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*Utah State University*

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ARE EXPERIMENTALLY DERIVED ESTIMATES OF THERMAL TOLERANCE USEFUL  
IN INTERPRETING SPECIES DISTRIBUTION MODELS?

by

Iva Sokolovska

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Watershed Science

Approved:

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Charles P. Hawkins  
Major Professor

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Wayne A. Wurtsbaugh  
Committee Member

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Susannah S. French  
Committee Member

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Vice President for Research and Dean  
of the School of Graduate Studies

UTAH STATE UNIVERSITY  
Logan, Utah

2014

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## ABSTRACT

Are Experimentally Derived Estimates of Thermal Tolerance Useful in Interpreting Species  
Distribution Models?

by

Iva Sokolovska, Master of Science

Utah State University, 2014

Major Professor: Dr. Charles P. Hawkins  
Department: Watershed Sciences

Direct interpretation of species distribution models assumes that the biota-environment relationships used in them are manifestations of causal mechanisms and are not spurious associations or confounded by co-variation between two or more environmental factors. However, in general, the mechanisms producing these associations have not been experimentally validated, which questions my confidence in both their interpretation and application. Given that temperature is one of the most important factors influencing the fitness and distribution of aquatic ectotherms, studying the thermal physiology of aquatic invertebrates could provide a useful approach for validating model predictions.

Experimental thermal tolerance studies, which assess the physiological limits to temperature, should be useful in interpreting the causal basis for species distribution models predictions. Critical Thermal Maxima experiments are frequently used to measure the thermal tolerance of ectothermic organisms. They represent the temperature at which organisms exhibit disorganized locomotor activity to the point that they lose their ability to escape conditions that will promptly lead to death. Critical Thermal Maxima experiments could, therefore, provide a test of the inferred mechanisms of species distribution models.

The objective of my study was to determine if Critical Thermal Maxima experiments are associated with the thermal limits inferred from species distribution models. If the models accurately describe causal relationships between probabilities of capture and environmental temperatures, and if the thermal maxima are associated with limits to organism fitness, I expected to see a strong correspondence between model-derived and experimentally-derived thermal limits. I observed little to no correspondence between the two different thermal tolerance estimates, which challenges the use and applicability of both the models and experiments.

(50 pages)

## PUBLIC ABSTRACT

Are Experimentally Derived Estimates of Thermal Tolerance Useful in Interpreting Species  
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Iva Sokolovska, Master of Science

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Major Professor: Dr. Charles P. Hawkins  
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Species distribution models are frequently used in ecology to predict the spatial and temporal occurrence of organisms. Direct interpretation of these models assumes that the relationships between the organisms and their environment are manifestations of causal mechanisms. However, in general, the mechanisms producing these associations have not been experimentally validated, which questions our confidence in their interpretation and application. Temperature is one of the most important factors influencing the fitness and distribution of aquatic organisms, and studying the thermal physiology of aquatic invertebrates could provide a useful approach for validating predictions of the species distribution models.

Experimental thermal tolerance studies, which assess the physiological limits to temperature, should be useful in interpreting the causal basis for species distribution model predictions.

Critical Thermal Maxima experiments are frequently used to measure the thermal tolerance of ectothermic organisms. They represent the temperature at which organisms exhibit disorganized locomotor activity to the point that they lose their ability to escape conditions that will promptly lead to death. Critical Thermal Maxima experiments could, therefore, provide a useful test of the inferred mechanisms of species distribution models.

The objective of my study was to determine if Critical Thermal Maxima experiments are associated with the thermal limits inferred from species distribution models. If the models accurately describe causal relationships between predicted distributions of organisms and environmental temperatures, and if the thermal maxima are associated with the limits to organism fitness, I expected to see a strong correspondence between model-derived and experimentally-derived thermal limits. A strong correspondence between model predictions and experimentally obtained thermal maxima would both validate a physiological interpretation of the species distribution models and justify the use of Critical Thermal Maxima experiments alone in predicting species distributions and responses to climate change.

## ACKNOWLEDGMENTS

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Iva Sokolovska



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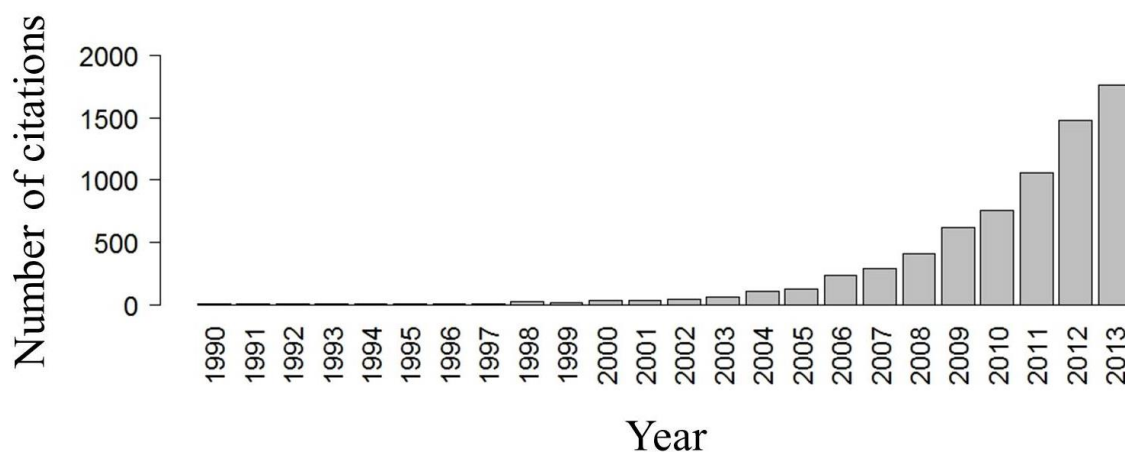
## CHAPTER 1

### INTRODUCTION

Direct interpretation of species distribution models (SDMs) assumes that the biota-environment relationships used in SDMs are manifestations of causal mechanisms and are not spurious associations or confounded by co-variation between two or more environmental factors (Austin, 2002; Barry and Elith, 2006; Kearney and Porter, 2009). However, the mechanisms generally have not been experimentally validated, which reduces our confidence in SDM interpretation. Given that temperature is one of the most important factors influencing the fitness and distribution of aquatic ectotherms (Vannote and Sweeney, 1980; Hawkins et al., 1997), studying the thermal physiology of aquatic invertebrates could provide a useful approach for validating SDM models that use temperature as a predictor. Experimental thermal tolerance studies, which assess the physiological limits to temperature, could be potentially useful in interpreting the causal basis for temperature-driven SDM predictions (Kearney and Porter, 2009; Huertas et al., 2011).

Considering the explosive growth in the development and use of SDMs (Araujo and Peterson, 2012; Araujo and Guisan, 2006) (Figure 1-1), there is a critical need to ensure that I have high confidence in the realism of their predictions. SDMs are typically statistical models that use associations between aspects of the environment and species presence/absence information to predict probabilities of observing a species under different environmental conditions (Austin, 2007; Araujo and Peterson, 2012). These probabilities of capture (PCs) are the core output of SDMs. They are often statistically

validated, i.e., their performance is evaluated with observational data that are independent of the data used to calibrate them (e.g., Allouche et al., 2006; Elith et al., 2006; Barry and Elith, 2006). SDMs are used to predict species' occurrences, distributional ranges, and sensitivities to variation in environmental factors (Guisan and Thuiller, 2005). Other applications include evaluation of the spreading potential of invading species (Peterson and Vieglais, 2001), identification and management of threatened species (Norris, 2004), conservation planning (Sánchez-Cordero et al., 2005), evaluation of the potential impact of climate change on patterns of species distribution (Domisch et al., 2013) and phylogenetic diversity (Pearson and Dawson, 2003), discovery of new populations or previously unknown species (Raxworthy et al., 2003), mapping risks of disease transmission (Costa et al., 2002), and identifying historical refugia for biodiversity (Graham et al., 2004).



**Figure 1-1.** Number of papers associated with the key phrase species distribution model published between 1990 and 2013. Data extracted from Google Scholar on February 23, 2014.

Most of the explicit and implicit assumptions SDMs make have never been tested or rigorously validated. Climate envelope models, as many SDMs are often referred to, assume that species distributions are in equilibrium with environmental variables (Barry and Elith, 2006). Many SDMs also assume that climatic variables are the primary determinants of geographic dispersal ranges (Walker and Cocks, 1991; Guisan and Zimmerman, 2000). One of the most important climatic variables used in SDMs is temperature, a key factor affecting the fitness of many species (Root, 1988; Walther et al. 2005). Temperature is frequently mentioned as being a primary determinant of macro-scale species distributions (McLanchlan and Bird, 1984; Araujo et al., 2007; Levinsky et al., 2007; Selzer and Payne, 1988), especially for freshwater macroinvertebrate species (Dallas, 2008; Hawkins et al., 1997; Ward and Stanford, 1982; Wethey and Woodin, 2008). Therefore, in SDMs using temperature predictors, I need to determine if SDMs actually describe the thermal tolerances of organisms. If SDMs accurately describe causal relationships between probabilities of capture and environmental temperatures, a strong correspondence between the predicted probabilities of capture and experimentally-derived thermal response should exist.

Critical Thermal Maxima (CTM) experiments are frequently used to measure the thermal tolerance of ectothermic organisms (Lutterschmidt and Hutchison, 1997). CTMs represent the temperature at which organisms exhibit disorganized locomotor activity to the point that they lose their ability to escape conditions that will promptly lead to death (Ernst et al., 1984). CTMs could, therefore, provide a meaningful test of the mechanisms inferred from temperature-driven SDM models.

The objective of this study was to determine if CTMs are associated with the thermal limits inferred from SDMs. If SDMs accurately describe causal relationships between probabilities of capture and environmental temperatures, and if CTMs are associated with organism fitness, I expected to see a strong correspondence between SDM-derived and experimentally-derived thermal limits. A strong correspondence between SDM predictions and CTMs would both validate a physiological interpretation of SDMs and justify the use of CTMs alone in predicting species distributions and responses to climate change.

## CHAPTER 2

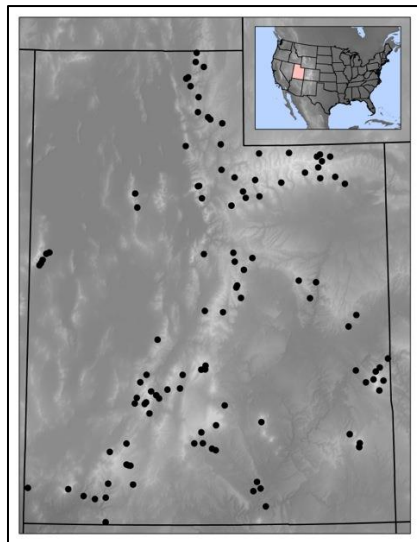
### METHODS

To address my objective, I identified the upper thermal limits for several taxa derived from a multi-taxon SDM and then experimentally measured CTMs for the same taxa.

#### *2.1 Multi-taxon species distribution model*

For this study I developed a multi-taxon SDM (Wright et al., 1998) from data collected at 111 least-disturbed (*sensu* Stoddard et al., 2006) reference sites in near natural condition in Utah (Figure 2-1).

This dataset consisted of stream macroinvertebrate presence and absence data and environmental data collected between 1998 and 2008 by the Utah Department of Environmental Quality. Samples were collected in summer or fall, i.e., between the 248th



**Figure 2-1.** Map of sampling sites in reference condition used to build the SDM. Every black circle marks a stream macroinvertebrate sampling site in Utah.



and 325th day of the year. I estimated upper thermal limits from the multi-taxon SDM for 41 taxa that occurred at 20 or more of these sites (see the Appendix).

To build the multi-taxon SDM, I first calculated the differences (Sørensen dissimilarities) in taxonomic composition (Sørensen, 1948) between sites and used flexible- $\beta$  clustering (Belbin et al., 1992) to identify groups (clusters) of taxonomically similar sites. I then used random forest models (Breiman, 2001) to predict the probabilities of cluster membership for each site from its environmental characteristics. Random forest is a non-linear modeling technique that is based on classification trees (Breiman, 1984) and has been used in related ecological applications (Cutler et al., 2007). Predicted probabilities of capture for each taxon can then be calculated by multiplying the probabilities of cluster membership predicted by the model by each taxon's occurrence frequencies within clusters (Moss et al., 1987). I used 23 candidate predictor variables estimated from either GIS layers or derived from stream temperature, water chemistry, or hydrology models (Table 1) to create the SDM. I then used a variable selection procedure to minimize both prediction error and the number of variables used in the model (Hill et al., 2013, 2014).

**Table 2-1.** Predictors used in the species distribution model. Sources: \*Sulochan Dhungel and Jacob Vander Laan, unpublished. \*\*Hill et al., 2013. \*\*\*Olson and Hawkins, 2012. \*\*\*\*GIS.

Predictor	Description
Predicted conductivity***	Predicted conductivity of the stream water. [ $\mu\text{S}/\text{m}$ ]
Mean summer stream temperature**	Predicted mean summer temperature (June, July, August) [ $^{\circ}\text{C}$ ].
Coefficient of variation of daily flows*	Ratio of the standard deviation of daily flows to the average of daily flows. Represents the overall variability of the streamflow regime.

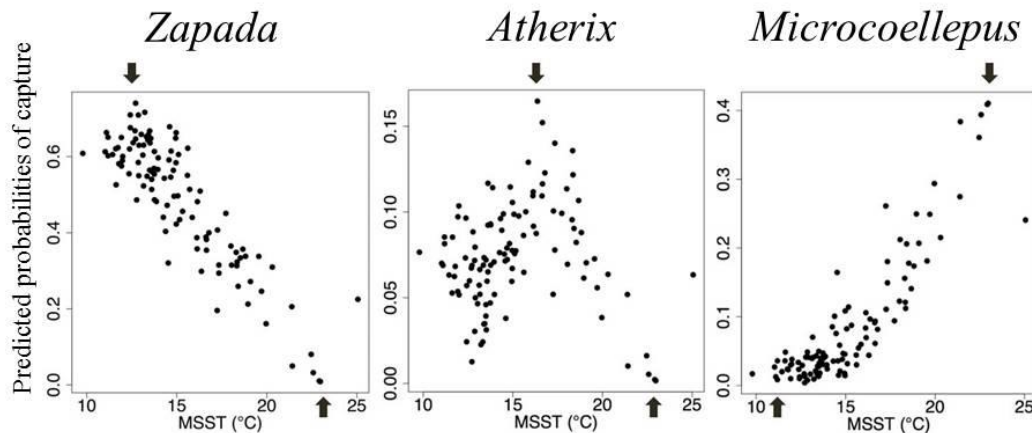
**Table 2.1.** Continued

Predictor	Description
Bank full flow*	The discharge that has a probability of exceedance of 1/1.67. This discharge is thought to represent the flow that is most effective in maintaining channel form [cfs].
Predictability, constancy and contingency of flow*	These variables are the measures of uncertainty. The indices quantify the persistence and temporal organization of seasonal processes. A stream is predictable if it has a constant flow throughout the year or it has the same seasonal pattern every year. If a stream has a low uncertainty regardless of the season, it has high constancy and when the uncertainty is low based upon the season, the stream has high contingency.
Date when 50% of the flow occurred*	The day of the water year by which 50% of the total flow has occurred measured in days from the start of water year (Oct 1).
Number of high flow events*	The average number of high pulse events per year for the entire period of record. A high pulse event is that period within a year when flow rises above the 95th percentile.
Extended low flow index*	A combination of two streamflow variables which have been used in research before: Base Flow Index is the ratio of lowest daily flow to annual average flow (expressed as percentage) and represents the stability of flow. Values near 1 indicate a fairly constant flow and a value near 0 indicate intermittent stream. Zero flow days is the average number of zero flow days in a year and quantifies low flow disturbance and intermittency in streamflow.
Duration of floods*	Flood duration quantifies the duration of flooding as the average number of days per year when the daily flow equals or exceeds Q167.
Day of flow peak*	The average day that peak flow occurs as calculated from the start of the water year (Oct 1).
Average 7-day maximum stream flow*	The average 7-day maximum discharge [cfs].

**Table 2.1.** Continued

Predictor	Description
Average 7-day minimum stream flow*	The average 7-day minimum discharge [cfs].
Number of low flow events*	The average number of low-flow events per year. A low-flow event is defined as a daily flow that is less than the 5 <sup>th</sup> percentile of mean annual flows.
Number of zero flow events*	The average number of zero-flow events per year.
Flow reversals per year*	The average number of reversals in the magnitude of daily flow values each year.
Daily mean discharge*	The mean daily discharge calculated over all years of record [cfs].
Watershed slope****	The mean slope of every 30 km pixel in a stream's watershed, calculated as the rise over run.

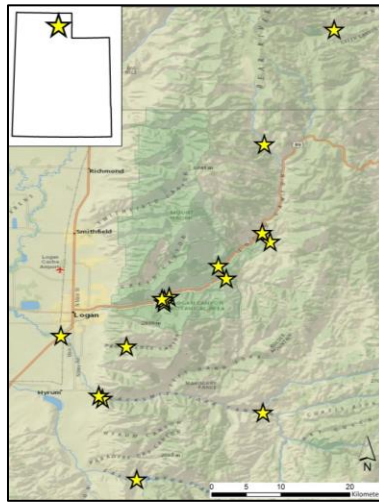
I compared the number of taxa observed at a reference site (O) by the number of taxa expected (E) from the SDM predictions to assess model accuracy and precision. I calculated E (the number of expected taxa) by summing all individual PC values. I used local probability of capture values  $\geq 0.5$  when calculating both O and E. I used the standard deviation of the ratio (O/E) of these values across all sites as a measure of model precision. I used the standard deviation of a null O/E index as an estimate of the lowest possible model precision (Van Sickle et al., 2005), where probabilities of capture of taxa are assumed to be identical across all sites and calculated as the frequency of occurrence of the taxa across all sites. I used an estimate of variation among replicate samples within a site (Van Sickle et al., 2005) as a measure of a model's theoretical best precision. I estimated upper-thermal tolerance limits as the temperature below which 95 percent of non-zero predicted probabilities of capture occurred (Figure 2-2).



**Figure 2-2.** Examples of predicted probabilities of capture for three taxa plotted against mean summer stream temperature (MSST). The arrows mark estimated thermal optima (top arrows) and limits (bottom arrows).

## 2.2. Critical thermal maxima experiments

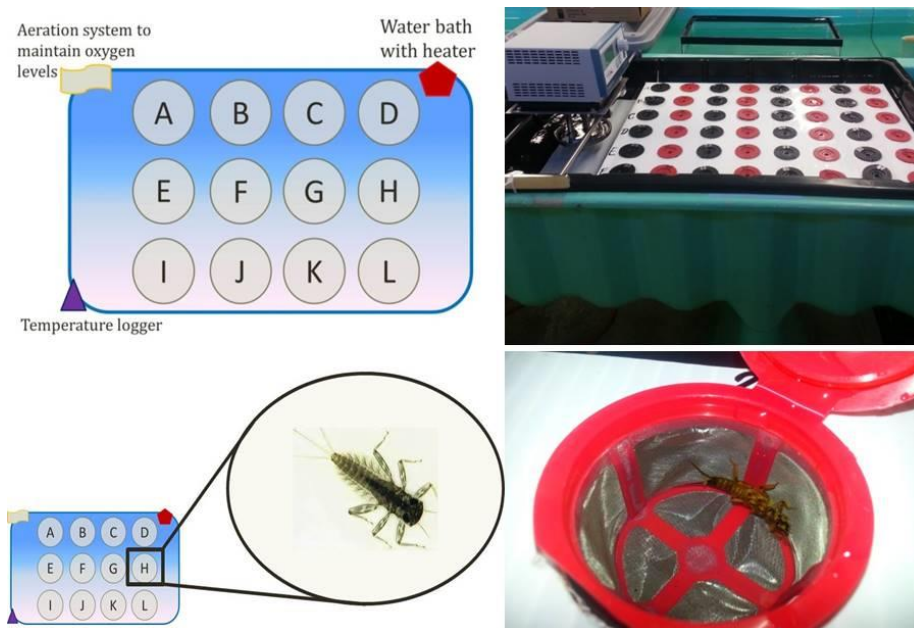
I estimated CTMs for stream macroinvertebrate taxa collected from several streams in northern Utah during late spring, early summer and early fall of 2013. I collected invertebrates during mid-morning to early afternoon from a diversity of streams in the Logan River, Blacksmith Fork, and Little Bear River drainages (Figure 2-3). These drainages contain streams with a variety of thermal regimes and are hydrologically independent. I sampled 19 different stream sites to collect individuals from a wide range of thermal environments. Some taxa were collected multiple times across different sites. Taxa collected at multiple sites allowed us to assess if CTMs vary across populations of the same species. I recorded the temperature at the time of sampling and used a stream temperature model (Hill et al., 2013) to predict the mean summer (July-August) stream temperature for every site.



**Figure 2-3.** Sampling sites in the Logan River, Blacksmith Fork, and Little Bear River drainages.

I conducted separate CTM experiments for each sampling site, testing all of the taxa collected at the site. Immediately after sampling, organisms were transferred to the lab and kept in aerated, non-chlorinated well water at approximately 12 °C for 12 hours prior to the start of the CTM experiments. Organisms were not fed during the pre-experimental period or during experiments. Short-term food restriction appears to have no to little effect on CTM estimates (Terblanche et al., 2011; Rezende and Santos, 2012) and elimination of feeding greatly simplified experiments. Up to 6 individuals of each taxon from a stream were placed into individual mesh chambers (Café Cup®, Spark Innovators) and submerged in a water bath (Figure 2-4). Water temperature was then continuously increased by 2 °C / hour with a programmable circulating water heater (VWR Signature Circulator with Programmable Controller) immersed in the water bath while water was aerated continuously. Individuals placed in an aerated water bath of 12 °C well water were used as controls. I checked individuals for critical thermal endpoint behavior every 15 – 30 minutes. When individuals reached their endpoint they were removed from the

treatment water bath and placed in an aquarium with 12 °C aerated water for recuperation. After 12 hours in the recuperation tank, the macroinvertebrates were preserved in 95% ethanol. Each individual was later identified by the Utah State University / U.S. Bureau of Land Management National Aquatic Monitoring Center, and then shipped for identification based on genetic differences (DNA barcoding) to the Molecular Ecology Research Branch of the National Exposure Research Laboratory of the U.S. Environmental Protection Agency in Cincinnati. I tested a total of 96 taxa, 32 of which I used for SDM comparisons. For the other analyses, I used the full set of tested taxa.



**Figure 2-4.** Experimental set-up (diagram and photos). Letters A-L in the diagram represent individual mesh chambers immersed in the water that contain a single individual.

### *2.3. Recuperation*

I carried out a preliminary analysis to determine if I should exclude individuals from analyses that died following the CTM experiments. Use of individuals that did not recover might over estimate CTM endpoints. I used Welch's t-test to determine if mean CTMs of recuperated and non-recuperated organisms were significantly different from one another. I also conducted mixed-effects analyses of variance with species as random factors and recovered and non-recovered individuals as the fixed treatment to examine how CTM values influenced recuperation.

### *2.4. Acclimation and local adaptation*

I tested for potential effects of acclimation or local adaptation on CTM estimates. To do so, I compared CTMs estimated for individuals from different streams with a mixed effects model with site as the fixed factor and species as the random factor. I also estimated CTMs for several taxa collected at the same site but subjected to different laboratory acclimation times (12 and 72 hours). If organisms had adapted or acclimated to different temperatures, I should observe higher CTMs for individuals within a species collected from warmer streams than for individuals that had been experimentally exposed to warmer temperatures prior to testing.

### *2.5. Mean assemblage CTM at thermally different sites*

As a separate assessment of whether differences among streams in assemblage composition were associated with stream temperature, I used mixed models to determine if mean assemblage CTM values varied across thermally different sites. I used data from both the sites at which I collected organisms for CTM experiments and an independent

set of 62 streams from which data on both macroinvertebrate composition and mean August water temperatures had been collected. These latter data were provided by the U.S. Bureau of Land Management's National Aquatic Monitoring Center.

#### *2.6. Factors associated with variation in CTMs*

I used two approaches to examine the factors associated with variation in CTMs. I used a random forest model to determine which of the following predictors was most strongly associated with variation in CTMs: organism wet weight, site temperature, mean summer stream temperature, and phylogenetic relatedness. I also used a mixed effects model to determine how much variance in CTMs was associated with each of these factors.

#### *2.7. Upper thermal limits correspondence*

I used ordinary correlation analysis (Pearson  $r$ ) and bivariate plots to examine the associations between the upper thermal limits estimated from the species distribution model and experimentally derived CTMs for each taxon.



## CHAPTER 3

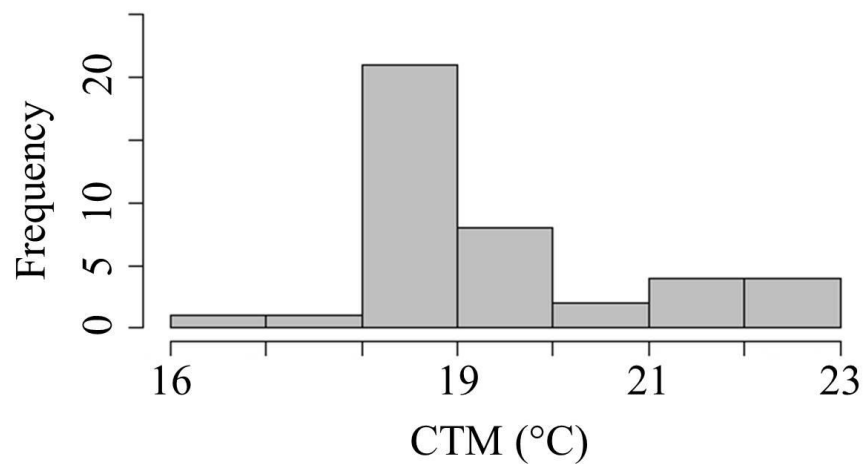
## RESULTS

*3.1. Multi-taxon species distribution model*

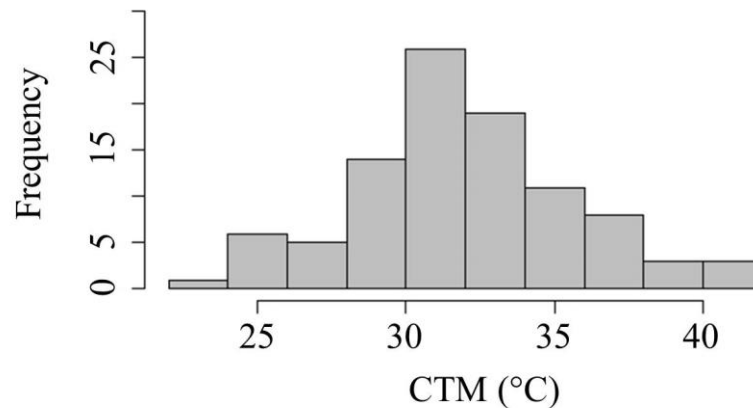
The most important predictors in the multi-taxon SDM were (in order of importance): coefficient of variation of daily flows, mean summer stream temperature, flow contingency, flow constancy, and bank full flow. The precision (SD) of the model was 0.17, which was substantially better than that of the null model (SD = 0.23) and nearly as good as the theoretically best model (SD = 0.16). Upper thermal limits derived from this model for taxa encountered at >20 sites varied from 16 to 23 °C (Figure 3-1).

*3.2. Critical thermal maxima experiments*

CTM-derived estimates of upper thermal limits for the 96 tested taxa varied from 15.5 to 43.7 °C (Figure 3-2).



**Figure 3-1.** SDM-derived upper thermal limits estimates at the lowest available taxonomic resolution.



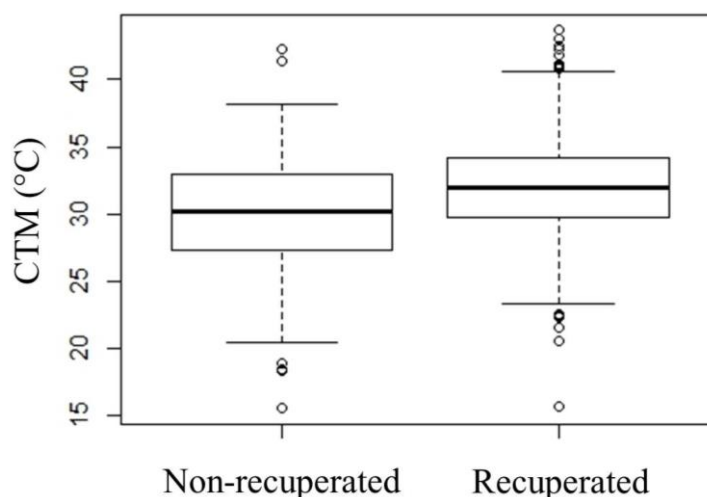
**Figure 3-2.** Mean taxon CTMs for the experimentally tested taxa.

### *3.3. Effects of recuperation on CTM estimates*

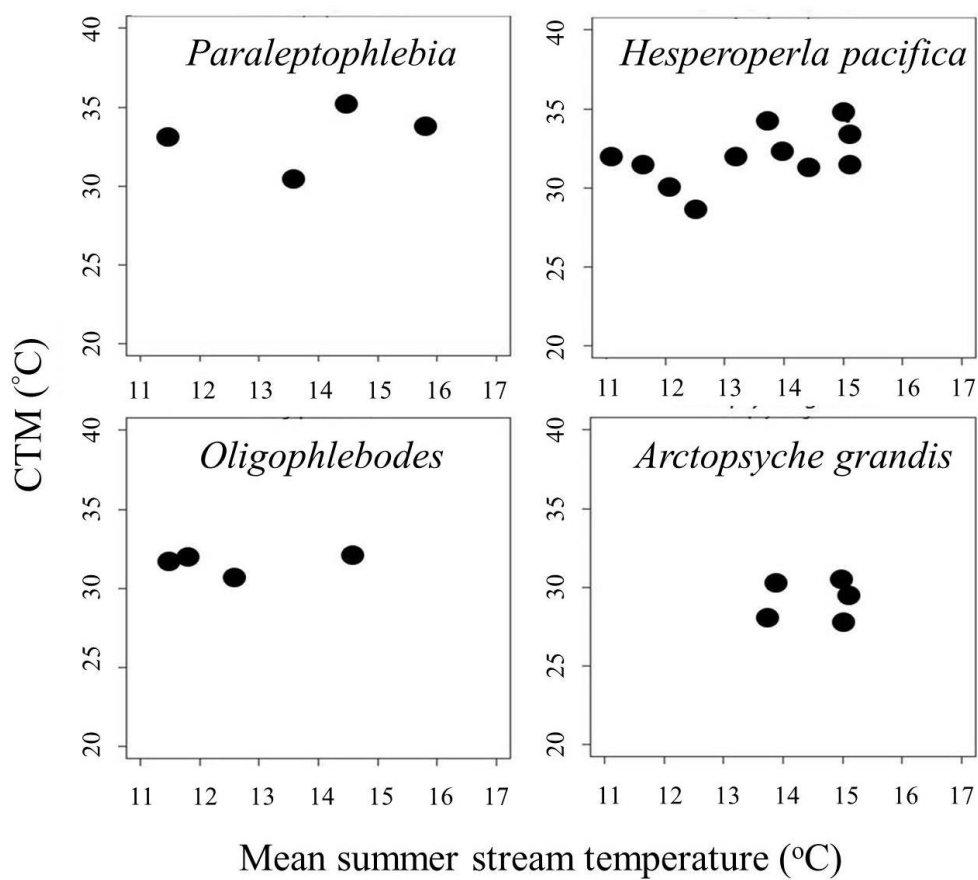
The Welch two sample t-tests for each taxon showed that CTMs for recuperated and dead individuals were not statistically significantly different from one another ( $p$ -values  $> 0.05$ ) (Figure 3-3). To be conservative, I therefore only used data from individuals that recuperated in subsequent analyses.

### *3.4. Acclimation and local adaptation*

I observed little evidence that acclimation or local adaptation influenced thermal tolerance estimates. When comparing the CTMs of taxa collected at thermally different sites, no discernible pattern of systematic variation in taxa-specific CTMs occurred across sites (Figure 3-4). Twelve- and 72-hour acclimation experiments also indicated that acclimation period had no statistically significant effect on CTMs for the 6 taxa tested ( $p$ -values  $> 0.05$ ).



**Figure 3-3.** Boxplots showing the distribution of CTM estimates for the non-recuperated and recuperated individuals. Heavy horizontal lines represents the mean, the values range is marked with the top and bottom of boxes, while single points signify outliers.



**Figure 3-4.** Plots of the mean CTMs estimated for 4 taxa collected at different sites that varied in predicted mean summer stream temperature.

### *3.5. Mean assemblage CTMs at thermally different sites*

Mean assemblage CTMs increased with stream temperature (predicted mean summer stream temperature) for data from my sampling sites, but not for the U.S. Bureau of Land Management data. Results from a mixed effect model based on my data showed that for every 1 °C increase in site temperature there was a 0.2 °C increase in the mean thermal endpoint for taxa (Figure 3-5). However, the same analysis showed no relationship ( $r^2=0.02$ ) between mean assemblage CTMs and mean August stream temperature for Utah streams sampled by the U.S. Bureau of Land Management in August 2013 (Figure 3-6).

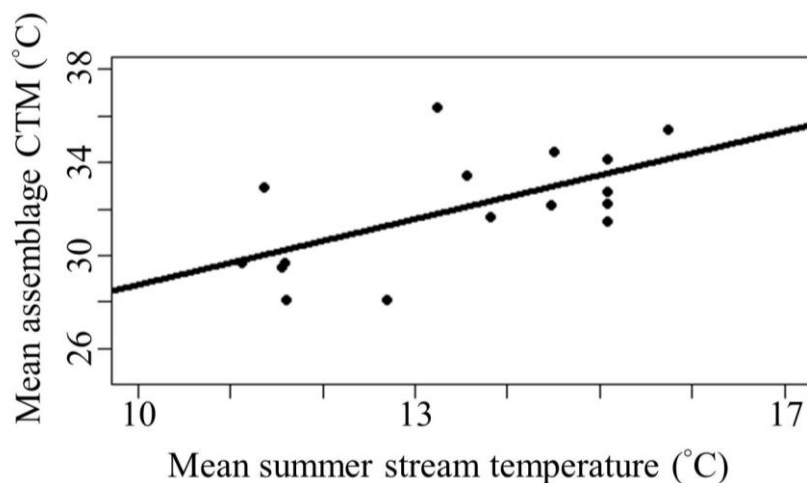
Of the taxa tested, taxonomic order was most strongly associated with CTMs based on the random forest model, followed by stream temperature, wet weight and MSST (Figure 3-7). The random forest model accounted for 64.7% of the variation among taxa in CTM values.

### *3.6. Factors associated with variation in CTMs*

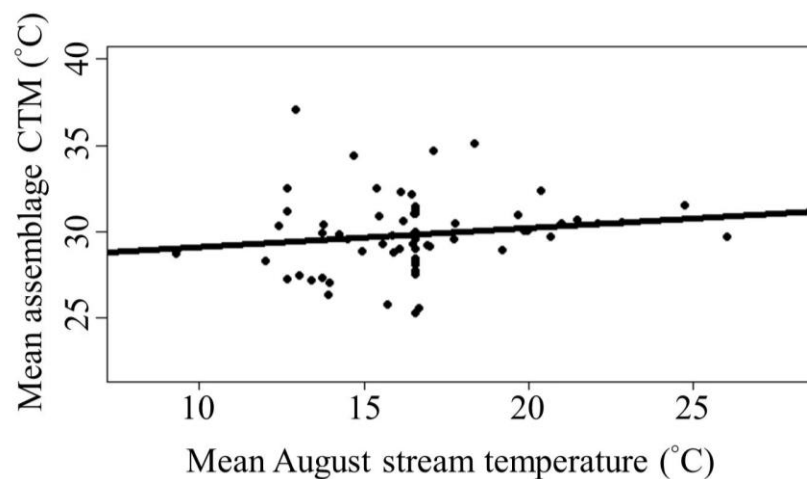
The mixed effects model where stream temperature and the wet weight of individuals were the fixed factors and species was the random factor, revealed that 78% of the variation of the CTM value was due to the taxonomic ID, i.e the species. Wet weight was not statistically significant, whereas the effect of MSST was. In general, as the stream temperature at a site increased so did the CTM value estimated for taxa collected at those sites. For every 1 °C increase in MSST, CTM values increased by 0.2 °C.

### 3.7. Relationship between SDM-derived upper thermal limits and CTMs

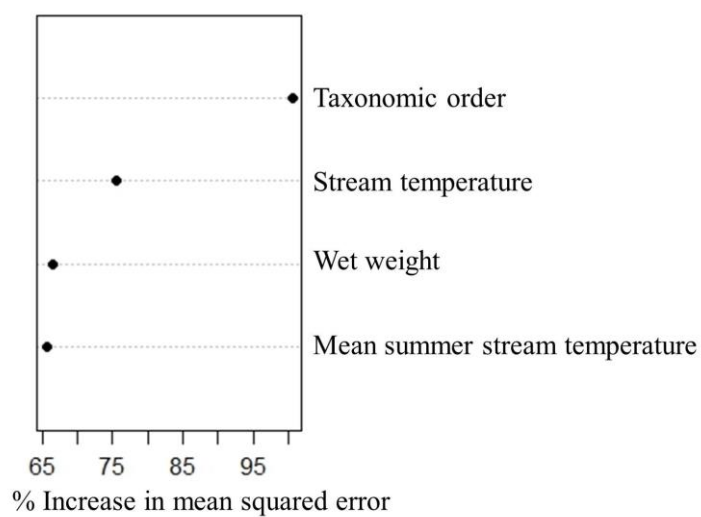
Contrary to expectations, my analyses showed that no correlation ( $r^2=0.0002$ ) existed between CTMs and SDM-derived thermal limits (Figure 3-8).



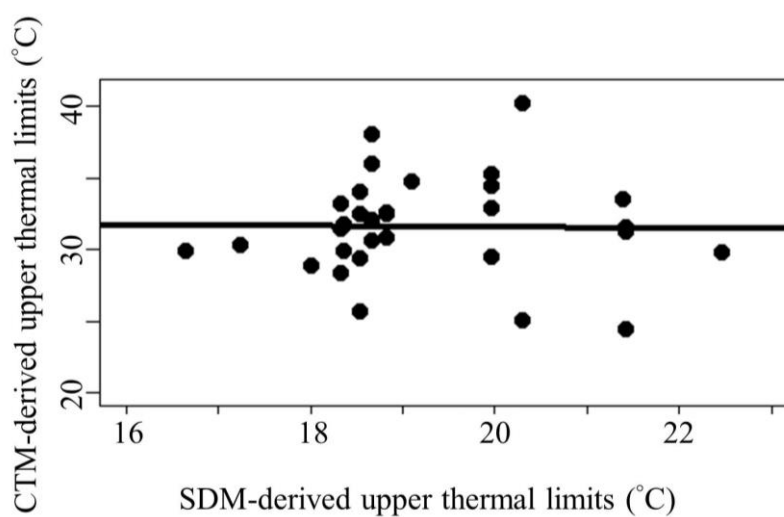
**Figure 3-5.** Positive relationship between assemblage CTMs and the predicted mean summer stream temperature at a site ( $r^2=0.37$ ).



**Figure 3-6.** Mean assemblage CTMs at different mean August stream temperatures for streams in Utah sampled by the U.S. BLM.



**Figure 3-7.** Ranked importance (percent increase in mean square error) of the predictor variables for CTM. Stream temperature refers to temperature measured at the time of sampling.



**Figure 3-8.** Relationship between mean species CTMs and SDM-derived upper thermal limits ( $r^2=0.0002$ ,  $p = 0.94$ ).

## CHAPTER 4

### DISCUSSION

My results imply that laboratory-derived estimates of near lethal temperatures (CTMs) may not be useful in interpreting species distribution models that use temperature predictors. If both CTMs and SDM-derived temperature limits were correlated with species fitness, we would expect to see a strong correlation between CTM- and SDM-derived upper thermal limits. The lack of a relationship between CTMs and SDM-derived thermal limits could have occurred for several reasons. First, I suspect that the two approaches are measuring different aspects of a species' niche, and more importantly neither approach may describe the upper thermal limits of the reproductive niche. Second, it is possible that CTMs were not a meaningful measure of upper thermal limits. However, this explanation is unlikely given the high correspondence between upper thermal limits and optimal temperatures of performance observed for some other taxa (Huey et al., 2009), strong correlations between CTMs and other measures of upper thermal limits (Lutterschmidt and Hutchinson, 1997); and findings that slow ramping rates in CTM experiments, like I used here, provide consistent results at different acclimation temperatures (Allen et al., 2012). Third, the temperatures that limit fitness, and hence distributions, may not be correlated with near lethal temperatures. Temperature influences many aspects of the existence of aquatic insects, such as metabolic rates, growth rates, feeding rates, fecundity, emergence, behavior, and ultimately survival (Vannote and Sweeney, 1980; Brittain and Campbell, 1991; Mckie et al., 2004; Kishi et al., 2005). Temperature also affects solvent properties of water, the amount of dissolved

oxygen, and water viscosity (Geng and Duan, 2010). In short, the numerous ways temperature influences stream biota may not be well represented by a single measure, such as near lethal CTMs. Finally, I hypothesized that the temperature measures I used in my models realistically represented overall thermal effects on species fitness. However, it is possible that the temperature predictors I used in the SDMs were not directly comparable with the highly resolved temperatures measured in the CTM experiments. The weak correlation between mean assemblage CTM and modeled stream temperatures in my data set and the lack of correlation between mean assemblage CTM and mean August stream temperature from the U.S. BLM data set suggests that we cannot predict species distribution at sites solely using stream temperature predictors. In fact, in my SDM the most important predictor of species distribution was a hydrologic variable (coefficient of variation of daily flows).

The lack of correlation between the CTM and SDM thermal limit estimates may also represent a discrepancy between the fundamental and realized thermal niches. A species' fundamental niche is that hypervolume defined by environmental dimensions (conditions and resources) within which that species can survive and reproduce in the absence of biotic interactions (Hutchinson, 1957). A species may be excluded from parts of its fundamental niche because of competition and other biotic interactions and this reduced hypervolume is the species' realized niche (Austin et al., 1990; Malanson et al., 1992). Thus, the macroinvertebrate observations used as input for the development of SDMs, estimate the upper limits of the realized thermal niches of taxa if competition excludes taxa from warmer streams that taxa could otherwise survive. In contrast, CTMs measure the fundamental, acute upper lethal limit of taxa in the absence of competition. We might



therefore not expect the two measures of thermal limits to be correlated with one another. Furthermore, the niche is N-dimensional; it encompasses biotic and abiotic interactions as well as movement constraints (Godsoe, 2010). Measuring the response to a single dimension, such as the upper thermal limit with CTM experiments, may not predict a species' distribution (Hortal et al., 2012) because the upper physiological limits alone will not characterize the realized niche of organisms (Kellermann et al., 2012; Gouveia et al., 2014). Figure 2-4 suggests evidence of a ceiling imposed by temperature with actual PCs at many sites well below this ceiling (i.e., the effect of other factors in controlling distributions).

CTMs may not be an appropriate validation method for model predictions. Despite finding poor correspondence between CTM- and SDM-based upper thermal limits, the SDMs performed very well statistically. My objective was to link CTMs to field temperature data in a way that realistically reflected the differences in the thermal regimes experienced by aquatic organisms. However, the temperature predictors I used in the SDMs might not accurately depict the temperatures stream biota experience on a daily basis. Instead, stream biota can experience microthermal heterogeneity (i.e., spatial and diel variation in warm and cool temperatures) that is most pronounced in the summer (Webb et al., 2008). This microthermal heterogeneity is important for behavioral thermoregulators (Ward and Standford, 1982; Berman and Quinn, 1991) like stream macroinvertebrates. (Greenwald, 1974; Huey and Stevenson, 1979), because it allows taxa to seek refuge or find better food sources. To improve the physiological realism of SDMs, it will be critical that we characterize temperature in a way that better measures actual thermal exposure experienced by stream organisms. Considering the importance of

a site's thermal history for upper thermal limits values (i.e., the history of thermal exposure is correlated with what taxa occur at a site) (Martin and Gentry, 1974; Clusella-Trullas et al., 2011; Dallas and Rivers-Moore, 2012), more finely resolved spatial and temporal temperature predictors might result in SDM-derived thermal limits that are more comparable to CTMs.

My results raise important questions regarding the use of CTMs in bioassessment. Despite being simple, quick, and inexpensive to conduct, this study suggests CTM experiments cannot be used to validate species distribution models. However, upper temperature limits, like the ones measured with CTMs, are relevant in understanding thresholds for fitness (Huey and Stevenson, 1979) and may be useful in addressing other questions. For example, CTMs are considered to be an effective method of determining relative thermal tolerances of organisms and useful in identifying potential bioindicators of thermal alteration (Dallas and Rivers-Moore, 2012). Data on thermal tolerances of aquatic organisms might be valuable in long-term management of thermal regimes and protection from thermal alteration effects (Dallas and Rivers-Moore, 2012; Stewart et al., 2013). CTMs appear to be useful in generating thermal indices and identifying thermally altered sites. For example, organisms in heated streams have been observed to have higher CTMs than conspecific organisms in streams with unaltered temperature (Martin and Gentry, 1974). However, my results (Figure 3-6) do not support these findings. I also considered the idea of using O/E models like the multi-taxon SDM (Hawkins, 2006) and calculating the observed and expected thermal tolerance of the aquatic community to determine the condition of a site. However, my mean assemblage CTM results showed that there was no relationship between mean CTM values and site temperatures. These

implications need to be further examined with experiments designed to rigorously test how useful CTMs are as indicators of thermal alteration by comparing CTMs of taxa collected at paired sites that differ only in thermal alteration (i.e., control and heated sites). If my initial results are confirmed and CTM values do not change with thermal alteration, the use of CTM experiments to create thermal indices should be questioned.

To validate species distribution models that use temperature as a predictor, further long-term experimental work is required. Studies that determine how field and laboratory measurements of upper thermal limits, lower thermal limits, and optima are related would be a good starting point to understand how physiological limits are related to distribution limits. However, we also need to understand and experimentally assess how temperature interacts with other factors (hydrology, substrate etc.) to influence species distributions.

## CHAPTER 5

### SUMMARY AND CONCLUSIONS

The results from this study show that estimates of thermal tolerance from laboratory thermal tolerance experiments do not appear to be useful in interpreting species distribution models that use temperature predictors. Even though it is possible that species distribution models are not accurately describing the upper thermal limits of organisms or CTMs might not be measuring the upper thermal limits accurately, I think the two approaches are measuring different aspects of a species' niche, and more importantly neither approach may describe the upper thermal limits of the reproductive niche.

Temperature influences many aspects of the existence of aquatic insects, such as metabolic rates, growth rates, feeding rates, fecundity, emergence, behavior, and ultimately survival (Vannote and Sweeney, 1980; Brittain and Campbell, 1991; Mckie et al., 2004; Kishi et al., 2005). For aquatic organisms, temperature also affects solvent properties of water, the amount of dissolved oxygen, and water viscosity (Geng and Duan, 2010). Because temperature can influence aquatic life in multiple ways, I assumed that temperature measures used in my models realistically represented overall thermal effects on species fitness. However, temperature might not be the most important predictor of stream macroinvertebrate distributions (my results show that hydrologic predictors are in fact more important than temperature predictors) and it is possible that the temperature predictors used in SDMs were not comparable with the highly resolved temperatures measured in the CTM experiments. The weak correlation between mean assemblage CTM and stream temperatures in my data set and the lack of correlation

between mean assemblage CTM and mean August stream temperature from the U.S. BLM data set suggests that we cannot predict species distribution at sites solely using stream temperature predictors. Temperature is often a strong causal determinant of species distributions (Vannote and Sweeney, 1980), however, I suspect that the temperatures that limit fitness, and hence distributions, may not be correlated with near lethal temperatures.

The lack of correlation might be a result of the discrepancy in upper thermal limits of the fundamental and realized niche. Hutchinson (1957) defined a species' fundamental niche as that hypervolume defined by environmental dimensions (conditions and resources) within which that species can survive and reproduce in the absence of biotic interactions. A species may be excluded from parts of its fundamental niche because of competition and other biotic interactions. The reduced hypervolume is then termed the realized niche (Austin et al., 1990; Malanson et al., 1992). The samples of macroinvertebrate assemblages and environmental data, used as input for the development of SDMs, estimate the upper limit of the realized thermal niches of taxa. CTMs measure the fundamental, acute upper lethal limit of taxa. If CTMs are not correlated with the upper limits of the organisms realized niche, we should not expect the realized and fundamental niche limits to mirror each other.

Seeing no correlation between the two thermal tolerance estimates coupled with my assemblage results raises important questions for the use of CTMs. Unfortunately, even though CTM experiments are simple, quick and non-expensive to conduct cannot be used to validate species distribution models. Using O/E models like the multi-taxon SDM (Hawkins, 2006) and calculating the observed and expected thermal tolerance of the

aquatic community at a site could be informative of the condition of the site. However, my mean assemblage CTM results show that there is no strong correlation between assemblage upper thermal limits and site temperatures.

To validate species distribution models that use temperature as a predictor, further experimental work is required. Studies to determine correspondence between field and laboratory measurements of upper thermal limits, lower thermal limits, and optima would be a good starting point to understand how physiological and ecological performances relate. However, we should seek to understand and experimentally assess how temperature interacts with other factors (hydrology, substrate etc.) that can influence species distributions.

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APPENDIX



**Appendix A. Model (SDM)-derived and experimentally (CTM) derived upper thermal limits (UTLs) for all tested taxa.**

**Table A-1.** Model- and experimentally derived upper thermal limits in degrees Celsius.

Class	Order	Family	SDM Taxon	SDM UTLs	CTM taxon	CTM UTLs
Insecta	Ephemeroptera	Ameletidae	Ameletus	18.3	Ameletus	28.4
					Ameletus celer	28.3
					Ameletus cooki	28.4
Insecta	Ephemeroptera	Baetidae	Baetidae	20.3	Baetidae	25.1
					Baetis bicaudatus	24.1
					Baetis tricaudatus	27.6
					Brachycentrus	34.0
Insecta	Trichoptera	Brachycentridae	Brachycentrus	18.5	Brachycentrus americanus	29.9
					Brachycentrus occidentalis	35.4
					Chironomidae pupae	24.5
Insecta	Diptera	Chironomidae	Chironominae	21.4	Chloroperlidae	32.6
					Sweltsa	31.7
					Sweltsa borealis	31.8
Insecta	Plecoptera	Chloroperlidae	Chloroperlidae	18.4	Sweltsa gaufini	30.9
					Suwallia starki	33.5
					Cinygmula	28.9
Insecta	Ephemeroptera	Heptageniidae	Cinygmula	18.0	Cinygmula	28.9
Insecta	Coleoptera	Elmidae	Cleptelmis	20.0	Cleptelmis addenda	34.5
Insecta	Diptera	Pediciidae	Dicranota	18.4	Dicranota	31.8
Insecta	Ephemeroptera	Ephemerellidae	Drunella doddsi	17.2	Drunella doddsii	30.3
Insecta	Ephemeroptera	Ephemerellidae	Drunella grandis	18.5	Drunella grandis	32.5
					Epeorus	30.9
					Epeorus albertae	31.2
Insecta	Ephemeroptera	Heptageniidae	Epeorus	18.8	Epeorus longimanus	29.9
					Ephemerella	32.2
					Ephemerella dorothea	32.3
					Ephemerella infrequens	32.3
Insecta	Ephemeroptera	Ephemerellidae	Ephemerella	18.7	Ephemerella tibialis	32.1

**Table A-1.** Continued.

Class	Order	Family	SDM Taxon	SDM UTLs	CTM taxon	CTM UTLs
Insecta	Plecoptera	Perlidae	Hesperoperla	18.8	Hesperoperla pacifica	32.5
Insecta	Coleoptera	Elmidae	Heterlimnius	18.3	Heterlimnius corpulentus	33.2
Insecta	Diptera	Tipulidae	Hexatoma	18.7	Hexatoma	38.0
					Hydropsyche / Ceratopsyche	31.6
Insecta	Trichoptera	Hydropsychidae	Hydropsyche / Ceratopsyche	21.4	Hydropsyche centra	30.8
					Hydropsyche oslari/occidentalis	31.9
					Isoperla	29.6
Insecta	Plecoptera	Perlodidae	Isoperla	20.0	Isoperla fulva	32.0
					Isoperla petersoni	29.3
					Lepidostoma	32.6
					Lepidostoma cinereum	35.5
Insecta	Trichoptera	Lepidostomatidae	Lepidostoma	18.8	Lepidostoma pluviale/aporna	31.3
					Lepidostoma unicolor	35.1
Insecta	Trichoptera	Brachycentridae	Micrasema	18.7	Micrasema bactro	36.0
Insecta	Trichoptera	Uenoidae	Neothremma	16.6	Neothremma alicia	29.9
Citellata	Oligochaeta		Oligochaeta	21.4	Oligochaeta	33.5
					Oligophlebodes	31.6
					Oligophlebodes ardis/minutus	31.3
Insecta	Trichoptera	Uenoidae	Oligophlebodes	18.3	Oligophlebodes minutus/ardis	31.3
					Optioservus quadrimaculatus	34.8
Insecta	Coleoptera	Elmidae	Optioservus	19.1	Optioservus quadrimaculatus	34.8
Insecta	Diptera	Chironomidae	Orthocladiinae	21.4	Orthocladiinae	31.2
					Paraleptophlebia	32.9
					Paraleptophlebia debilis	33.1
Insecta	Ephemeroptera	Leptophlebiidae	Paraleptophlebia	20.0	Paraleptophlebia heteronea	32.8
					Pteronarcella badia	30.2
Insecta	Plecoptera	Pteronarcyidae	Pteronarcella	18.7	Pteronarcella badia	30.2

**Table A-1.** Continued.

Class	Order	Family	SDM Taxon	SDM UTLs	CTM taxon	CTM UTLs
Insecta	Ephemeroptera	Heptageniidae	Rhithrogena	18.5	Rhithrogena	29.5
					Rhithrogena sp	31.0
					Rhithrogena robusta	27.4
					Rhyacophila	29.9
Insecta	Trichoptera	Rhyacophilidae	Rhyacophila	18.4	Rhyacophila brunnea	30.2
					Rhyacophila coloradensis	28.1
					Rhyacophila oreta	31.7
					Rhyacophila vao	29.6
					Simuliidae	30.1
					Simulium	26.1
Insecta	Diptera	Simuliidae	Simuliidae	22.5	Simulium arcticum/saxosum/brevicercum	34.3
					Simulium canadense	29.7
					Simulium piperi	29.2
					Simulium vittatum	31.4
					Tipula	35.2
Insecta	Diptera	Tipulidae	Tipula	20.0	Tipula	35.2
Insecta	Coleoptera	Elmidae	Zaitzevia	20.3	Zaitzevia parvulus	40.2
					Zapada	25.7
					Zapada cinctypes	25.5
Insecta	Plecoptera	Nemouridae	Zapada	18.5	Zapada columbiana	25.9
					Zapada columbiana	25.9
					Zapada columbiana	25.9