-group combination with which they were most strongly associated. These site-group associations served as the initial candidate thermal guilds. All indicator value analyses were conducted using the indicspecies package in R (De Cáceres and Legendre 2009).

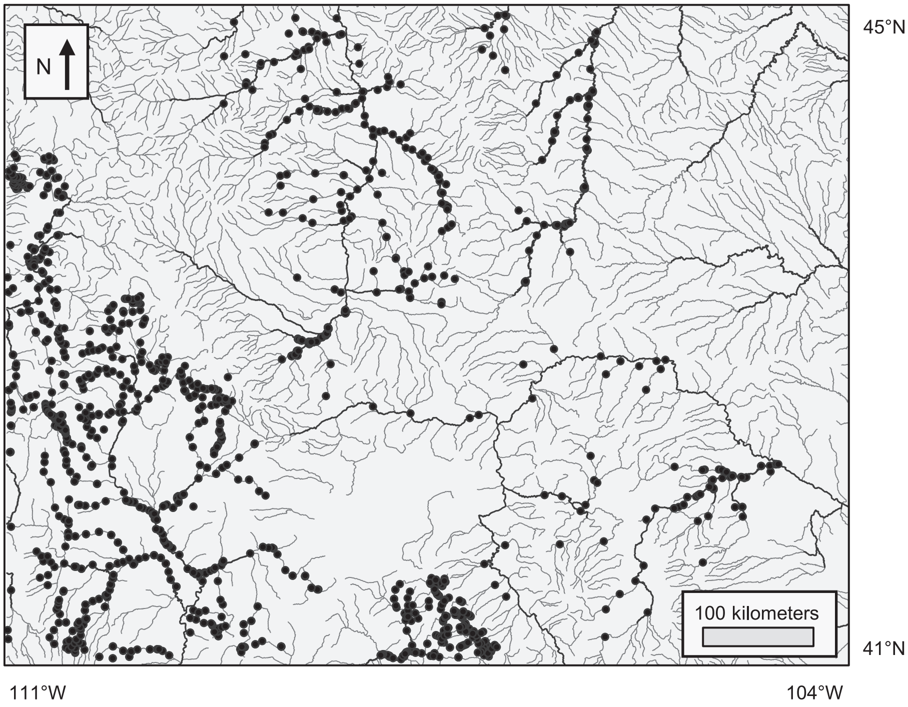


FIGURE 2. Map of Wyoming showing the sites included in the stream fish species assemblage database (n = 1,763). All surveys were conducted between 1989 and 2016. Data were provided by the Wyoming Game and Fish Department.

Laboratory-Derived Thermal Tolerance Values

We conducted a literature review to compile data on the acute and chronic upper thermal tolerance for each stream fish species expected to be found in Wyoming. We targeted studies whose major output was one or more of the physiological metrics relevant to the criteria development protocols in Environmental Protection Agency guidance (e.g., survival, growth, metabolic rate) (Brungs and Jones 1977). We defined the acute thermal tolerance for each species in terms of daily maximum temperature (DM) and the chronic thermal tolerance in terms of maximum weekly average temperature (MWAT). We derived species' acute and chronic tolerance values following the approach outlined by Todd et al. (2008; CWQCC 2011), which is closely based on Environmental Protection Agency guidance (Brungs and Jones 1977). This approach entailed using previously developed equations to standardize various laboratory tests of species' thermal optima and maxima to produce the acute and chronic tolerance values (Todd et al. 2008). For both acute and chronic values, this approach is characterized by three steps: the identification of a numeric threshold, the definition of an appropriate averaging time for the evaluation of stream temperature against the numeric threshold, and the application of a safety factor to ensure the desired level of individual survival in streams that have reached the numeric threshold (Sullivan et al. 2000).

To reduce variability in the quality of studies accepted in our literature review, we identified eight considerations that studies were required to meet before their results could be used in our analyses: (1) the study must have been subject to external review, (2) it must have been conducted in a laboratory environment, (3) it must have used commonly applied methods consistent with typical experimental design, (4) the life stage of the fish in the study must have been recorded as either juvenile or adult, (5) the temperature and rate of acclimation must have been recorded, and acclimation temperatures must be within the species' normal summer temperature range, (6) the full range of temperatures applied in the study must have been recorded, (7) it must have been recorded whether fish were fed during the study, and (8) the study must have been replicated appropriately (Todd et al. 2008; Peterson 2017).

Integration of Field and Laboratory Data

Through a series of four steps, the candidate guilds derived from field data were modified based on laboratory thermal tolerance data and, where those data were unavailable, the professional judgment of biologists familiar with the regional distribution of Wyoming fish species (Figure 1). Step 1 consisted of the initial classification of species based on field data. In Step 2, laboratory data were used to identify and reclassify species whose thermal tolerance differed from that of the species with which they tend to occur (cases D, E, and G in Table 1) and to classify species that occurred too infrequently in our database to be classified by field-based methods (case F in Table 1). In Step 3, professional judgment was used to classify the six species with insufficient data for classification in the first two steps and to reclassify species with unavailable laboratory data as needed. We used these three steps to ensure that all species could be classified using as many lines of evidence (i.e., field data, laboratory data, and professional judgment) as possible (Figure 1). A fourth step allowed for increasing the resolution of the guild system so that it consisted of the greatest number of thermal guilds that could be feasibly implemented in a regulatory context. For the purpose of this study, candidate guilds were considered feasible if at least three out of four measures of each guild's thermal criteria (mean MWAT, minimum MWAT, mean DM, and minimum DM) were at least 1°C warmer than the equivalent measure of the next-coldest guild.

RESULTS

Field-Derived Thermal Distributions

Modeled mean August temperature ranged from 4.4°C to 23.1°C at the 1,763 sites in the species assemblage database. The species varied widely in terms of frequency of observation and observed thermal range (Figure 3). The lower community threshold identified by TITAN was 15.5°C and the higher threshold was 19.9°C (Table 2). Our results suggest the presence of a true threshold, as indicated by the narrow confidence limit band for the sum $z-$ and sum $z+$ change points (Baker and King 2013). The confidence limits of the two thresholds do not overlap, suggesting the possibility of one or more unique transitional communities with species assemblages that are distinct from those on either the warm or cold end of the thermal gradient (Table 2).

Of the 1,763 sites in the species assemblage database, 551 were classified in the coldwater site-group (<15.5°C), 1,064 in the coolwater site-group (15.5–19.9°C), and 148 in the warmwater site-group (>19.9°C). All 52 species in the TITAN analysis were associated with either one of these three site-groups or one of the four potential combinations of these site-groups, and 50 of these associations were significant ($P < 0.05$) (Table 3). Because there were no species associated with the cold–warm or cold–cool–warm combinations of site-groups, all species were effectively classified into five site-group combinations: the coldwater site-group, the cold–cool site-group combination, the coolwater site-group, the cool–warm site-group combination, and the warmwater site-group (Table 3).

Laboratory-Derived Thermal Tolerance Values

The completed database of laboratory thermal testing results contained information on the 73 stream fish species expected to be found in Wyoming, gathered from 221 peer-reviewed journal articles (Peterson 2017). This information was sufficient to calculate acute thermal tolerance values (DM) for 54 of the 73 species and chronic thermal tolerance values (MWAT) for 38 of the 73 species (Table 3). Eighteen species had insufficient data to derive either thermal tolerance value.

Integration of Field and Laboratory Data

Following the four data integration steps in our flow diagram (Figure 1), we used a combination of species' upper thermal tolerance values and professional judgment to identify and reclassify species characterized by cases D through G in Table 1 into a total of five proposed thermal guilds (Table 3). Step 1 reflects the initial use of field data to classify species into site-groups, which serve as the first iteration of candidate guilds. In this step, the cool–warm site-group, which consisted of just two species, White Sucker and Lake Chub, was merged with the warmwater site-group due to the cool–warm group's small size. In Step 2, three species were reclassified based on their thermal tolerance values into the adjacent warmer candidate guild, 10 species were reclassified into the adjacent colder guild, and one species was reclassified to be two guilds colder. Of the 21 species that could not be classified by field-based methods because they occurred at three or fewer sites, 15 were classified based on their thermal tolerance values derived from laboratory studies. In Step 3, the remaining six species with insufficient data to be classified by field- or laboratory-based methods were classified by the professional judgment of biologists familiar with the fish species of Wyoming. Additionally, two species were reclassified based on professional judgment: Paiute Sculpin was reclassified to be one guild warmer and Utah Sucker was reclassified to be two guilds warmer.

In Step 4, all candidate guilds containing four or more species (cold–cool, cool, and warm) were subdivided into two subguilds, one consisting of species with thermal tolerance values below the mean of the subdivided candidate guild and the other of species with thermal tolerance values above the mean. All but the coldest candidate guild were divided in this process, resulting in seven new candidate guilds. This system of seven guilds proved to be infeasible to implement in a regulatory standard because it failed the criteria that adjacent guilds should be distinct by at least 1°C in at least three of four thermal metrics (Figure 1). For example, the mean DM of the third-coldest guild was 28.4°C while that of the fourth-coldest guild was 28.8°C and the minimum DM of the third-coldest guild was 27.9°C while that of the fourth-coldest guild was 27.8°C. As a result, all adjacent candidate guilds where more than two of the four test metrics were separated by less than 1°C were merged. This resulted in the third coldest of the seven subguilds being merged with the fourth coldest and the fifth-coldest subguild being merged with the sixth coldest. We used the same test of feasibility on the resulting five consolidated guilds, and none of the new guilds failed the test. Thus at the end of Step 4, the 73 stream fish species were classified into five proposed thermal guilds that provide greater resolution than the guilds produced by Steps 1–3, while meeting the feasibility criteria (Table 3).

DISCUSSION

Our thermal guild development approach used species' field-based associations with thermally distinct assemblages as a primary data source and laboratory-derived thermal tolerance values as a secondary data source to produce five thermal guilds. This integrated approach addressed the limitations associated with the independent use of either field or laboratory data. As a result, we expect that these guilds will allow for more effective thermal regulation than guilds developed using either type of data alone. Integration of the two data sources enabled us to classify a greater proportion of the 73 Wyoming fish species into guilds: 92% (67 of 73) could be classified without relying upon professional judgment. In contrast, 75% (55 of 73) could be classified if thermal guilds were based only on laboratory data and 71% (52 of 73) if thermal guilds were based only on field occurrence data (Table 3).

We found that 50 out of 52 species were significantly associated with one or more temperature site-groups. The two species with nonsignificant associations, Iowa Darter ($P = 0.083$) and Northern Leatherside Chub ($P = 0.639$), each had low occurrence frequencies and inhabited a thermal range that was close to evenly split between two site-groups. The application of additional lines of evidence through our series of four steps (Figure 1) reduces the subjectivity inherent in classifying such transitional species.

Our use of TITAN to identify thresholds improves upon earlier multivariate threshold identification methods through its sensitivity to species with low occurrence frequencies, which are common in our species assemblage database (Baker and King 2010; Beauchene et al. 2014). Additionally, TITAN reduces the likelihood of falsely identifying thermal thresholds by providing a set of clear diagnostics for interpreting results (Baker and King 2010; King and Baker 2014). A challenge associated with our application of TITAN is that TITAN can identify only two thresholds, and therefore the highest possible resolution for the classification of species based on TITAN results is into three site-groups plus the resulting four site-group combinations. Any further subdivision of species must rely on additional methods.

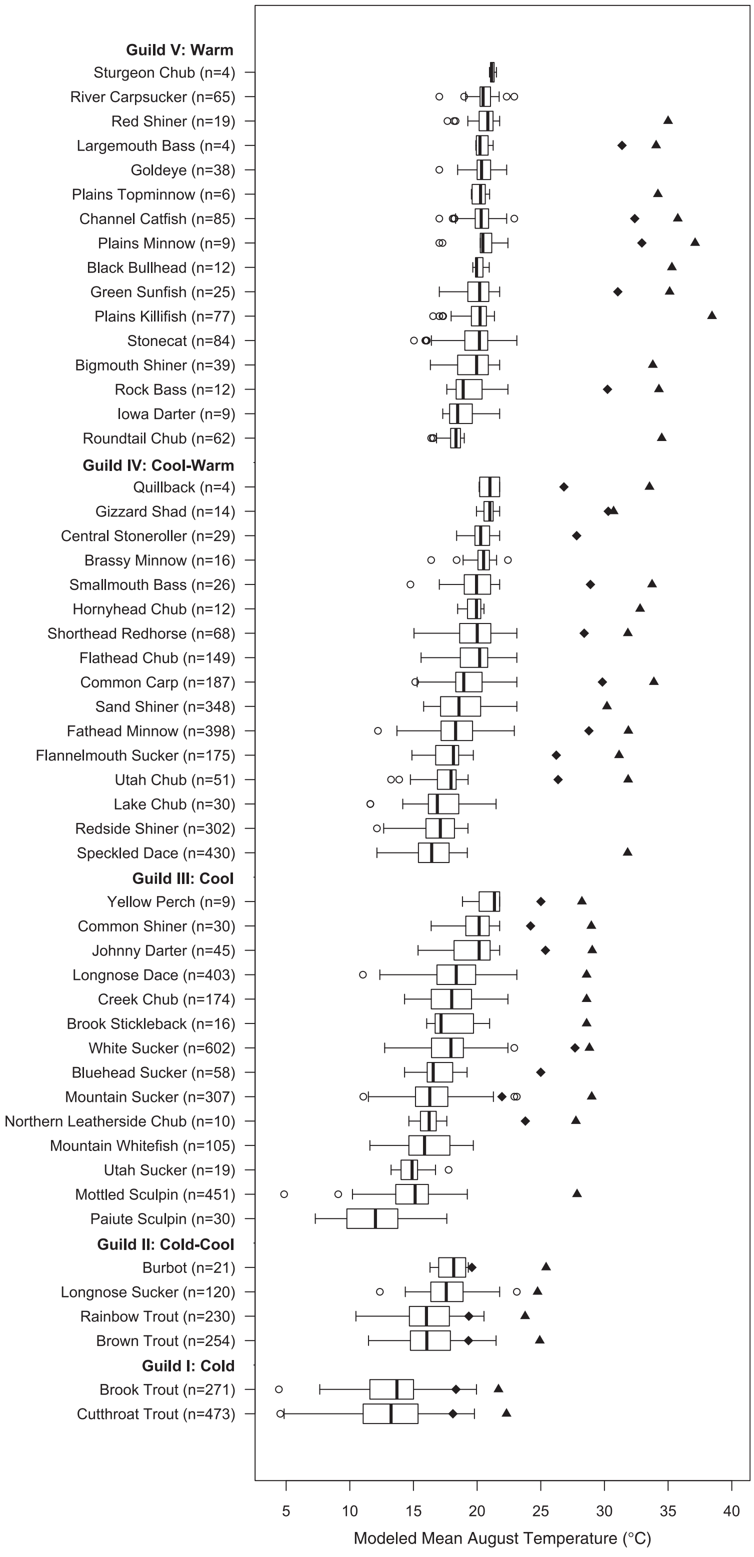


FIGURE 3. Distribution of modeled mean August stream temperature for all species observed at four or more sites (*n* = 1,763). The center bar in each box indicates the modeled mean August stream temperature, the box dimensions indicate the range between the 25th and 75th percentiles, the whiskers indicate the 5th and 95th percentiles, and the circles represent outliers. For species with available thermal tolerance data, MWAT is indicated by black diamonds and DM is indicated by black triangles. The *n* after the species name indicates the number of sites at which that species was observed. Species are grouped according to thermal guild recommendations (Table 3).

TABLE 2. Community-level thresholds identified by TITAN. Change point indicates the community-level thresholds identified by TITAN, and the 0.05, 0.10, 0.50, 0.90, and 0.95 columns represent the 5, 10, 50, 90, and 95% confidence intervals, respectively, for the thresholds. Confidence intervals were developed through 500 bootstrap replications. The bold italicized values represent the 5% confidence interval of the first community-level threshold and the 95% confidence interval of the second community-level threshold, which were used as the thresholds between site-groups for indicator value analysis, following the precedent set by Beauchene et al. (2014). All values are given in degrees Celsius.

Method	Change point	0.05	0.10	0.50	0.90	0.95
Sum $z-$	15.8	***15.5***	15.6	15.8	15.9	15.9
Sum $z+$	19.8	19.4	19.4	19.7	19.9	***19.9***

Our use of modeled mean August stream temperatures allowed us to conduct analyses with a larger sample size than would be possible using measured temperature data. However, we noted some assumptions in our use of modeled temperatures. First, we assumed that modeled temperatures correspond to the actual temperatures experienced by fish communities. When the stream temperature models used in our study were tested against observed temperatures they showed a strong correlation to observed temperature ($R^2 = 0.91$) (Isaak et al. 2017a). However, the uncertainty in temperature predictions (root mean squared prediction error = 1.10°C; mean absolute percentage error = 0.72°C) results in a corresponding degree of uncertainty regarding species' observed thermal distributions in the field (Isaak et al. 2017a). Furthermore, it should be noted that the 1-km resolution of the modeled temperature database is unable to capture the finer-scale thermal refugia that fish may use to survive in stream segments with otherwise inhospitable temperatures (Kurylyk et al. 2015; Westhoff et al. 2016).

Next, we assumed that the mean monthly temperature in August is an appropriate metric to measure fish community response. In reality, no single metric can completely describe the relationship between stream thermal regimes and species' distributions (Poole et al. 2004; Benjamin et al. 2016). Nevertheless, mean August temperature was chosen for this study because it is readily available and because it correlates well with several different ways of measuring stream temperature. While some species may respond more to temperature maxima than mean temperatures or to temperatures averaged over a different duration, mean August temperature is highly correlated with some common measures of maximum temperature, including some which incorporate a different averaging period (e.g., maximum weekly maximum temperature [$R^2 = 0.92$], average weekly maximum temperature [$R^2 = 0.95$]) (Isaak et al. 2016). As such, we considered mean August temperature to be an appropriate metric for our study.

Further, we assumed that Wyoming stream fish species assemblages are relatively consistent throughout the summer months, defined broadly here as May through October, making it appropriate to pair modeled mean August temperature values with species observations collected during these months. The range of May through October was chosen to maximize the number of fish observations available for this study, while remaining reasonably confident in consistent fish distribution patterns. Diadromous species or species that migrate from reservoirs or lakes could produce seasonal variation in stream fish assemblages, but such species are uncommon in Wyoming.

Finally, we emphasize the limitations of our choice to derive species' associations using only modeled temperature data rather than considering additional habitat variables. Recent work by Isaak et al. (2017b) demonstrates that individual species' thermal niches are better predicted by models that account for multiple habitat variables than by stream temperature alone. Because such detailed modeling methods as described by Isaak et al. (2017b) are available to improve predictions of individual species' thermal distributions, we suggest that drawing conclusions about the realized thermal niches of individual taxa is not the best use of our results. Rather, our pairing of modeled temperature with species assemblages should be used for its insights into broad thermal thresholds between species assemblages that may be useful for statewide thermal regulation, regardless of localized variations in habitat variables throughout the state.

The standardized acute and chronic thermal tolerance values calculated from laboratory data served as an essential second line of evidence in guild development to improve our understanding of individual species' thermal requirements. The developers of TITAN analysis call for such an approach, noting that TITAN results are likely inappropriate for developing regulations on their own but may be successfully combined with additional lines of evidence, including laboratory studies (King and Baker 2014). The site-groups produced by TITAN are most helpful for defining species' realized thermal niches, which are essential for classifying species together with others that most often share similar thermal habitat. Species' acute and chronic thermal tolerance values derived in the laboratory are most helpful for defining species' fundamental thermal niches, which are useful for setting protective regulatory criteria. Both lines of evidence are important for developing regulations.

However, it is important to note that, as with field occurrence data, there are also assumptions associated with our use of laboratory data. Most significantly, there is uncertainty about the level of precision with which laboratory metrics can provide meaningful insight into species' realized relationship to temperature on the landscape (Rezende et al. 2014; Kingsolver and Umbanhowar 2018).

TABLE 3. Site-groups and strengths of association for the 52 species observed frequently enough ($n > 3$) to be included in indicator value analysis, and standardized upper thermal tolerance values (maximum weekly average temperature [MWAT] and daily maximum temperature [DM], both in °C) for all species with sufficient laboratory data to calculate these values. The phi coefficient of association measures species' association with a site-group relative to its degree of association with other site-groups. The statistical significance of species' strengths of association was determined by conducting indicator value analysis on 999 random permutations. Species' classification codes refer to the steps described in the second panel of Figure 1. For species that were reclassified based on Steps 2 and 3 in Figure 1 (second panel), the up and down arrows indicate whether the species were reclassified into a colder (down arrow) or warmer (up arrow) candidate guild. Species with two arrows were moved two candidate guilds in the indicated direction. Species are classified according to the final five proposed guilds derived by adjusting the initial site-group associations as outlined in Figure 1.

Species	MWAT	DM	Site-group	Phi coefficient	Significance	Classification code
Guild I: cold						
Brook Trout *Salvelinus fontinalis*	18.34	21.68	Cold	0.453	0.001	1
Cutthroat Trout *Oncorhynchus clarkii*	18.10	22.31	Cold	0.505	0.001	1
Guild II: cold–cool						
Brown Trout *Salmo trutta*	19.32	24.92	Cold–cool	0.196	0.001	1
Burbot *Lota lota*	19.59	25.42	Cool	0.115	0.001	2A ▼
Longnose Sucker *Catostomus catostomus*		24.80	Warm	0.161	0.001	2A ▼▼
Rainbow Trout *Oncorhynchus mykiss*	19.35	23.77	Cold–cool	0.194	0.001	1
Guild III: cool						
Bluehead Sucker *Catostomus discobolus*	25.00		Cool	0.160	0.001	1
Brook Stickleback *Culaea inconstans*		28.60	Warm	0.092	0.015	2A ▼
Common Shiner *Luxilus cornutus*	24.20	28.97	Warm	0.291	0.001	2A ▼
Creek Chub *Semotilus atromaculatus*		28.60	Warm	0.244	0.001	2A ▼
Johnny Darter *Etheostoma nigrum*	25.37	29.04	Warm	0.341	0.001	2A ▼
Longnose Dace *Rhinichthys cataractae*		28.60	Warm	0.521	0.001	2A ▼
Mottled Sculpin *Cottus bairdii*		27.85	Cold	0.340	0.001	2A ▲
Mountain Sucker *Catostomus platyrhynchus*	21.95	29.00	Cold–cool	0.107	0.010	1
Mountain Whitefish *Prosopium williamsoni*			Cold–cool	0.155	0.001	1
Northern Leatherside Chub *Lepidomeda copei*	23.79	27.76	Cool	0.044	0.639	1
Northern Pearl Dace *Margariscus nachtriebi*						3A
Orangethroat Darter *Etheostoma spectabile*	24.41	29.98				2B
Paiute Sculpin *Cottus beldingii*			Cold	0.115	0.006	3B ▲
Utah Sucker *Catostomus ardens*			Cold	0.119	0.001	3B ▲▲
White Crappie *Pomoxis annularis*	23.56	29.48				2B
White Sucker *Catostomus commersonii*	27.69	28.82	Cool–warm	0.372	0.001	2A ▼
Yellow Perch *Perca flavescens*	25.01	28.23	Warm	0.190	0.001	2A ▼
Guild IV: cool–warm						
Black Crappie *Pomoxis nigromaculatus*	26.56	32.10				2B
Brassy Minnow *Hybognathus hankinsoni*			Warm	0.241	0.001	1
Central Stoneroller *Campostoma anomalum*	27.82	33.84	Warm	0.293	0.001	1
Common Carp *Cyprinus carpio*	29.84	33.88	Warm	0.471	0.001	1
Emerald Shiner *Notropis atherinoides*	28.86	30.15				2B
Fathead Minnow *Pimephales promelas*	28.78	31.88	Warm	0.494	0.001	1
Finescale Dace *Chrosomus neogaeus*		30.00				2B
Flannelmouth Sucker *Catostomus latipinnis*	26.22	31.15	Cool	0.307	0.001	1
Flathead Chub *Platygobio gracilis*			Warm	0.632	0.001	1
Gizzard Shad *Dorosoma cepedianum*	30.30	30.72	Warm	0.258	0.001	1
Golden Shiner *Notemigonus crysoleucas*	27.71	31.56				2B
Grass Carp *Ctenopharyngodon idella*	29.96	35.95				2B
Hornyhead Chub *Nocomis biguttatus*		32.80	Warm	0.164	0.001	1
Kendall Warm Springs Dace *Rhinichthys osculus thermalis*		31.75				2B

TABLE 3. Continued.

Species	MWAT	DM	Site-group	Phi coefficient	Significance	Classification code
Lake Chub *Couesius plumbeus*			Cool–warm	0.155	0.001	1
Northern Pike *Esox lucius*		30.00				2B
Pumpkinseed Sunfish *Lepomis gibbosus*	29.78	32.74				2B
Quillback *Carpiodes cyprinus*	26.82	33.54	Warm	0.136	0.001	1
Redside Shiner *Richardsonius balteatus*			Cool	0.271	0.001	1
Sand Shiner *Notropis stramineus*		30.20	Warm	0.638	0.001	2A ▼
Sauger *Sander canadensis*						3A
Shorthead Redhorse *Moxostoma macrolepidotum*	28.41	31.84	Warm	0.385	0.001	2A ▼
Shovelnose Sturgeon *Scaphirhynchus platorynchus*						3A
Smallmouth Bass *Micropterus dolomieu*	28.90	33.74	Warm	0.216	0.001	1
Speckled Dace *Rhinichthys osculus*		31.82	Cold–cool	0.317	0.001	2A ▲
Spottail Shiner *Notropis hudsonius*	29.21	31.94				2B
Utah Chub *Gila atraria*	26.36	31.86	Cool	0.139	0.002	1
Walleye *Sander vitreus*	25.99	31.68				2B
Guild V: warm						
Bigmouth Shiner *Notropis dorsalis*		33.80	Warm	0.274	0.001	1
Black Bullhead *Ameiurus melas*		35.30	Warm	0.146	0.001	1
Bluegill *Lepomis macrochirus*	31.59	33.14				2B
Channel Catfish *Ictalurus punctatus*	32.38	35.76	Warm	0.537	0.001	1
Flathead Catfish *Pylodictis olivaris*						3A
Freshwater Drum *Aplodinotus grunniens*	30.19	32.02				2B
Green Sunfish *Lepomis cyanellus*	31.05	35.12	Warm	0.245	0.001	1
Goldeye *Hiodon alosoides*			Warm	0.363	0.001	1
Iowa Darter *Etheostoma exile*			Warm	0.060	0.083	1
Largemouth Bass *Micropterus salmoides*	31.38	34.06	Warm	0.113	0.004	1
Plains Killifish *Fundulus zebrinus*		38.45	Warm	0.476	0.001	1
Plains Minnow *Hybognathus placitus*	32.94	37.12	Warm	0.174	0.001	1
Plains Topminnow *Fundulus sciadicus*		34.20	Warm	0.127	0.002	1
Red Shiner *Cyprinella lutrensis*		35.00	Warm	0.258	0.001	1
River Carpsucker *Carpiodes carpio*			Warm	0.540	0.001	1
Rock Bass *Ambloplites rupestris*	30.24	34.28	Warm	0.079	0.017	1
Roundtail Chub *Gila robusta*		34.50	Cool	0.198	0.001	2A ▲
Stonecat *Noturus flavus*			Warm	0.467	0.001	1
Sturgeon Chub *Macrhybopsis gelida*			Warm	0.136	0.001	1
Suckermouth Minnow *Phenacobius mirabilis*						3A
Western Mosquitofish *Gambusia affinis*	29.04	34.80				2B
Western Silvery Minnow *Hybognathus argyritis*						3A

Nevertheless, the relative availability of laboratory thermal tolerance data and the insight they provide into potential outcomes for species subjected to various levels of thermal impairment make them an essential line of evidence in our approach.

Another assumption is that all thermal tolerance studies accepted in our literature review are equally reliable. Although we applied strict standards to the selection of thermal tolerance studies, the reality is that the standardized MWAT and DM values calculated for each species are not equally robust. The first reason is that the number of relevant studies varied widely among the species included in our review; the number of laboratory test values used to calculate species' standardized DM values ranged from 1 to 33, and the number of values used to calculate species' standardized MWAT values ranges from

1 to 35 (Peterson 2017). Values developed with a large sample size are likely more robust. Finally, the method used to calculate species' standardized thermal tolerance values also contributes to the level of confidence that can be placed in these values. In order to increase the number of laboratory studies used to calculate MWAT and DM values, thereby increasing the robustness of those values, there are multiple equations that can be used to calculate MWAT and DM values from several different laboratory metrics (CWQCC 2011). The available laboratory metrics and resulting choice of calculation method can affect a species' calculated tolerance values (Peterson 2017).

The range of modeled mean August water temperatures at sites identified as coolwater habitat in Wyoming is 15.5°C through 19.9°C. This is similar to the coolwater range of approximately 15°C through 19–20°C for mean July water temperature identified in three rivers in the South Saskatchewan River basin in Alberta, Canada, another Rocky Mountain headwaters system (Mee et al. 2018). The range of coolwater habitat identified in the eastern and Midwestern United States is slightly warmer; the coolwater range of mean July water temperature in Connecticut was defined as 18.5–22.3°C (Beauchene et al. 2014) and the coolwater range of June–August mean water temperature in Wisconsin and Michigan was defined as 17–20.5°C (Lyons et al. 2009). This difference is likely due to Wyoming's status as a high-elevation headwaters region but may also be influenced by differences in approaches used to identify thermal thresholds. The Wyoming coolwater range identified in this study is warmer than a transitional zone identified in another headwaters region in British Columbia, which ranged from 12–13°C to 19–20°C in terms of summer MWAT (Parkinson et al. 2016).

The coolwater range is increasingly understood to harbor a unique species assemblage, in addition to a mixture of warm- and coldwater species (Wehrly et al. 2003; Lyons et al. 2009). This is true for the coolwater range identified in Wyoming: 7 out of 52 species in Wyoming were exclusively associated with the coolwater site-group, which comprises 60% of the sites in our database (Table 3). An additional seven species had broad distributions that overlapped with the coolwater site-group based on the TITAN and indicator value analyses (Table 3). This suggests that Wyoming's coolwater habitat is an important part of the state's aquatic resource and that it would benefit from targeted thermal regulation. Similar prevalence of coolwater habitat in other regions (e.g., Lyons et al. 2009; Beauchene et al. 2014) indicates that further characterization of coolwater species assemblages is an important research goal.

Due to the transitional nature of coolwater habitat, the coolwater guild (Guild III) contains species with the most variable initial site-group associations (Table 3). Many of these species were reclassified into Guild III to address some of the limitations outlined in Table 1. For example, Longnose Dace was initially identified by indicator value analysis as part of the warmwater site-group. Longnose Dace illustrates case D (Table 1): as a generalist species, it often co-occurs with warmwater species but its relatively low acute thermal tolerance suggests that it cannot withstand temperatures as high as some of the species with which it co-occurs (Figure 3). Utah Sucker was reclassified from the coldwater site-group into Guild III; it is an example of case E (Table 1), a species that occupies a narrower thermal niche in Wyoming than in its full geographic range. Its co-occurrence with coldwater species in Wyoming is due more to a correlation between temperature and other habitat variables than to stream temperature itself.

The guilds at the extreme ends of the thermal spectrum, Guild I (cold) and Guild V (warm), contain almost exclusively species that were initially classified into the coldwater and warmwater site-groups, respectively. Most species in Guild IV (cool–warm) were also initially classified into the warmwater site-group. The differentiation between Guild IV and Guild V is largely based on laboratory-derived data, illustrating case G (Table 1): Guild IV and Guild V species tend to co-exist on the landscape, despite Guild IV species being less tolerant of warm temperatures. This difference in thermal requirements is not reflected on the landscape because Wyoming does not have many aquatic habitats that are warm enough to exclude the Guild IV species. Potential warming due to climate change may necessitate different protections for Guild IV and Guild V species in the future.

The four steps for integrating field and laboratory data (Figure 1) provided a reproducible mechanism to recognize species that would not be protected by classification based only on field data and to reclassify such species into a more protective guild based on laboratory data. This approach is designed to give equal consideration to all species, despite the discrepancy in number and quality of available thermal studies among species. The application of a series of reproducible steps to classify species into guilds by integrating multiple lines of evidence (primarily field-derived and laboratory-derived data, with professional judgment applied as needed) is a concept that could transfer easily to other regions, though the specifics of the steps would likely differ based on regional habitat availability, species assemblages, and regulatory goals. Step 4, in particular, could be revised to meet the divergent needs of different regulatory agencies and geographic areas. We propose applying a replicable test of feasibility to determine whether a system of guilds could be practically applied within a regulatory standard (in our case, separation between guilds by more than 1°C), but the specifics of this test should be decided based on regional regulatory goals and resources.

Furthermore, it is critical to note that a system of thermal guilds is only the first step to developing thermal regulations. For thermal guilds to be applied in a regulatory context, each guild must be associated with one or more regulatory criteria. Streams can then be regulated for compliance with the criteria of the guild that most resembles the assemblage expected to be present in the stream. The process of determining the guild most likely to be present in a stream could be based on observations of species presence or the observed, remotely sensed, or modeled presence of habitat variables that have been shown to correlate with species presence.

Once a stream has been identified as belonging to a guild, it can then be regulated for compliance with that guild's criteria. The thermal criteria in use by regulatory agencies in the United States vary widely, but many agencies define acute upper limits in terms of DM and chronic upper limits in terms of MWAT (e.g., CWQCC 2011). We used these metrics to define species-specific thermal tolerance because of their common application in regulations, but guilds derived using the methods in this study could be readily associated with other types of regulatory criteria. The taxonomic composition of a guild often plays a role in defining the numerical value of its criteria; for example, guild criteria could be defined by the thermal tolerance of the most sensitive species in the guild or by a percentage of that tolerance (e.g., CWQCC 2011). If the five guilds derived in this study were to be regulated by the thermal tolerance of their most sensitive species, then streams classified into the Guild I (cold) would have a maximum allowable MWAT of 18.1°C (this is the MWAT value of Cutthroat Trout, the Guild I species with the lowest MWAT value) and a maximum allowable DM of 21.7°C (this is the DM value of Brook Trout, the Guild I species with the lowest DM value). Using the same method to calculate criteria for each of the remaining four guilds, the results would be as follows: Guild II = MWAT 19.3°C and DM 23.8°C; Guild III = MWAT 22.0°C and DM 27.8°C; Guild IV = MWAT 26.0°C and DM 30.0°C; and Guild V = MWAT 29.0°C and DM 32.0°C. When the taxonomic composition of a system of thermal guilds is used to define the guilds' regulatory criteria in addition to defining where these criteria are applied, it is especially critical that thermal guilds provide a nuanced depiction of species' thermal distribution on the landscape.

It is important to acknowledge that while the division of species into thermal guilds and subsequent definition of guild criteria is a common model for thermal regulation, other approaches have been proposed. Calls to look beyond thermal magnitude and consider more nuanced aspects of the thermal regime, including the frequency, variability, duration, and timing of temperature exposure, are increasing (Poole et al. 2004; McCullough et al. 2009; Falke et al. 2016; Benjamin et al. 2016; Steel et al. 2017) . Alongside this growing body of research, however, the common application of guild-based thermal regulations ensures that it remains important to continue refining guild development approaches.

As stream temperatures are predicted to increase due to climate change, many stream fish assemblages will inhabit streams that are closer to their thermal thresholds and it will therefore be increasingly important to detect further sources of impairment (Isaak et al. 2010; Comte and Grenouillet 2013; Paukert et al. 2016; Pyne and Poff 2017). And with recent research indicating that climate change impacts on stream temperature may differ in severity at a relatively fine scale along the thermal gradient in headwaters systems (Isaak et al. 2016), it is increasingly important to ensure that thermal regulations are crafted with sufficient nuance to capture distinct species assemblages along the thermal spectrum. The integration of laboratory-derived and field-derived data to classify species into thermal guilds is a broadly applicable approach that has the potential to improve the ability of regulatory agencies to prevent and respond to thermal impairment.

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ORCID

Caitlin P. Mandeville https://orcid.org/0000-0002-1361-607X

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.