DETERMINATION OF CHIRONOMIDAE THERMAL PREFERENCES AND THERMAL PARTITIONING AMONG CLOSELY RELATED TAXA IN A MINNESOTA STREAM USING SURFACE FLOATING PUPAL EXUVIAE

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With 3 figures

ABSTRACT: The thermal preferences of a chironomid community in a northern temperate stream were determined using surface floating pupal exuviae. In general, thermal preferences fit predictions with Diamesinae and Orthocladiinae emerging at lower temperatures than Chironominae and Tanypodinae. Thermal preference ranges were greater for larger genera compared to small genera suggesting that thermal partitioning is occurring within large genera and may reduce competition among closely related species.

RESUMO: As preferências térmicas duma comunidade de quironomídeos foram determinadas utilizando exuviae pupais flutuantes. As preferências térmicas concordaram com as nossas previsões, nomeadamente a ocorrência da eclosão de Diamesinae e Orthocladiinae nas alturas de baixas temperaturas quando comparados com Chironominae e Tanypodinae. A gama de tolerâncias térmicas foi maior nos géneros com um maior número deespécies, que possivelmente reduza a competição entre espécies com um maior grau de afinidade.

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INTRODUCTION

Thermal regime is a major regulator of the life history, phenology, and taxonomic composition and structure of macroinvertebrate communities in lotic waters. Temperature frequently controls the growth and development of aquatic insects as sufficient heat energy is necessary for an aquatic insect to become an adult capable of reproduction. The energy required for the growth and development of different insect species varies as aquatic insects have evolved a wide range of temperature tolerances and requirements. Therefore, the amount and pattern of heat energy in an aquatic habitat determines its suitability depending on the requirements of a species. For example, at optimal thermal regimes, species tend to be more abundant and larger with greater fecundity. As thermal regime becomes less optimal, abundance, size, and fecundity tend to decrease until the population is no longer self-sustaining or is completely absent (VANNOTE & SWEENY, 1980). Therefore, the broadscale distribution of an aquatic insect is largely determined by a species' optimal temperature requirements as it relates to meteorological conditions.

Several studies have identified seasonal patterns in chironomid communities from temperate streams where taxa from the subfamilies Diamesinae and Orthocladiinae tend to emerge during cooler months and Chironominae and Tanypodinae emerge during warmer months (*e.g.* BECKETT, 1992; COFFMAN & DE LA ROSA, 1998). However, thermal preferences at the species and genus levels are less well known and could have implications for assessing interspecific competition, the evolutionary history of chironomid species, and broadscale diversity patterns for aquatic insects. For example, COFFMAN (1989) hypothesized that increased thermal variability in streams (*e.g.* temperate surface water dominated [SWD] streams) creates additional niche partitioning and permits a greater number of species to utilize the habitat. This would suggest that species utilizing similar resources (*e.g.* food, substrate) can divide these resources through time. Closely related species would be expected to utilize similar resources; therefore we can further hypothesize that closely related taxa may be more likely to partition resources through time by possessing different thermal preferences. As a result, larger genera would be expected to have a greater diversity of thermal preferences to reduce competition among closely related species whereas the thermal preferences of smaller genera should reflect the evolutionary history of higher taxonomic levels.

METHODS

The sampling site was located on a 3rd order section of Chub Creek (Dakota County, Minnesota, USA; 44.5216°N, 93.1811°W), a tributary of the Cannon River located in south-eastern Minnesota. The water shed is dominated by cropland although similar sections of the stream have been assessed as possessing good biological condition (Dakota County Soil and Water Conservation District, 2001) possibly the result of good riparian buffers and relatively high habitat diversity. Average daily temperatures during 2003 ranged from 0.1 to 25.6°C with ice cover occurring during January, February, and December. Chironomidae surface floating pupal exuviae (SFPE) samples were collected on a bi-weekly basis for one year during 2003 following the methods of Ferrington *et al.* (1991). Samples consisted of a timed 10 minute sampling period within a 30 m sample reach. Collections were made by scooping SFPE into a pan from areas where they collect (*e.g.* snags, overhanging vegetation, behind rocks) and pouring this material through a 125 µm sieve. Samples were then transferred to 118 ml jars and preserved in 80% ethanol. To measure temperature regime, a temperature logger (Onset StowAway TidbiT) was deployed in the stream for the duration of sampling and downloaded bi-weekly during sampling events. Once returned to the laboratory, SFPE were picked from debris in water, slide mounted, and identified under a compound microscope to species or morphospecies. Specimens which were broken, covered in extensive fungal hyphae, or dried were not picked to avoid identification problems or uncertainty regarding the age of exuviae.

Emergence abundance for subfamily, genus, and species taxonomic levels were compiled and related to the average daily temperature at which the specimens were collected. Violin plots were created for subfamilies and genera using NCSS (HINTZE, 2001) to show relative emergence abundance at different temperatures. Thermal preference ranges for genera were calculated as the difference between the mean emergence temperature of the two species with the highest and lowest mean emergence temperature. However, greater thermal diversity in larger genera may be a function of the number of species in a genus rather than thermal partitioning. To examine this, simulated genera were generated by calculating all possible two, three, four, five, and ten species combinations for genera from which multiple combinations could be generated for each genus size. For example, all genera with three or more species were used to generate two species simulated genera. Comparisons for genera with six, seven, eight, and nine species were not made because no genera were this size. The ranges for all possible combinations were then averaged for each genus from which simulated genera were generated. By calculating simulated genera we can determine if in larger genera there was increased thermal variability independent of genus size. Box plots were created using NCSS (HINTZE, 2001) to compare the thermal preference ranges of different sized genera for both natural (*i.e.* unmodified) and simulated (*i.e.* average of all possible combinations) genera. Relationships between genus size and thermal preference range were not tested for significance because there were too few genera for some genus size categories which invalidated test assumptions.

RESULTS

A total of 128 species from 54 genera were identified from Chub Creek during

2003. Chironominae was the most diverse subfamily with 60 species followed by Orthocladiinae with 48 species. Less diverse were the Tanypodinae with 19 species and the Diamesinae with one species identified. Mean emergence temperatures for subfamilies ranged from 5.32 to 20.19°C with Diamesinae emerging at the lowest temperatures and Tanypodinae at the highest (Fig. 1). Orthocladiinae and Chironominae had mean emergence temperatures of 16.83 and 18.48°C, respectively. Mean emergence temperatures for genera ranged from 5.32°C (*Diamesa*) to 24.52°C (*Paramerina*) (Fig. 2). At lower temperatures there was a greater prevalence of Orthocladiinae genera, but at warmer temperatures, Chironominae and Tanypodinae genera were more common (Figure 2). There were a few notable exceptions to these generalizations with *Micropsectra* emerging on average at 11.71°C and *Corynoneura* emerging on average at 22.51°C. Several other genera also did not match subfamily predictions (*e.g. Glyptotendipes*, *Parachironomus*, *Epoicocladius*, *Eukiefferiella*; Fig. 2), but the small number of specimens collected for these genera cause some uncertainty regarding their thermal preferences.

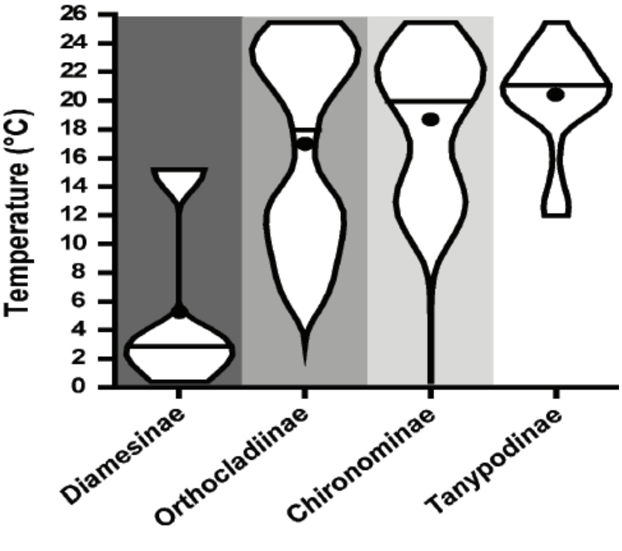

Fig. 1. Violin plots of subfamily relative abundance at emergence temperatures (plot width = relative abundance; line = median, and solid circle is mean).

The thermal preference ranges for both natural and simulated genera increased from smaller to larger genera (Fig. 3). For two, three, and four species genera, simulated genera had greater thermal preference ranges. In contrast, natural genera had similar thermal preference ranges for five species genera and greater ranges for ten species genera when compared to simulated genera. The thermal preference ranges for natural two and three species genera were more variable than other genera sizes and treatments. This larger variation was the result of one genus among the two species genera and three genera among three species genera which had considerably larger thermal preferences ranges than the other genera with similar genus sizes.

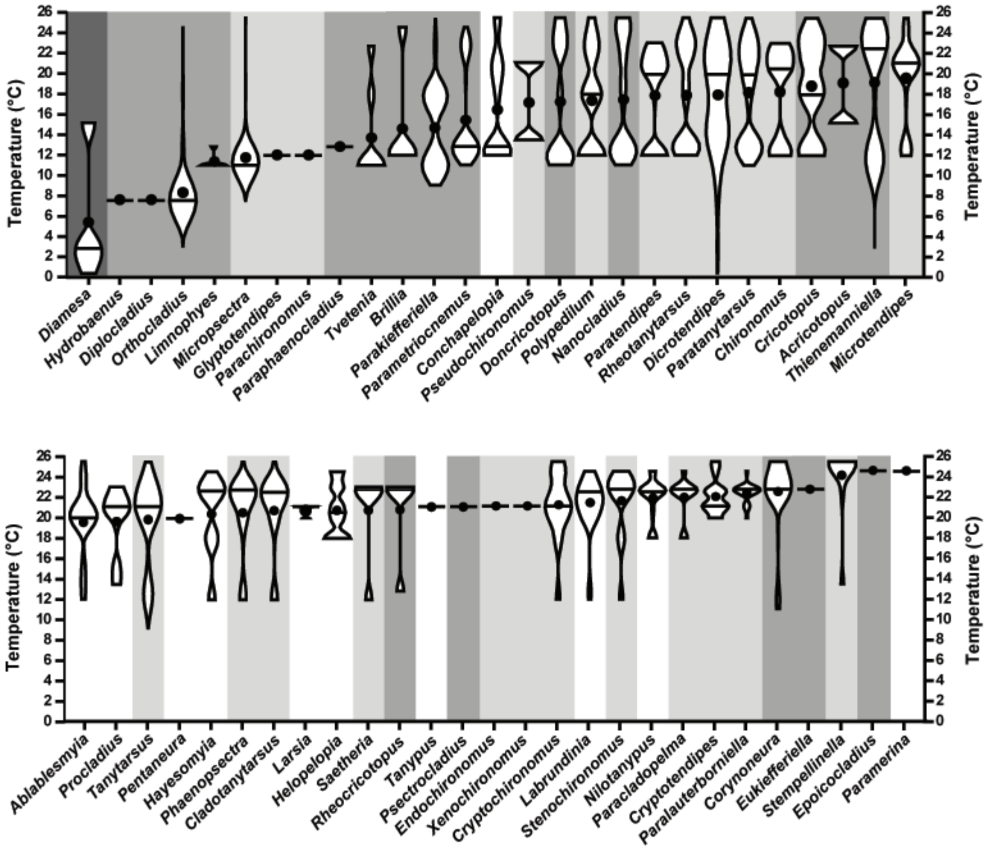

Fig. 2. Violin plots of relative abundance for genera at emergence temperatures (plot width = relative abundance; line = median; solid circle = mean; dark grey = Diamesinae; medium grey = Orthocladiinae; light grey = Chironominae; white = Tanypodinae).

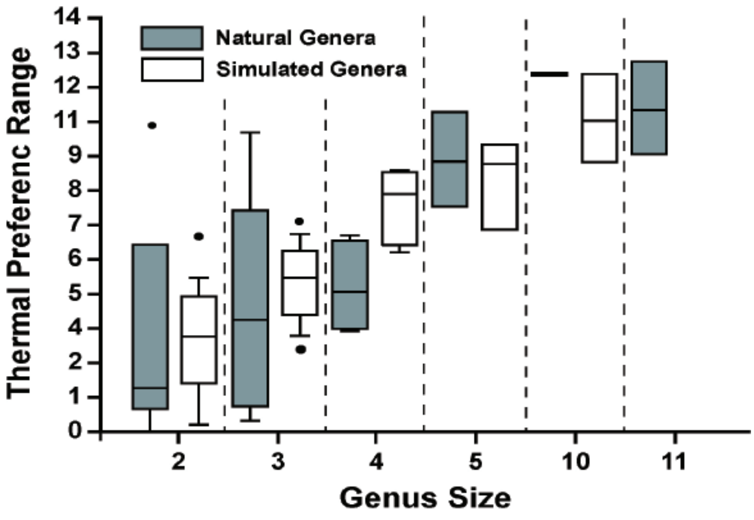

Fig. 3. Box plots of thermal preference ranges for natural and simulated genera of different sizes (middle line = median; upper and lower bounds of the box = 25th and 75th percentiles; whisker caps = 10th and 90th percentiles; circles = outliers).

DISCUSSION

Thermal preference patterns have been identified at the subfamily level, with Diamesinae, Prodiamesinae, and Orthocladiinae tending to be more cool water adapted while Chironominae and Tanypodinae are warmer water adapted (BECKETT, 1992; COFFMAN & DE LA ROSA, 1998). As predicted, Diamesinae and Orthocladiinae were more likely to emerge at cooler water temperatures while Chironominae and Tanypodinae were more likely to emerge at warmer temperatures. However, this pattern was not completely consistent as some genera emerged at temperatures different than most other genera in their respective subfamily (*e.g. Corynoneura*, *Micropsectra*). In general, these results suggest that thermal preferences are relatively rigid at the subfamily and genus levels and reflect the evolutionary history of higher taxonomic levels. The results from this study support the general thermal preference patterns observed in other studies; however, caution must be exercised as several taxa do not fit these predictions. Additional research will improve determination of thermal preferences and help make this information useful in biological monitoring and ecological studies.

Many factors determine the composition of an insect community in lotic habitats. At large scales, the regional species pool determines the potential species that can colonize a habitat. The community is further filtered by environmental characteristics and resources. Among these factors, temperature is likely a major determinant for many insect species as poikilotherms are limited to habitats with thermal regimes that meet their requirements for growth and development. Different thermal requirements in insects appear to help reduce competition among closely related taxa which are potentially utilizing similar resources. The reduction of competition implied by this would allow a greater number of species to be packed into a habitat and would therefore be an additional determinant of the species which can occur at a given site. Therefore, chironomid community composition in streams is a result of recruitment from the regional species pool and local environmental conditions which may be further refined by interspecific interactions.

In this study there was a clear pattern of increasing thermal preference range from smaller to larger genera (Fig. 3). Furthermore, simulated ranges calculated from genera with many species were greater than those from natural genera with two, three, and four species. There is considerable overlap for two and three species genera between natural and simulated genera, but this overlap is caused by four small, yet thermally heterogeneous, natural genera with unusually high thermal preference ranges. Five and ten species genera had different responses between natural and simulated genera; however, this response was possibly the result of the low number of genera with more than 5 species (n = 3). Although there were some inconsistencies in the pattern of increased thermal preference range in simulated genera, in general this pattern is evident suggesting that thermal partitioning is occurring in larger genera. Future work is needed to add more genera to these analyses which will increase the power of this investigation. However, based on these results we can conclude that genus size does influence emergence temperature range. As a result, we can assume that there are likely at least two factors influencing this pattern: 1) larger genera have greater thermal diversity simply by chance (*i.e.* more species results in a greater chance that there will be greater thermal diversity independent of species interactions) and 2) in larger genera increased thermal partitioning is occurring as a result of interspecific interactions.

Other factors such as disturbance may also be important in determining aquatic insect communities (CONNELL, 1978). For example, lotic habitats, especially SWD streams, are dynamic and expose insects to environmental variation through changing flow and temperature. These changing environmental characteristics can reduce potential competition and increase diversity (REICE, 1994). Besides thermal partitioning, resource partitioning can also reduce competition in co-occurring, closely-related aquatic insect species (*e.g.* KEIPER & FOOTE, 2000) and could also account for the overlap in emergence for some species. In addition, apparent thermal preferences may be secondary and the result of seasonal resource patterns. However, more detailed studies on the ecology and life history of these species is needed to identify potential interactions among these species.

Although most subfamilies and genera demonstrate predictable thermal preferences, at finer resolutions some have less typical thermal preferences. These results suggest that thermal preference is a relatively rigid characteristic within higher chironomid taxonomic groupings, but taxa with atypical preferences may reflect apomorphic characteristics. However, without detailed evolutionary and biogeographical information it is difficult to assess how thermal preferences evolved in these species. Thermal preference differences may also influence community composition by allowing some species to coexist by partitioning the habitat temporally; therefore, the evolution of different thermal preferences may be the result of interspecific interactions (*e.g.* competition). The results of this research do support the occurrence of temporal partitioning in the chironomid community in this SWD stream. Research is currently underway to include data from additional streams to improve thermal preference estimation and to give analyses greater power to elucidate thermal partitioning patterns among chironomid communities.

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