CHIRONOMUS Journal of Chironomidae Research No. 40, 2025: 37-63. Special Issue LCF Memorial.

MIDGES BELOW ZERO: A REVIEW OF HIBERNAL EMERGENCE OF CHIRONOMIDAE IN TEMPERATE REGIONS

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Abstract

The Chironomidae are one of several groups of aquatic insects with representatives that possess cold hardening strategies that allow pronounced hibernal activity, including species that complete their life and reproduce only during the coldest months of the year. Although these winter-active species are often ignored in aquatic studies, relatively recent research has demonstrated that these insects are not only interesting, but they can also be an important and diverse element of aquatic insect communities. This review synthesizes existing literature on winter-emerging Chironomidae, focusing largely on Holarctic species emerging from temperate streams that are at least partially ice-free throughout the winter season. We found that there are currently at least 215 chironomid taxa present during winter, predominated by Orthocladiinae (n = 127), Chironominae (n = 42) and Diamesinae (n = 35). Our review highlights cold hardening strategies, such as supercooling, that permit winter activity, and we also discuss growth and emergence for species that have been extensively studied, such as *Diamesa mendotae* Muttkowski. Winter-active species tend to be long-lived at cold temperatures, and we discuss how consequences of climate change, including warmer temperatures and reduced snowpack, may negatively impact certain winter-active species. Although there is a growing base of studies featuring winter-active species, our review demonstrates that research is largely restricted to a handful of localities, and autecology studies are limited to only select species. We emphasize the importance of extending field work into the winter season and expanding research on winter Chironomidae to a broader geographic range to better gauge species accounts and enhance our understanding of the importance of winter-emerging Chironomidae.

Introduction

Several aquatic insect groups include species that are active during the winter season in northern temperate regions of the Holarctic when air temperatures can be below 0°C (Lencioni 2004, Soszyńska 2004, Hågvar 2010, Soszyńska-Maj et al. 2016, Bouchard and Gelhaus 2020). These insects exhibit a myriad of physical, behavioral, ecological, and biochemical adaptations to survive freezing and subfreezing temperatures (≤0 °C) (Lee 1989, Block 1990, Oswood et al. 1991, Lencioni 2004, Danks 2008). Most aquatic insects are not active at temperatures below 0°C and have strategies for avoiding (e.g. migration, occupying protected microhabitats) or surviving (e.g. freeze tolerance, depression of supercooling point [SCP]) exposure to freezing temperatures. For example, many aquatic insects in temperate regions occupy or disperse to aquatic habitats that do not freeze in winter (e.g. deep waters and away from habitat margins) or they will burrow into benthic sediments or the hyporheic zone (Danks 2008). Other aquatic insects have the ability to survive freezing and may hibernate in frozen substrates. Additionally, certain aquatic insects can protect themselves from freezing by lowering their SCP. This strategy allows these species to remain active during winter because they do not need to enter hibernation. Among aquatic insects, select Diptera (e.g. Chironomidae, Limoniidae), Plecoptera, Trichoptera, and Ephemeroptera emerge from ice-free aquatic environments as active adults and can be observed walking or mating on the snow or occasionally flying short distances (Lencioni 2004, Bouchard et al. 2009, Hågvar 2010, Soszyńska-Maj et al. 2016, Bouchard and Gelhaus 2020, Anderson et al. 2022). This winter activity is often ignored or treated as a curiosity in aquatic studies, but relatively recent research has demonstrated that these insects can be taxonomically diverse and an important element of aquatic communities.

Although life during winter for ectothermic organisms comes with challenges, including cold and snowy environmental conditions, insects adapted to emerge during this season are afforded some benefits. Winter-emerging species likely encounter reduced risk of predation, as many potential predators are dormant or inactive (e.g. certain insectivorous herpetofauna, mammals, or predatory insects/invertebrates), have migrated (e.g. many bird species), or are active but have reduced metabolic requirements at low temperatures (e.g. fish). Given that relatively few aquatic insect species are adapted to winter development and emergence, competition is also reduced. Although winter is often viewed as an extreme time of year, in some ways it is no more harsh than other seasons. Insects emerging during other seasons often face significant daily air temperature fluctuations; although also true during winter, winter-emerging taxa may find refuge within the snowpack or near the air-water margin of spring-fed streams to buffer them from seasonal fluctuations (e.g. Hågvar 2010, Anderson et al. 2013). Additionally, larvae developing during winter may face reduced probability of flooding or drying events, which can alter habitat and food resources. Lastly, required habitats may be primarily available only during winter for some species. For example, Ferrington and Sæther (1987), describe certain intermittent streams which harbor populations of *Orthocladius (Orthocladius) ferringtoni* Soponis; streams harboring this species flow primarily from fall-spring, therefore, development can only occur over this period when suitable habitat is available. Thus, the cost for aquatic insects to employ successful strategies for surviving subfreezing temperatures can be offset by conditions that may be favorable during the winter months.

The fly family Chironomidae contains many winter-active representatives and is the largest, most diverse group of winter-active invertebrates studied thus far. Studies of winter-emerging Chironomidae are rare as compared to their summer counterparts; however, this is not due to the novelty of the phenomenon. Instead, as suggested 50 years ago by Jonsson and Sandlund (1975), this rarity is because of the dearth of entomological sampling that occurs during the winter season. Although rare in comparison to work during warmer seasons, the emphasis on winter entomological field research and focus on the importance of the findings has increased in recent years. Dr. Leonard Ferrington, Jr., who held long-term positions at both the University of Minnesota and the University of Kansas, championed a significant portion of the winter chironomid research in temperate habitats in recent years, driving or inspiring many research projects in both the Nearctic and Palearctic ecoregions.

This review synthesizes existing literature on winter-emerging Chironomidae, focusing largely on Holarctic species emerging from temperate streams that are at least partially ice-free throughout the winter season. We define winter-emerging as species observed to emerge from streams as adults from December through March. Our discussion is restricted primarily to seasonal, temperate ecosystems that experience freezing or subfreezing temperatures for a significant portion of the year but include discussion outside these areas where appropriate. We cover a suite of topics including the diversity of winter-emerging species, cold hardiness, emergence and growth patterns, longevity, behavior, and the ecological importance of winter emergence.

Diversity

Chironomidae contain over 5,000 species described across all continents including Antarctica and projections suggest up to 20,000 species exist worldwide (Ferrington and Berg 2019). Given the immense species-richness of the group, there is significant diversity when considering ecological adaptations and tolerances. In terms of environmental temperature, certain species are well adapted to extreme highs and occur in habitats such as thermal springs (Hayford et al. 1995) whereas others are cold adapted and can survive near and at subfreezing conditions (Kohshima 1984, Lee 1989, Lencioni 2004, Bouchard et al. 2006a, 2006b, Danks 2007). Chironomidae are thought to have evolved in upper reaches of cool, spring-fed mountain streams in temperate forest regions (Brundin 1966). Danks (1971) further deduced that these ancestral chironomids were cold-adapted given that most major genera include representative species exhibiting cold tolerance. Given this, it is not surprising that many species are known to withstand and even thrive in cold winter temperatures.

Across the 11 chironomid subfamilies and 22 nominal tribes, the Diamesinae, Prodiamesinae, Podonominae, and Orthocladiinae are considered most cold-tolerant (Bouchard 2007, Eggermont and Heiri 2012), although winter-emerging Podonominae are not yet known to the Holarctic. While recognized as somewhat less cold tolerant than Diamesinae and Prodiamesinae (Oliver 1971, Bouchard 2007, Bouchard and Ferrington 2008), Orthocladiinae generally comprise a larger percentage of winter taxa, due in-part to the immense species-richness of the subfamily (e.g. Coffman 1973, Rempel and Harrison 1987, Chou et al. 1999, Anderson et al. 2010, Anderson and Ferrington 2013, Soszyńska-Maj et al. 2016). The subfamilies Tanypodinae and Chironominae are also species rich but are more typical of warmer waters (Coffman and De La Rosa 1998).

However, these patterns do not always hold. Certain genera, such as the Chironominae genus *Micropsectra*, tend to emerge at cooler temperatures and are often present during winter (Table 1), whereas *Corynoneura* and *Parametriocnemus,* while also found in winter, are restricted to warmer temperatures than other winter-emerging orthoclads (e.g. Ferrington 2000, Bouchard and Ferrington 2008, Nyquist et al. 2020). This thermal partitioning may allow species to reduce competition between closely related taxa (Bouchard and Ferrington 2008).

Taxonomic composition and diversity of the winter chironomid community have also been shown to vary both longitudinally within a stream system and over the winter season, following predictable patterns. For example, Nyquist et al. (2020) found that taxonomic composition was variable within a 300m reach in a groundwater-dominated stream due to thermal heterogeneity between sites. Taxa such as *Corynoneura, Parametriocnemus,* and *Eukiefferiella* (Orthocladiinae)*,* were found near a spring source, which provided "winter warm" reaches in the stream. In contrast, *Orthocladius* and *Diamesa,* were found in cooler reaches. Cooler reaches also exhibited greater taxonomic diversity (Nyquist et al. 2020). Studies examining seasonal emergence follow similar patterns, with Diamesinae and Orthocladiinae emerging during the colder period of the winter season and orthoclads predominating throughout winter. Tanytarsini, Chironomini, and Tanypodinae species do not commonly emerge during the winter, but rather begin to emerge at the end of the winter season as temperatures begin to warm; many Diamesinae and Orthocladiinae taxa also follow this pattern (Coffman 1973, Boerger 1981, Chou et al. 1999, Ferrington 2000, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2013, Soszyńska-Maj et al. 2016).

We assessed the literature to document the diversity of winter-emerging Chironomidae found in the Holarctic. Although several cold-adapted taxa are known from glaciers/glacial-fed streams and polar or alpine regions during non-winter months as defined in this paper (e.g. Oliver 1968, Kohshima 1984, Lencioni 2004, Lencioni et al. 2008), our discussion of diversity is restricted to species emerging from December through March. However, certain references (e.g. Soszyńska-Maj et al. 2016) defined winter based on weather or snow cover and/or did not specify specific winter emergence periods. While some taxa from these studies may emerge predominantly in early spring, we include these taxa in our list of winter-active species because they were found to emerge within our defined winter period. We document evidence of emergence either as collections of adult chironomids, or as collections of pupal exuviae. Where species-level designations were not reported or could not be determined from the literature, we record the taxa to the highest defined taxonomic level (e.g. *Diamesa* spp. when multiple undistinguished species were presented or *Diamesa* sp. when one was presented). Each taxon was counted once for each associated region to obtain a conservative estimate of total number of winter-active taxa per region.

Our literature survey yielded 39 studies across the Holarctic that documented the presence of winter chironomid emergence. These records indicate at least 215 taxa present during the winter season (Table 1). Although we recognize that winter may not be the primary emergence period for many of the species recorded, these taxa are documented at low temperatures at some time during the winter period as we define in this paper. We anticipate that certain species that are currently incidental winter emergers may become more common as temperatures become warmer with climate change. The most common winter-active groups from our literature survey are Orthocladiinae (total taxa=127), Diamesinae (total taxa=35), and Tanytarsini (total taxa=28). Chironomini (total taxa=14), Tanypodinae (total taxa=8), and Prodiamesinae (total taxa=3) were also collected from various regions but were less common (Table 1). This pattern holds with what is reported in the literature with orthoclads typically documented as the most abundant (Coffman 1973, Anderson et al. 2010, Anderson and Ferrington 2013, Soszyńska-Maj et al. 2016) and Chironomini and Tanypodinae as the least winter-active subfamilies/tribes in Chironomidae (Coffman and De La Rosa 1998). Table 1 provides a comprehensive overview of these winter-active

Chironomidae, including locations they are known from and literature references.

Figure 1 highlights currently known winter chironomid diversity by region. As for many biodiversity efforts, documentation of winter-active Chironomidae is biased based on human artifacts related to deference for collecting biodiversity data in certain geographic regions (geographic bias), focusing on taxa that are commonly found or studied most often (taxonomic bias), collecting specimens when field work is optimal (temporal bias), or collecting taxa that are easy to see or find based on size or reproductive patterns (bias based on functional traits) (Meyer et al. 2015, Daru and Rodriguez 2023). Some bias may also be driven by public interest (Troudet et al. 2017), and by complex interactions among geographic accessibility and socio-economic factors (Meyer et al. 2015). Thus, the total number of taxa we report for various regions is not only a conservative estimate, but also only represents regions where studies have been conducted and where, most likely, chironomid researchers are located (Fig. 1). Our review also points to research voids, and regions where additional research focus would benefit. For example, Figure 1 shows that Minnesota and Kansas are known to have more than 40 winter-active chironomid taxa, whereas far fewer are documented from neighboring states/provinces. Given the significant amount of work completed in Minnesota and Kansas, led largely by Dr. Ferrington, it is perhaps not surprising that so many species are known in these areas. Additional research focus would undoubtedly yield far more taxa in surrounding areas.

The phenomenon of cryptic species, or biological groups that are morphologically near-identical, incapable of interbreeding, and genetically distinct (Pfenninger and Schwenk 2007), also suggests that the results presented here are conservative. Chironomidae are known to contain many cryptic

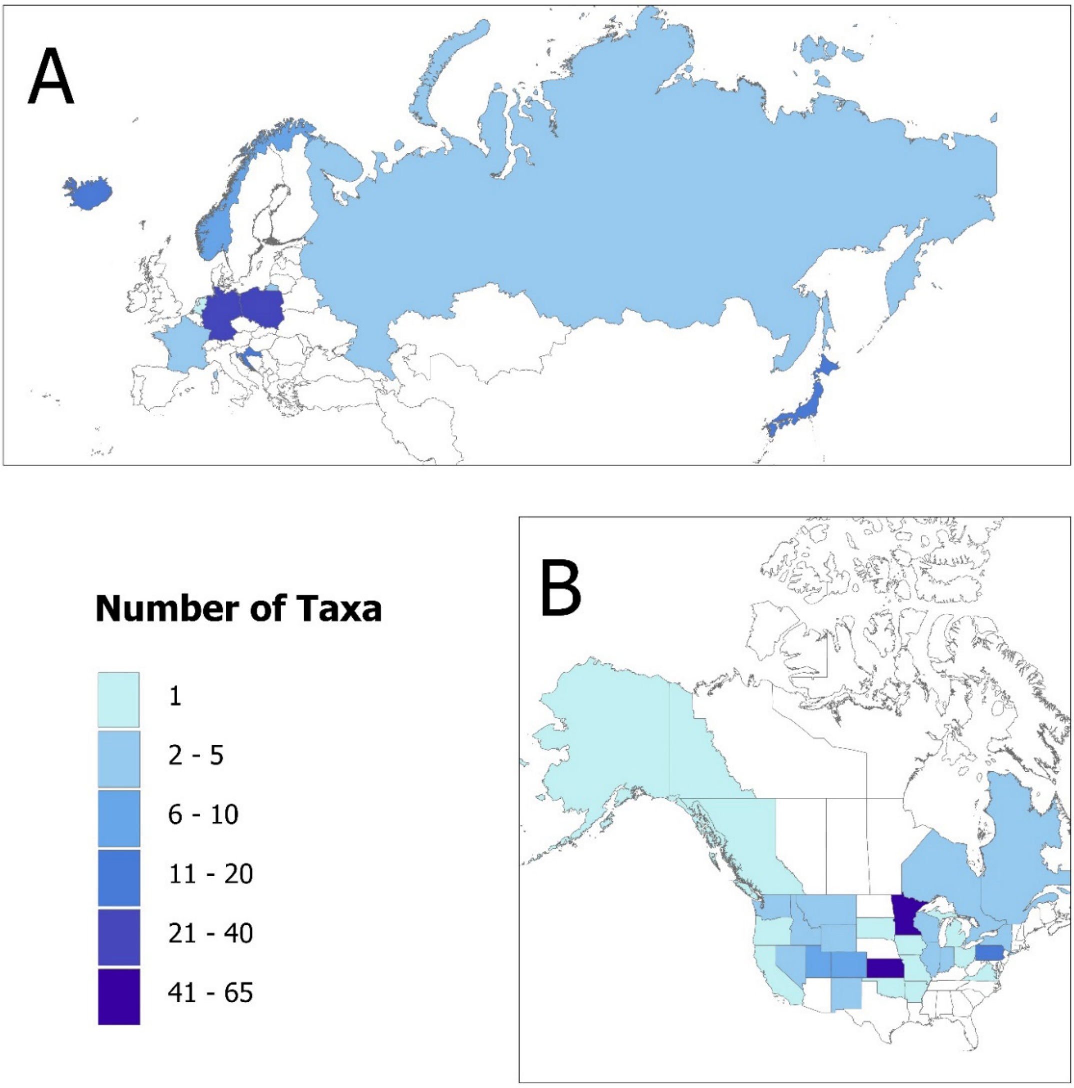

Figure 1. Distribution of known winter-emerging Chironomidae in the north-temperate Holarctic, with number of taxa currently known to specific localities. A. Palearctic region. B. Nearctic region.

Table 1. Taxa with representatives that emerge during winter. Locations of reported emergence and reference sources provided. Where species-level designations were not reported or could not be determined from the literature, we record the taxa to the highest defined taxonomic level (e.g. *Diamesa* spp. when multiple undistinguished species were presented or *Diamesa* sp. when one was presented). Asterisks (*) next to taxonomic names reflect species with junior synonyms; accepted names are used here, while a reference documenting the taxon utilizes a junior synonym.

Taxon	Location(s) Recorded	References
Orthocladiinae (127 taxa)		
Acricotopus lucens (Zetterstedt, 1850)	Crimea	Baranov and Ferrington 2013
Brillia bifida (Kieffer, 1909)*	Crimea, Croatia, Germany, Poland (lowlands)	Illies 1971, Ringe 1974, Siebert 1980, Baranov and Ferrington 2013, Soszyńska-Maj et al. 2016, Dorić et al. 2024
Brillia flavifrons (Johannsen, 1905)	USA: Minnesota	Bouchard 2007
Brillia retifinis Sæther, 1969	USA: Minnesota	Anderson and Ferrington 2012
Bryophaenocladius akiensis (Sasa, Shimomura & Matsuo, 1991)	Crimea	Baranov and Ferrington 2013
Bryophaenocladius sp.	Crimea	Baranov and Ferrington 2013
Cardiocladius fuscus Kieffer, 1924	Croatia	Dorić et al. 2024
Chaetocladius dentriforceps gr.	USA: Minnesota	Bouchard 2007, Anderson and Ferrington 2012
Chaetocladius dissipatus (Edwards, 1929)	Iceland	Nyquist 2022
Chaetocladius grandilobus Brundin, 1956	Poland (lowlands and mountains)	Soszyńska-Maj et al. 2016
Chaetocladius insolitus Caspers, 1987	Crimea	Baranov and Ferrington 2013
Chaetocladius laminatus Brundin, 1947	Germany, Norway, Poland (lowlands and mountains)	Lehmann 1971, Hågvar and Østbye 1973, Ringe 1974, Soszyńska-Maj et al. 2016
Chaetocladius longivirgatus Stur & Spies, 2011	Germany	Stur and Spies 2011
Chaetocladius nr. *melaleucus/dissipatus*	Iceland	Nyquist 2022
Chaetocladius perennis (Meigen, 1830)	Germany, Poland (lowlands)	Lehmann 1971, Soszyńska-Maj et al. 2016
Chaetocladius piger gr., sp.	Poland (lowlands and mountains), USA: Minnesota	Bouchard 2007, Anderson and Ferrington 2012, Soszyńska-Maj et al. 2016
Chaetocladius spp.	USA: Kansas, Minnesota	Kavanaugh 1984, Chou et al. 1999, Ferrington 2000, Ferrington 2007, Bouchard 2007, Anderson et al. 2010
Corynoneura lacustris Edwards, 1924	Crimea	Baranov and Ferrington 2013
Corynoneura lobata Edwards, 1924	Poland (mountains)	Soszyńska-Maj et al. 2016
Corynoneura spp.	USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Kavanaugh 1984, Chou et al. 1999, Ferrington 2000, Ferrington 2007, Bouchard 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Cricotopus (*Cricotopus*) *bicinctus* (Meigen, 1818)	Croatia	Dorić et al. 2024
Cricotopus annulator Goetghebuer, 1927	USA: Minnesota	Anderson and Ferrington 2012
Cricotopus spp.	USA: Kansas, Minnesota	Coler 1981, Kavanaugh 1984, Ferrington 2000, Ferrington 2007, Bouchard 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Cricotopus skirwithensis (Edwards, 1929)*	Croatia	Dorić et al. 2024
Cricotopus tremulus (Linnaeus, 1758)	USA: Minnesota	Anderson and Ferrington 2012
Cricotopus triannulatus (Macquart, 1826)	USA: Minnesota	Anderson and Ferrington 2012

Taxon	Location(s) Recorded	References
Cricotopus trifascia Edwards, 1929	USA: Minnesota, Poland (mountains)	Anderson and Ferrington 2012, Soszyńska-Maj et al. 2016
Diplocladius cultriger Kieffer, 1908	Germany, USA: Kansas	Ringe 1974, Chou et al. 1999, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Diplocladius sp.	USA: Minnesota, Pennsylvania	Coffman 1973, Bouchard 2007
Eukiefferiella brevicalcar (Kieffer, 1911)	Germany	Ringe 1974
*Eukiefferiella claripennis (*Lundbeck, 1898)	Crimea, Minnesota	Bouchard 2007, Anderson and Ferrington 2012, Baranov and Ferrington 2013
Eukiefferiella devonica (Edwards, 1929)	Germany	Ringe 1974
Eukiefferiella ilkleyensis (Edwards, 1929)	Crimea, USA: Minnesota	Bouchard 2007, Anderson and Ferrington 2012, Baranov and Ferrington 2013
Eukiefferiella minor (Edwards, 1929)	Iceland, Germany	Illies 1971, Ringe 1974, Siebert 1980, Nyquist 2022
Eukiefferiella gracei (Edwards, 1929)*	USA: Minnesota	Anderson and Ferrington 2012
Eukiefferiella spp.	USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Coler 1981, Kavanaugh 1984, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Heterotrissocladius marcidus gr.	USA: Minnesota	Anderson and Ferrington 2012
Heterotrissocladius sp.	USA: Kansas	Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Heterotrissocladius subpilosus gr.	USA: Minnesota	Nyquist et al. 2020
Hydrobaenus johannseni (Sublette, 1967)	USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Coler 1981, Bouchard 2007
Hydrobaenus kisosecundus Sasa & Kondo, 1991	Japan	Kondo and Sasa 1994
Hydrobaenus korneyevi (Baranov, 2011)*	Crimea	Baranov and Ferrington 2013
Hydrobaenus kondoi Sæther, 1989	Japan	Kondo and Sasa 1994
Hydrobaenus nr. *spinnatus*	USA: Kansas	Chou et al. 1999
Hydrobaenus pilipes (Malloch, 1915)	USA: Kansas	Coler 1981, Chou et al. 1999
Hydrobaenus pilipodex Sæther , 1976	USA: Kansas	Chou et al. 1999
Hydrobaenus simferopolus Moubayed-Breil & Baranov, 2018	Crimea	Moubayed-Breil and Baranov 2018
Hydrobaenus spp.	USA: Kansas	Kavanaugh 1984, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Hydrosmittia kisotriangulata Sasa & Kondo 1993*	Japan	Kondo & Sasa 1994
Limnophyes borealis Goetghebuer, 1933	Canada: British Columbia	Cranston and Oliver 1988
Limnophyes cf. *pumilio* (Holmgren, 1869)	USA: Minnesota	Nyquist et al. 2020
Limnophyes gurgicola (Edwards, 1929)	Croatia	Dorić et al. 2024
Limnophyes minimus (Meigen, 1818)	Crimea	Baranov and Ferrington 2013
Limnophyes natalensis (Kieffer, 1914)	Poland (mountains)	Soszyńska-Maj et al. 2016
Limnophyes pentaplastus (Kieffer, 1921)	Crimea, Poland (mountains)	Baranov and Ferrington 2013, Soszyńska-Maj et al. 2016
Limnophyes prolongatus (Kieffer, 1921)	Germany	Illies 1974, Ringe 1974

Taxon	**Location(s) Recorded**	**References**
Limnophyes sp.	USA: Kansas, Minnesota	Kavanaugh 1984, Chou et al. 1999, Ferrington 2000, Ferrington 2007, Bouchard 2007, Anderson et al. 2010
Limnophyes spinigus Sæther, 1991	Crimea	Baranov and Ferrington 2013
Metriocnemus albolineatus (Meigen, 1818)	Poland (lowlands)	Soszyńska-Maj et al. 2016
Metriocnemus eurynotus (Holmgren, 1883)	Crimea, Iceland	Baranov and Ferrington 2013, Nyquist 2022
Metriocnemus fuscipes (Meigen, 1818)	Germany	Ringe 1974
Metriocnemus martinii Thienemann, 1921*	Croatia	Dorić et al. 2024
Metriocnemus picipes (Meigen, 1818)	Poland (mountains)	Soszyńska-Maj et al. 2016
Metriocnemus spp.	Germany, USA: Kansas	Illies 1974, Kavanaugh 1984, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Nanocladius crassicornis Sæther, 1977	USA: Kansas	Coler 1981
Nanocladius rectinervis (Keiffer, 1911)	USA: Minnesota	Nyquist et al. 2020
Nanocladius sp.	USA: Kansas	Coler 1981, Ferrington 2007, Anderson et al. 2010
Nanocladius spiniplenus Sæther, 1977	USA: Minnesota	Nyquist et al. 2020
Oliveridia hugginsi Ferrington & Sæther, 1987	USA: Kansas	Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Orthocladiinae sp.	Poland (lowlands)	Soszyńska-Maj et al. 2016
Orthocladiinae spp.	Poland (mountains), USA: Kansas, Pennsylvania	Coffman 1973, Ferrington 2007, Anderson et al. 2010, Soszyńska-Maj et al. 2016
Orthocladius (Euorthocladius) abiskoensis Thienemann & Krüger, 1937	USA: Kansas	Kavanaugh 1984, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Orthocladius (Euorthocladius) rivicola Kieffer, 1911	USA: Kansas, Minnesota	Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Orthocladius (Euorthocladius) rivulorum Kieffer, 1909	USA: Kansas, Minnesota	Kavanaugh 1984, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Orthocladius (Euorthocladius) sp.	USA: Kansas, Pennsylvania	Coffman 1973, Coler 1981
Orthocladius (Euorthocladius) thienemanni Kieffer & Thienemann, 1906	Germany, Poland (lowlands), USA: Kansas	Lehmann 1971, Siebert 1980, Chou et al. 1999, Ferrington 2000, Ferrington 2007, Anderson et al. 2010, Soszyńska-Maj et al. 2016
Orthocladius (Orthocladius) appersoni Soponis, 1977	Canada: Yukon Territory	Soponis 1977
Orthocladius (Orthocladius) cf. *lignicola* Kieffer, 1915	Germany, USA: Pennsylvania	Coffman 1973, Ringe 1974
Orthocladius (Orthocladius) ferringtoni Soponis, 1983	USA: Kansas	Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Orthocladius (Orthocladius) frigidus (Zetterstedt, 1838)	Germany, Japan, Poland (mountains), USA: Minnesota	Illies 1971, Lehmann 1971, Ringe 1974, Siebert 1980, Kondo and Sasa 1994, Bouchard 2007, Anderson and Ferrington 2012, Soszyńska-Maj et al. 2016
Orthocladius (Orthocladius) mallochi Kieffer, 1919	USA: Kansas, Minnesota	Ferrington 2000, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Orthocladius (Orthocladius) manitobensis Sæther, 1969	USA: Minnesota	Anderson and Ferrington 2012

Taxon	Location(s) Recorded	References
Orthocladius (Orthocladius) nigritus Malloch, 1915	USA: Kansas, Minnesota, Pennsylvania, Utah, Virginia	Soponis 1977, Chou et al. 1999, Bouchard 2007, Anderson and Ferrington 2012
Orthocladius (Orthocladius) obumbratus Johannsen, 1905	USA: Illinois, Iowa, Kansas, Minnesota, Pennsylvania, South Dakota	Soponis 1977, Chou et al. 1999, Bouchard 2007, Anderson and Ferrington 2012
Orthocladius (Orthocladius) oliveri Soponis, 1977	USA: Arkensas, Illinois, Indiana, Minnesota, Missouri, New York, Oklahoma, Oregon	Soponis 1977, Bouchard 2007
Orthocladius (Orthocladius) spp.	USA: Kansas, Pennsylvania	Coffman 1973, Coler 1981, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010
Orthocladius (Orthocladius) vaillanti Langton & Cranston 1991	USA: Minnesota	Anderson and Ferrington 2012
Orthocladius excavatus Brundin, 1947	Germany	Ringe 1974
Orthocladius glabripennis (Goetghebuer, 1921)	Crimea, Japan	Kondo and Sasa 1994, Baranov and Ferrington 2013
Orthocladius kanii (Tokunaga, 1939)	Japan	Kondo and Sasa 1994
Orthocladius rhyacobius Kieffer, 1911	Poland (mountains)	Soszyńska-Maj et al. 2016
Orthocladius saxicola Kieffer, 1911	Germany	Illies 1971
Orthocladius spp.	Crimea, USA: Minnesota	Anderson and Ferrington 2012, Baranov and Ferrington 2013
Orthocladius tamarutilus Sasa, 1981	Japan	Kondo and Sasa 1994
Orthocladius wetterensis Brundin, 1956	Germany, Poland (lowlands, mountains)	Lehmann 1972, Soszyńska-Maj et al. 2016
Parachaetocladius abnobaeus (Wülker, 1959)	USA: Kansas	Cranston and Oliver 1988
Parachaetocladius lenferringtoni Bouchard, Namayandeh & Hudson 2024	USA: Kansas, Minnesota	Bouchard et al. 2024
Parachaetocladius spp.	USA: Minnesota, Pennsylvania	Coffman 1973, Bouchard 2007
Paracladius conversus (Walker, 1856)	Crimea	Baranov and Ferrington 2013
Paracricotopus niger (Kieffer, 1913)	Poland (mountains)	Soszyńska-Maj et al. 2016
Parakiefferiella spp.	USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Coler 1981, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Parakiefferiella bathophila (Kieffer, 1912)*	Japan	Kondo and Sasa 1994
Parametriocnemus lundbeckii (Johannsen, 1905)	Kansas	Koler 1981
Parametriocnemus spp.	Croatia, USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Kavanaugh 1984, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012, Nyquist et al. 2020, Dorić et al. 2024
Parametriocnemus stylatus (Spärck, 1923)	Crimea, Croatia	Baranov and Ferrington 2013, Dorić et al. 2024
Paraphaenocladius impensus contractus (Walker, 1856)	Crimea	Baranov and Ferrington 2013
Paraphaenocladius sp.	USA: Kansas	Coler 1981, Kavana 1984
Paratrissocladius excerptus (Walker, 1856)	Poland (lowlands)	Soszyńska-Maj et al. 2016

Taxon	Location(s) Recorded	References
Psectrocladius yunoquartus Sasa, 1984	Japan	Kondo and Sasa 1994
Pseudorthocladius sp.	Crimea	Baranov and Ferrington 2013
Pseudosmittia forcipatus (Goetghebuer, 1921)	USA: Kansas	Chou et al. 1999
Rheocricotopus (*Psilocricotopus*) *atripes* (Kieffer, 1913)	Croatia	Dorić et al. 2024
Rheocricotopus fuscipes Kieffer, 1909	Germany, Poland (mountains)	Ringe 1974, Soszyńska-Maj et al. 2016
Rheocricotopus sp.	USA: Kansas	Ferrington 2007, Anderson et al. 2010
Smittia aterrima (Miegen, 1818)*	Japan, Poland (mountains)	Kondo and Sasa 1994, Soszyńska-Maj et al. 2016
Smittia stercoraria Rossaro & Lencioni, 2000	Poland (lowlands)	Soszyńska-Maj et al. 2016
Stilocladius sp.	USA: Minnesota	Bouchard 2007
Thienemannia gracilis Kieffer, 1909	Croatia, Germany, Poland (mountains)	Ringe 1974, Soszyńska-Maj et al. 2016, Dorić et al. 2024
Thienemannia sp.	Poland (mountains)	Soszyńska-Maj et al. 2016
Thienemanniella clavicornis (Kieffer, 1911)	Crimea	Baranov and Ferrington 2013
Thienemanniella obscura Brundin, 1947	Germany	Ringe 1974
Thienemanniella spp.	USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Kavanaugh 1984, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Thienemanniella vittata (Edwards, 1924)	Crimea, Croatia	Baranov and Ferrington 2013, Dorić et al. 2024
Thienemanniella xena (Roback, 1957)	USA: Minnesota	Bouchard 2007
Trissocladius brevipalpis Kieffer & Thienemann, 1908	Poland (lowlands)	Soszyńska-Maj et al. 2016
*Tvetenia bavarica (*Goetghebuer, 1934)*	Germany	Siebert 1980
Tvetenia spp.	USA: Kansas, Minnesota	Kavanaugh 1984, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Prodiamesinae (3 taxa)		
Odontomesa fulva (Kieffer, 1919)	USA: Minnesota	Bouchard 2007, Anderson and Ferrington 2012
Odontomesa sp.	USA: Kansas	Ferrington 2007, Anderson et al. 2010
Prodiamesa olivacea (Meigen, 1818)	Poland (lowlands), USA: Minnesota	Bouchard 2007, Anderson and Ferrington 2012, Soszyńska-Maj et al. 2016, Nyquist et al. 2020
Diamesinae (35 taxa)		
Diamesa aberrata Lundbeck, 1898	Iceland	Nyquist 2022
Diamesa ancysta Roback, 1959	USA: Colorado, Idaho, Montana, Nevada, Utah, Washington	Hansen and Cook 1976
Diamesa arctica (Boheman, 1865)*	USA: Utah	Young, 1964
Diamesa bertrami Edwards, 1935	Iceland	Nyquist 2022
Diamesa bohemani Goetghebuer, 1932	Iceland	Nyquist 2022
Diamesa cheimatophila Hansen, 1976	USA: New York, Pennsylvania	Hansen and Cook 1976, Ferrington and Masteller 2015
Diamesa chiobates Hansen, 1976	USA: Minnesota, Wisconsin	Hansen and Cook 1976

Taxon	**Location(s) Recorded**	**References**
Diemesa cinerella Meigen, 1835	Germany, Poland (mountains)	Ringe 1974, Siebert 1980, Soszyńska-Maj et al. 2016
Diamesa davisi Edwards, 1933	USA: Utah, Wyoming	Hansen and Cook 1976
Diamesa davisi gr.	USA: Colorado	Hermann et al. 1987
Diamesa garretti Sublette & Sublette, 1965	USA: Colorado, Idaho	Hansen and Cook 1976, Hermann et al. 1987
Diamesa hamaticornis Kieffer, 1924	Germany, Poland (mountains)	Illies 1971, Lehmann 1971, Ringe 1974, Soszyńska-Maj et al. 2016
Diamesa heteropus (Coquillett, 1905)	USA: Alaska, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, Washington	Hansen and Cook 1976
Diamesa incallida (Walker, 1856)	Iceland, USA: Wyoming	Hansen and Cook 1976, Nyquist 2022
Diamesa insignipes Kieffer, 1908*	Germany, Poland (mountains), USA: Wyoming	Illies 1971, Lehmann 1971, Ringe 1974, Hansen and Cook 1976, Soszyńska-Maj et al. 2016
Diamesa latitarsis (Goetghebuer, 1921)	Iceland, Norway, Poland (mountains), Pyranees	Serra-Tosio, 1972, Jonsson and Sadlund 1975, Soszyńska-Maj et al. 2016, Nyquist 2022
Diamesa leona Roback, 1957*	Poland (mountains), Russia, USA: Colorado, Idaho, Montana, Nevada, New Mexico, Utah, Washington	Hansen & Cook 1976, Makarchenko 1985, Hermann et al. 1987, Giłka et al. 2013, Soszyńska-Maj et al. 2016, Makarchenko et al. 2022
Diamesa leoniella Hansen, 1976	USA: California, Utah	Hansen and Cook 1976
Diamesa mendotae Muttkowski, 1915	USA: Minnesota, Wisconsin	Hansen and Cook 1976, Mazack 2013, Durnin 2021
Diamesa nivoriunda (Fitch, 1847)	Canada: Ontario, Quebec, USA: Indiana, Minnesota, New York, Wisconsin	Hansen and Cook 1976, Durnin 2021
Diamesa spinacies Sæther, 1969	USA: Idaho, Utah	Hansen and Cook 1976
Diamesa spp.	USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Kavanaugh 1984 Ferrington 2000, Ferrington 2007, Bouchard 2007, Anderson et al. 2010, Anderson and Ferrington 2012, Nyquist et al. 2020
Diamesa thomasi Serra-Tosio, 1970	Croatia	Baranov et al. 2013
Diamesa tonsa (Haliday, 1856)*	Germany, Norway, Poland (mountains)	Lehmann 1971, Jonsson and Sandlund 1975, Soszyńska-Maj et al. 2016
Diamesa tsutsuii Tokunaga, 1936	Russia (Former USSR regions), Japan	Makarchenko 1985, Makarchenko 2023
Diamesa vockerothi Hansen, 1976	Canada: Ontario, Quebec	Hansen and Cook 1976
Diamesa zernyi Edwards, 1933	Iceland	Nyquist 2022
Pagastia sp.	USA: Minnesota	Mazack 2013
Pagastia partica (Roback, 1957)	USA: Colorado	Hermann et al. 1987
Potthastia sp.	USA: Kansas, Pennsylvania	Coffman 1973, Coler 1981, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Prodiamesa olivacea (Meigen, 1818)	Germany	Lehmann 1971
Pseudodiamesa branickii (Nowicki, 1873)	Iceland, Norway, Poland (mountains), USA: Colorado	Hågvar and Østbye 1973, Hermann et al. 1987, Soszyńska-Maj et al. 2016, Nyquist 2022

Taxon	Location(s) Recorded	References
Pseudodiamesa nivosa (Goetghebuer, 1928)	Iceland, Norway	Willassen 2011, Nyquist 2022
Sympotthastia sp.	USA: Kansas	Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Chironomini (14 taxa)		
Biwatendipes motoharui Tokunaga, 1965	Japan	Kondo and Sasa 1994
Chironomus nipponensis Tokunaga, 1940	Japan	Kondo and Sasa 1994
Chironomus riparius Meigen, 1804	USA: Kansas	Coler 1981
Chironomus spp.	USA: Kansas	Coler 1981, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Dicrotendipes fumidus (Johannsen, 1905)	USA: Kansas, Minnesota	Ferrington 2000, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Dicrotendipes nervosus (Staeger, 1839)	Crimea	Baranov and Ferrington 2013
Dicrotendipes sp.	USA: Kansas	Kavanaugh 1984
Microtendipes sp.	USA: Kansas	Coler 1981
Paracladopelma sp.	USA: Kansas	Coler 1981
Phaenopsectra sp.	USA: Minnesota	Bouchard 2007
Polypedilum trigonum Townes, 1945	USA: Minnesota	Anderson and Ferrington 2012
Polypedilum sp.	USA: Kansas	Anderson et al. 2010, Ferrington 2000, Ferrington 2007
Stictochironomus sticticus (Fabricius, 1781)*	Japan	Kondo and Sasa 1994
Stictochironomus spp.	USA: Kansas, Minnesota	Coler 1981, Kavanaugh 1984, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012
Tanytarsini (28 taxa)		
Cladotanytarsus atridorsum Kieffer, 1924	Crimea	Baranov and Ferrington 2013
Micropsectra apposita (Walker, 1856)*	Crimea, Croatia, USA: Minnesota	Anderson and Ferrington 2012, Baranov and Ferrington 2013, Dorić et al. 2024
Micropsectra atrofasciata (Kieffer, 1911)	Crimea, France, Germany, Japan	Ringe 1974, Siebert 1980, Stur and Ekrem 2006, Baranov and Ferrington 2013
Micropsectra attenuata Reiss, 1969	USA: Minnesota	Anderson and Ferrington 2012
Micropsectra bavarica Stur & Ekrem, 2006	France, Poland (mountains)	Stur and Ekrem 2006, Soszynska-Maj et al. 2016
Micropsectra bidentata (Goetghebuer, 1921)	Germany	Siebert 1980
Micropsectra dives gr. sp.	USA: Pennsylvania	Coffman 1973
Micropsectra geminata Oliver & Dillon, 1994	USA: Minnesota, Ohio	Oliver and Dillon 1994, Nyquist et al. 2020
Micropsectra junci (Meigen, 1818)	Germany, Poland (lowlands and mountains)	Siebert 1980, Soszynska-Maj et al. 2016
Micropsectra klinki Stur & Ekrem, 2006	Netherlands	Stur and Ekrem 2006
Micropsectra longicrista Stur & Ekrem, 2006	Germany	Stur and Ekrem 2006
Micropsectra nigripila (Johannsen, 1905)	Canada: Ontario, USA: Minnesota	Oliver and Dillon 1994, Bouchard 2007, Anderson and Ferrington 2012
Micropsectra notescens (Walker, 1856)	Poland (mountains)	Soszynska-Maj et al. 2016
Micropsectra pallidula (Meigen, 1830)	Croatia	Dorić et al. 2024
Micropsectra polita (Malloch, 1919)	USA: Minnesota	Bouchard 2007, Anderson and Ferrington 2012

Taxon	**Location(s) Recorded**	**References**
Micropsectra spp.	Germany, USA: Kansas, Minnesota, Pennsylvania	Coffman 1973, Ringe 1974, Coler 1981, Kavanaugh 1984, Chau et al. 1999, Ferrington 2000, Bouchard 2007, Ferrington 2007, Anderson et al. 2010, Anderson and Ferrington 2012, Nyquist et al. 2020
Micropsectra subletteorum Anderson, Stur, & Ekrem, 2013	USA: Minnesota	Anderson et al. 2013, Nyquist et al. 2020
Paratanytarsus sp. 1 *laccophilus* gr.	USA: Minnesota	Nyquist et al. 2020
Paratanytarsus sp. 2 *inopertus* gr.	USA: Minnesota	Nyquist et al. 2020
Paratanytarsus spp.	USA: Kansas	Coler 1981, Kavanaugh 1984, Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Rheotanytarsus curtistylus (Goetghebuer, 1921)	Croatia	Dorić et al. 2024
Rheotanytarsus distinctissimus (Brundin, 1947)	USA: Minnesota	Anderson and Ferrington 2012
Rheotanytarsus sp.	USA: Kansas	Kavanaugh 1984
Tanytarsini sp.	USA: Pennsylvania	Coffman 1973
Tanytarsus arduennensis Goetghebuer, 1922	Croatia	Dorić et al. 2024
Tanytarsus nearcticus Butler, 2000	USA: Minnesota	Anderson and Ferrington 2012
Tanytarsus spp.	USA: Kansas	Ferrington 2000, Ferrington 2007, Anderson et al. 2010
Tanytarsus yunosecundus Sasa, 1984	Japan	Kondo and Sasa 1994
Tanypodinae (8 taxa)		
Ablabesmyia (*Ablabesmyia*) *longistyla* Fittkau, 1962	Croatia	Dorić et al. 2024
Ablabesmyia spp.	USA: Kansas	Coler 1981
Conchapelopia rurika Roback, 1957	USA: Kansas	Coler 1981
Conchapelopia sp.	Croatia	Chou et al. 1999, Ferrington 2007, Dorić et al. 2024
Conchapelopia flavifrons (Johannsen, 1905)*	USA: Kansas	Kavanaugh 1984
Psectrotanypus dyari (Coquillett, 1902)	USA: Kansas	Coler 1981
Zavrelimyia sinuosa (Coquillett, 1905)	USA: Kansas, Minnesota	Coler 1981, Kavanaugh 1984, Ferrington 2000, Anderson et al. 2010, Anderson and Ferrington 2012
Zavrelimyia sp.	USA: Kansas	Coler 1981

species and studies suggest that the most accurate identifications include morphological characteristics and molecular techniques used in parallel (Anderson et al. 2013, Montagna et al. 2016, Lin et al. 2018, Makarchenko et al. 2018). For example, Anderson et al. (2013) described three cryptic *Micropsectra* species in spring-fed streams of the Driftless Area of southeastern Minnesota, USA including one known to emerge during winter (*M. subletteorum* Anderson, Stur, & Ekrem) using mitochondrial and nuclear DNA. Additional research in this region by Durnin (2021) suggested that winter-emerging *Diamesa nivoriunda* (Fitch) may contain two or more cryptic species and recommends that testing for reproductive compatibility and further examination of habitat requirements would likely support these results. Stable environmental conditions promote consistent selective pressures whereby organisms become selectively constrained in morphology (Fišer et al. 2018). Spring-fed streams often provide consistent, stable conditions because of the constant input of thermally and chemically stable groundwater (Williams and Vondracek 2010), leading to constant selective pressure. These environments are also often geographically isolated, which may contribute to speciation and the presence of cryptic species (Murphy et al. 2008). As we show here, many winter-emerging chironomids are found in spring-fed streams with recent studies discovering cryptic diversity in these habitats. It is likely that ongoing research will identify additional cryptic species.

Cold Hardiness

Cold hardiness is the ability of an organism to survive at low temperatures. Two different cold-hardiness strategies are observed in aquatic insects, which permit survival at subfreezing temperatures: freeze tolerance and freeze avoidance. Freeze-tolerant insects can raise and control the SCP of haemolymph using ice-nucleating agents (Lencioni 2004), which allows these insects to slow and control the formation of ice crystals within their bodies to avoid damaging tissues. Freeze avoidant species are unable to survive freezing of their haemolymph and have attributes or mechanisms to avoid the freezing of their tissues including lowering their SCP, melanism, increased hairiness, reduced wing size, cocoon construction, and seeking microhabitats that do not freeze (Lencioni 2004). Depending on the habitat, life stage, and life history, different strategies are observed in aquatic insects to survive and in some cases, to remain active when air temperatures are below 0 °C.

Considering Chironomidae are the most widespread and commonly observed winter-active insect family, it is not surprising that some species have been demonstrated to be very cold hardy. Both freeze tolerance and freeze avoidance strategies are documented in the Chironomidae; however, only freeze avoidance is observed in adults, whereas both freeze tolerance and avoidance are observed in larvae. Cold hardiness strategies of the egg and pupal stages are poorly known. Freeze tolerance is most often observed in diapausing Chironomidae larvae in habitats that freeze, such as wetlands, small streams, and the margins of lakes and rivers (Lencioni 2004, Danks 2008), but this strategy has also been documented in larvae from habitats that do not freeze (Bouchard et al. 2006b). Most larvae have not been tested for freeze tolerance, so it is unknown how widespread this ability may be in Chironomidae larvae. Although freeze avoidance is observed in both larvae and adults, specific mechanisms may differ between life stages. Most freeze avoidant larvae seek habitats that do not freeze (e.g. deep lakes, large streams, groundwater fed streams, springs, hyporheic zones; Lencioni 2004). Although freeze-avoidant larvae may diapause in protected habitats, many also remain active during the winter if conditions are suitable. Adult Chironomidae are not known to diapause and many winter-active species may have morphological adaptations (e.g. melanism, increased hairiness) or seek protected microhabitats to avoid freezing. However, an interesting strategy to avoid freezing has been studied in several winter-active midge adults. These species lower their SCP (i.e. the temperature at which they freeze) through the production of antifreezes and thermal hysteresis proteins (Lencioni 2004, Lencioni et al. 2015). The diversity of cold hardiness strategies observed in different life stages and species in Chironomidae demonstrate how well adapted this group is for surviving and thriving in a variety of winter habitats.

Although the ability of many Chironomidae species to diapause as larvae and survive subfreezing temperatures is a fascinating and productive area of research, observations of adult flies in winter habitats are particularly intriguing, given their ability to maintain activity in sub-freezing environments. Many winter-active species are morphologically specialized due to adaptations for surface mating such as reduced antennae, enlarged hypopygium, or wing reduction (e.g. Hansen and Cook 1976, Ferrington and Sæther 1987). In addition, it is unusual for ectothermic species to maintain activity at subzero air temperatures which raises questions regarding how and why these species are active in the winter. These flies are often considered an oddity, but more recent research has indicated that winter activity may be a beneficial strategy in some Chironomidae species. In temperate and high elevation habitats, detailed research has focused on the genus *Diamesa*. Members of this genus are commonly observed in the winter and are often active at temperatures below freezing and are also known to fly at subfreezing temperatures (Young 1969, Hågvar and Østbye 1973). For example, *Diamesa mendotae* Muttkowski is commonly found on snow near groundwater-dominated streams during the winter indicating that winter activity is an integral part of their life cycle, and these winter-active individuals are not “leakage” from the main population (see labile life cycle hypothesis; Ferrington et al. 2010). Associated with observations of adult activity at low temperatures, research on *D. mendotae* has demonstrated that this species can greatly lower its SCPs (-21.6 °C; Bouchard et al. 2006a). The ability to survive low temperatures in a winter-active insect has interesting implications such as increasing the life span of these insects, and with that, the likelihood of locating a mate (Bouchard et al. 2006a). This behavior may be particularly important in habitats where adults are unable to swarm if temperatures are too cool (see section on Longevity and Behavior). A longer life span may be beneficial in surface-mating species because mate searching may require more time than in aerial swarming species and periods of poor weather conditions (e.g. torpor inducing temperatures, high winds) could also lengthen the period between emergence and mating. The ability to survive and remain active at low, subfreezing air temperatures allows species, such as *D. mendotae* to successfully occupy winter habitats and may contribute to their importance in these habitats.

The ability to lower SCPs may be widespread in adult Chironomidae; but has not been extensively studied. Among Chironomidae, Diamesinae are most associated with adult activity at subzero temperatures, but many other subfamilies are also observed in the fall, winter, or spring in temperate habitats where subzero air temperatures are possible (see Diversity section). Although adults of other subfamilies are less likely to be observed at subzero temperatures, there is evidence that they may also have low SCPs. For example, 48 adult midges from several different subfamilies and tribes (Prodiamesinae, Orthocladiinae, Tanytarsini, and Chironomini) collected from a Minnesota stream and a lake in May had average SCPs ranging from -26.9 to -11.0 °C (R.W. Bouchard, Jr., unpublished data). One genus (*Odontomesa*: SCP = -26.1 °C [n = 12]) had an average SCP lower than that of *Diamesa mendotae* (-21.6 °C; Bouchard et al. 2006a) and two genera were only slightly higher than *D. mendotae*: *Stictochironomus*: -20.5 °C (n=4); *Micropsectra*: -20.7 °C (n=7)). These genera are often observed emerging at relatively low temperatures (Bouchard 2007), whereas other genera with higher SCPs (e.g. *Parametriocnemus*, *Chironomus*, *Dicrotendipes*, *Paratendipes*, *Polypedilum*; SCPs -17.9 to -11.7 °C) are less commonly observed emerging at low temperatures. Interestingly, aquatic insects from other families and orders observed from similar Minnesota habitats during winter and early spring have higher SCPs (e.g. *Allocapnia* [Bouchard et al. 2009] and *Phantolabis* [Bouchard and Gelhaus 2020]). Given that Chironomidae are thought to have evolved in cold habitats (Brundin 1966), cold hardiness may be an ancestral trait of the family. Why this ability has apparently been retained in species that are not frequently exposed to subzero temperatures is not clear, although in temperate, polar, and high-altitude regions there may be an evolutionary advantage as low temperatures are possible during the period of adult emergence. The retention of physiological mechanisms associated with cold hardiness may also be adaptive as they can serve other purposes such as resistance to desiccation (Danks 2000). Although only a small fraction of winter-active chironomids has been studied in detail, available research demonstrates that the ability to survive low temperatures is widespread within the family and deserves additional study.

Growth patterns and emergence of winter-active Chironomidae

In temperate regions, we can identify two main habitat types from which winter-active insects emerge: groundwater-fed habitats and surface water-fed habitats. There are gradients between these two types of habitats, but habitats with large emergences of winter-active chironomids are typically not covered with surface ice throughout the winter and water temperatures remain high enough for larval growth and development (Bouchard and Ferrington 2009). In surface water-fed habitats in high latitudes, aquatic habitats are frozen or water temperatures are near 0 °C through much of the winter and most emergence will not occur until the spring thaw, although there may be some limited emergence through cracks or small openings in the ice (Coffman 1973, Hansen and Cook 1976, Herrmann et al. 1987). Large emergences of winter-active midges from surface water-fed habitats occur at lower latitudes where winter air temperatures are high enough to keep the habitat ice free. However, even if ice cover is limited during the winter, water temperatures in these temperate habitats can be low, slowing the growth and developmental rate of chironomid larvae (Nolte and Hoffman 1992, Bouchard and Ferrington 2009, Schütz and Füreder 2019). Regardless, some chironomids are known to successfully use surface water-fed streams in the winter (Ferrington 2000). In contrast, groundwater-fed streams in the winter create a highly suitable habitat for cold stenothermic species as groundwater inputs provide a thermally buffered habitat, yielding ideal water temperatures for growth and development throughout winter. However, even if water temperatures are suitable, the adults of these species, especially those at higher latitudes, may then be challenged by low air temperatures when they emerge.

Summer poses a different challenge for cold-adapted chironomids in temperate regions. In most habitats, the larvae of these cold stenothermic species presumably aestivate in hyporheic zones during warmer periods (Lencioni 2004). Less commonly, habitats that are sufficiently buffered by groundwater may allow winter-active species to continuously grow throughout a significant portion of the year. For example, multiple species of *Diamesa,* including *D. cheimatophila* Hansen, *D. mendotae,* and *D. nivoriunda* are reported to emerge from September to May (Hansen and Cook 1976). Yet, detailed life histories for most midge species are unknown, and the exact habitat for cold stenothermic species during the summer in temperate regions is not well known in Chironomidae.

The larvae of chironomids with winter-active adults are often cold stenothermic and are limited to habitats with cool water temperatures, including habitats that remain cold year-round or seasonally cold habitats. Based on the typically short duration of the adult stage (hours or days) compared to the larval stage (although see section on Longevity and Behavior), the water temperature at the time of adult emergence is linked to larval thermal requirements. For example, Rossaro (1991) examined optimum water temperature for 127 species of chironomids, finding that larvae of cold stenothermic species are tolerant of only a narrow temperature range, with most exhibiting temperature optima near the minimum tolerance value. Moreover, the study included 12 species of *Diamesa,* a particularly cold-stenothermic genus. Mean water temperature where these larvae were found ranged from 4.2 to 9.8°C, exemplifying the need for low temperatures to facilitate larval development (Rossarro 1991). Therefore, this indicates that for winter-active insects, adults must survive and be active at cold air temperatures to provide suitable habitat for their offspring. As such, the phenology of winter-active chironomids is often linked to the growth and development of the larvae and emergence patterns of adults may be useful for estimating thermal preferences of larval midges. However, this may be complicated by species that diapause, are semivoltine, or those with facultative thermal preferences.

In many temperate habitats, most Chironomidae species likely diapause during winter because aquatic habitats may completely freeze to the benthic substrates (Danks et al. 1994) or water temperatures are too low for growth and development. Many chironomid larvae that are not active in winter can tolerate freezing or avoid freezing by occupying habitats that do not freeze (e.g. forming cocoons, producing ice-nucleation proteins; Danks 1971). In habitats with consistently cold water temperatures (<2 °C), most chironomid larvae typically undergo diapause during winter regardless of whether they are freeze tolerant or freeze avoidant. There are some species, however, that can grow at very low temperatures including species that inhabit streams with maximum temperatures below 1 °C (e.g. *Diamesa*; Burgheer and Ward 2001). *Diamesa incallida* (Walker) (Nolte 1992) and *D. mendotae* (Bouchard and Ferrington 2009) larvae grow continuously during the winter at temperatures below 10 °C and are known to emerge throughout the winter months of temperate regions. This prolonged emergence period may be advantageous, especially for populations that emerge under especially inhospitable winter conditions (Jonsson and Sandlund 1975). However, the ability to produce multiple generations during the winter (e.g. labile life cycle hypothesis) appears to be limited to a small subset of species that are especially well adapted for activity at low temperatures. In general, the life histories of most winter-active species are understudied, especially larval growth and development patterns.

Most winter-active midges appear to be more marginal in terms of their cold hardiness because their activity is often limited to late winter or early spring in northern temperate habitats or regions with mild winters. These species often have a single, distinct emergence period in late winter indicating a univoltine life cycle (e.g. *Parachaetocladius lenferringtoni* Bouchard and Namayandeh [Bouchard et al. 2024], *Chaetocladius* spp. [Bouchard 2007]). Although it is likely that these less cold hardy species with winter-active adults can also grow and develop at low water temperatures, the thermal requirements for the larvae of most species are unknown.

Longevity and Behavior

A general assumption of chironomid biology is that the adult lifespan is short (Armitage 1995). However, winter-active chironomids display surprisingly long lifespans given their small size and the extreme conditions they inhabit (Table 2). Most of our understanding of winter-active chironomid longevity stems from a single focal species: *Diamesa mendotae.* The mean longevity for *D. mendotae* has been determined to be between 12–33 days and maximum longevity between 25-54 days when maintained at 6 °C (Ferrington et al. 2010), which is supported by additional studies on this species (e.g. Ferrington 2019, Anderson et al. 2022, Bodmer et al. 2023). Differences in mean longevity across collection events could reflect site-specific environmental factors, such as higher mean water temperature during larval development, which may influence adult longevity (Bodmer et al. 2023). Sex may also influence longevity, with mean female longevity measured to be 6 days longer than males (Ferrington et al. 2010). However, longevity has also been determined to be significantly influenced by reproductive status,

Table 2. Maximum and mean longevities of *Diamesa* mendotae reported in recent studies of winter-emerging populations in the Midwest USA. Male and female longevities are given separately, unless these values were not individually reported in the below studies.

Study	Collection Location	Collection Date	Treatment	Sample size (m/f)	Max longevity (m/f)	Mean longevity (m/f)
Ferrington et al. 2010	Stream at Pine Needles Preserve; Washington County, MN	13 Feb, 1 Mar, 16 Mar 2001	6°C	470 / 259	48 / 54	18.6
	Stream at Arcola Mills Historic Site; Washington County, MN	16 Mar 2001				
	Valley Creek; Washington County, MN	20 Dec, 26 Dec 2002, 13 Feb 2003				
	Kinnickinnic River; Pierce County, WI (River Falls)	19 Feb, 27 Feb 2003				
	Kinnickinnic River; Pierce County, WI (Downstream)	12 Mar 2003				
	Trout Brook; Dakota County, MN	30 Jan 2003				
Anderson et al. 2013	Kinnickinnic River; St Croix County, WI	16 Feb 2004	Under snow 4 days, then 6°C	10 / 10	48 / 57	41.3 / 42.5
			Under snow 8 days, then 6°C	10 / 10	56 / 57	40.3 / 47
			Under snow 12 days, then 6°C	10 / 10	51 / 58	42.4 / 48.4
			Under snow 16 days, then 6°C	10 / 10	66 / 61	48.3 / 45.8
			Under snow 20 days, then 6°C	10 / 10	62 / 66	47.4 / 43.4
			Under snow 24 days, then 6°C	10 / 10	65 / 61	55 / 50
			Under snow 28 days, then 6°C	10 / 10	60 / 61	44.7 / 50.5
Mazack et al. 2014	Valley Creek; Washington County, MN	3 Mar 2010	–5°C for 7 days, then 6°C	5 / 4	35 / 42	28.4 / 29.5
			–5°C for 14 days, then 6°C	4 / 2	32 / 38	29.2 / 32.5
			–5°C for 21 days, then 6°C	3 / 3	43 / 35	33.3 / 37.3
			–5°C for 28 days, then 6°C	3 / 2	58 / 38	44.7 / 34.5
			–5°C for 34 days, then 6°C	3 / 3	50 / 56	44.3 / 46.3
			–5°C for 42 days, then 6°C	4 / 1	64 / 43	51.5 / 43
			–5°C for 49 days, then 6°C	2 / 0	53 / --	51.5 / --
			–5°C for 56 days, then 6°C	1 / 0	58 / --	58 / --
			–5°C for 63 days, then 6°C	2 / 1	81 / 73	79.5 / 73
			–5°C for 70 days, then 6°C	2 / 1	92 / 76	83 / 76

Study	Collection Location	Collection Date	Treatment	Sample size (m/f)	Max longevity (m/f)	Mean longevity (m/f)
Ferrington 2019	Hay Creek; Goodhue County, MN	17 Feb 2019	6°C	17 / 19	28 / 30	
			18°C	18 / 20	12 / 12	
			24°C	19 / 20	4 / 6	
	Trout Brook; Dakota County, MN	14 Feb 2019	6°C	29 / 13	27 / 28	
			18°C	29 / 13	10 / 8	
			24°C	29 / 13	5 / 2	
	Valley Creek; Washington County, MN	23 Feb 2019	6°C	26 / 12	23 / 19	
			18°C	26 / 12	7 / 5	
			24°C	26 / 12	4 / 4	
Anderson et al. 2022	Tributary to Redwood River; Lyon County, MN	22 Jan, 28 Jan, 6 Feb, 21 Feb, 24 Feb 2020	2°C	92 / 33	60	19.8
			6°C	86 / 48	34	14.9
			Ambient outdoor conditions	58 / 36	37	13.9
Bodmer et al. 2023	Ike's Creek; Hennepin County, MN	5 Jan, 23 Jan 2020	6°C	41 / 6	32 / 20	18.0 / 16.3
			22°C for 24hr, then 6°C	42 / 4	37 / 19	17.0 / 7
	Pickwick Creek; Winona County, MN (Site 1, Upstream)	4 Jan 2021	6°C	39 / 11	26 / 23	15.2 / 14
			22°C for 24hr, then 6°C	37 / 11	30 / 23	14.2 / 13.6
			22°C for 48hr, then 6°C	37 / 12	28 / 30	12.4 / 11.9
	Pickwick Creek; Winona County, MN (Site 2, Downstream)	4 Jan 2021	6°C	36 / 14	26 / 23	16.4 / 15.6
			22°C for 24hr, then 6°C	35 / 13	26 / 20	13.1 / 10
			22°C for 48hr, then 6°C	34 / 13	23 / 18	11.3 / 8.5

NOTES — Ferrington et al. (2010) combines mean and maximum longevity for all streams and mean male and female longevity. Ferrington 2019 does not report mean longevity. Anderson et al. (2022) does not report separate mean and maximum longevities for males and females, and notes that although most specimens were *D. mendotae,* non-*Diamesa* chironomids may be included in estimates.

with males and ovipositing females living significantly longer than non-ovipositing females (Anderson et al. 2022). Further work on chironomid longevity, particularly by investigating additional taxa, is necessary to elucidate the drivers of within and between-population differences in longevity.

Winter-active chironomids often display prolonged adult lifespans under extreme, subfreezing conditions. In one study, all *D. mendotae* survived burial under snow for 4–28 days, with mean longevity increasing in longer treatment durations (Anderson et al. 2013). Similarly, *D. mendotae* maintained at –5 °C for treatments of 7–70 days before returning to 6 °C had higher mean longevities when kept under subfreezing conditions longer, with a maximum longevity of 92 and 76 days for males and females, respectively (Mazack et al. 2014). Chironomid longevity also increased when maintained at constant lower temperatures: chironomids held at constant 2 °C lived significantly longer (19.8 days) than those at constant 6 °C (14.9 days) or exposed to ambient outdoor conditions (13.9 days) (Anderson et al. 2022). Therefore, these cold-adapted insects may be disproportionately impacted as climate change threatens the duration and intensity of cold winter temperatures.

Recent research on chironomid longevity has assessed how cold-adapted taxa are impacted by climate change (e.g. Nyquist et al. 2021, Bodmer et al. 2023). The winter season in north temperate regions is predicted to experience significant warming in coming decades due to climate change (Notaro et al. 2014, Gulev et al. 2021), which intensifies the need for a comprehensive understanding of cold-adapted, winter-active taxa. At constant high temperatures, Icelandic *Diamesa* spp. had mean longevities of 19.9 days when held at 6 °C, compared to 3.8 days at 20 °C (Nyquist et al. 2021). Although sample sizes were small, this pattern also held for other genera in the study, including *Eukiefferiella*, *Micropsectra*, and *Thienemanniella* (Nyquist et al. 2021). Even short-term warm temperature spikes may impact chironomid longevity. *D. mendotae* from southeastern Minnesota had higher longevities when held at constant 6°C than when exposed to 22°C for 24hrs or 48hrs (Bodmer et al. 2023). Short-term high temperature exposure also reduced successful reproduction, with fewer females producing egg masses that hatched into larvae compared to control 6 °C groups (Bodmer et al. 2023). In similar research, short term exposure to 22 °C reduced adult Orthocladiinae longevity (Bodmer and Nyquist 2022). However, the presence of parasitic nematodes unexpectedly increased orthoclad longevity by increasing survivorship in early life (Bodmer and Nyquist 2022). It is therefore critical that future studies address the impacts of winter warming on chironomids and other cold-adapted taxa to better predict the myriad of ways these communities may respond to climate change and warming winters.

Ferrington (2019) proposed a standardized behavioral assay to estimate individual adult activity level. This assay can be used to predict whether or not adult flies could survive under natural conditions to better understand how climate change may impact winter-active Chironomidae fitness. Although winter-active chironomids have relatively long lifespans, only a subset of their total lifespan is spent successfully mating and reproducing (Bodmer et al. 2024). As *D. mendotae* aged, the proportion of time spent performing inactive behaviors, such as lying on their backs in water, increased steadily until death (Bodmer et al. 2024). Flies that displayed active behaviors soon after collection lived significantly longer than inactive flies, which may allow researchers to predict the age of flies collected off snow (Bodmer et al. 2024). These findings illustrate the limitations of using longevity alone to predict changes in population structures as winter warming progresses. Instead, researchers can use behavior to better predict how individual-level responses to warm temperatures may accumulate to produce population and community-level shifts under climate change.

Mating behavior of winter-emerging chironomids is also notable, with some species either mating on the snow surface (e.g. *Chaetocladius laminatus* Brundin*, Diamesa permacer* (Walker)*, D. mendotae* as described by Hågvar and Østbye 1973 and Ferrington et al. 2010) or exhibiting surface-mating behavior, where mating pairs glide across the surface of the water (e.g. *Oliveridia hugginsi* Ferrington and Sæther*,* as described by Ferrington and Sæther 1987). These behaviors contrast with mating swarms more typical of warmer seasons and are better suited for maximizing rapid contact with mates during winter while also limiting the potential of inadvertent wind-blown dispersal (Ferrington and Sæther 1987). Flight may be impeded or impossible due to low temperatures, and smooth, white snow cover can facilitate location of potential mates (Hågvar and Østbye 1973, Anderson et al. 2013). Morphological adaptations follow suit: the winter-active species *Oliveridia hugginsi* and *Orthocladius ferringtoni* Soponis exhibit adaptations, such as broadened and elongated legs, elaboration of the hypopygium, and a reduced antennal plume — traits that favor surface mating as opposed to those needed to recognize and mate with females during flight (Lencioni 2004). Although several winter-emerging species have been observed in flight, especially on warmer winter days (Young 1969, Bouchard and Ferrington 2009, Anderson et al. 2022), brachypterous and apterous conditions are also reported. Wing-variations are reported within *Diamesa leona* Roback (*D. starmachi* Kownacki & Kownacka as a synonym, see Makarchenko et al. 2022). Seasonal wing variation, with brachypterous forms emerging during winter and fully-winged spring to summer-emerging forms are reported from the Palearctic (Giłka et al. 2013 and Makarchenko et al. 2022. Although, Makarchenko et al. (2022) reports that macropterous forms are incapable of flight due to underdeveloped flight muscles. Winter-emerging *D. leona* from Colorado, USA exhibit similar variation; however, both forms occurred together with brachypterous forms reported to dominate populations at higher elevations and macropterous forms more common at lower elevations (Herrmann et al. 1987).

Ecological Importance

Chironomids are important members of stream food webs and are key food sources for fish, birds, and other insects in winter. Research from Minnesota trout streams found that chironomids are an important component of the winter diet of brown trout (*Salmo trutta* Linnaeus) (French et al. 2016) and are actively selected for by brown trout in some streams (Anderson et al. 2016, Cochran-Biederman and Vondracek 2017). Smaller fish tended to exhibit preference for chironomid larvae and exhibited size-selective predation for larger larvae, comprised primarily of late-instar *Diamesa* (Anderson et al. 2016). Additionally, both stomach-content analysis (French et al. 2014, 2016) and stable isotope analysis (French 2014) found chironomids are important prey for brown trout during winter. Research from the Iberian Peninsula has also found that certain overwintering passerine birds, including *Motacilla alba* Linnaeus (White Wagtail), *Saxicola rubicola* Linnaeus (Common Stonechat), and *Erithacus rubecula* Linnaeus (European Robin) feed upon recently emerged chironomids; *E. rubecula* was observed feeding upon chironomids that were visible on the snow surface (Braz et al. 2014).

Some assemblages dominated by *Diamesa* may decline or disappear due to continued climate warming and increasing water temperatures (Dočkalová et al. 2024, Lencioni et al. 2024). Specifically, increases in water temperature have been shown to reduce or halt emergence of *D. mendotae,* with temperatures above 10 °C unsuitable for continued larval growth and survival (Bouchard and Ferrington 2009); maximum growth rates of *D. mendotae* are recorded at water temperatures between 6-8 °C (Mazack 2013). Similarly, a drop in the abundance of *D. steinboecki* Goetghebuer has been reported in kryal streams that exhibited climate-associated temperature increases, along with an increase in overall invertebrate diversity (Lencioni et al. 2022). Considering that the longevity of at least some cold-adapted species decline with higher temperatures, certain chironomid populations may become less abundant (e.g. Nyquist et al. 2021, Bodmer et al. 2023). Communities currently dominated by *Diamesa* may become more diverse as temperatures rise (Dočkalová et al. 2024). The combination of these observations suggests that the winter chironomid community will change; however, other taxa may replace those that are reduced or lost.

What a future cold-adapted chironomid community might include, and whether there may be ecological consequences, is unknown, especially given the current role of *Diamesa* in food webs. A reduction in emergence of some of these winter-active groups or changes in their activity period could lead to mismatches in phenology and asynchrony between species interactions (Kharouba et al. 2018). A study on Diptera in the United Kingdom found that peak flight biomass of active adult flies changed significantly from 1974 to 2014, which could have negative repercussions for birds and other animals that feed on them (Grabener et al. 2020). Additionally, significant differences in the rate of phenological change in trophic levels have been described in marine and freshwater systems (Thackeray et al. 2010). When the rate of phenological change is great enough and the synchrony between species interactions is in different directions, this can decouple relationships resulting in negative fitness consequences for the species involved (Kharouba et al. 2018) and ecosystem disruption (Thackeray et al. 2010). Further work on cold-adapted Chironomidae is necessary to investigate rates of change in key life-stage events like hatching and emergence to be able to draw further conclusions on the effect that climate change may have on food webs reliant on winter emergence.

Winter-emerging taxa appear highly resistant to extreme late summer floods which suggests that certain taxa may exhibit an opportunistic response to flooding disturbance, taking over niches left vacant by less resistant summer taxa (Anderson and Ferrington 2013). Many chironomids use the hyporheos as a “nursery” for eggs, early larvae, or quiescent stages (Chou et al. 1999, Lencioni et al. 2008, Dole-Olivier 2011, Lencioni and Spitale 2015, Mugnai et al. 2019). Among those taxa known to use the hyporheos are several genera within the Orthocladiinae and Diamesinae that include winter-emerging taxa, such as *Diamesa, Chaetocladius, Cricotopus, Parametriocnemus, Orthocladius,* and *Micropsectra* (e.g. Lencioni et al. 2008, Lencioni and Spitale 2015, Mugnai et al. 2019). Use of the hyporheic zone may allow these taxa to avoid displacement and mortality associated with streambed disturbance (Anderson and Ferrington 2013). Additionally, Anderson and Ferrington (2013) suggest the hyporheos is important for predators, such as stream fish recovering from disturbance events that utilize these insects as a food source. The potential consequences of climate change, including the very likely increase in prevalence and intensity of heavy precipitation events that result in flooding (Seneviratne et al. 2021) combined with a likely scenario of reduced prevalence of certain winter-emerging species due to temperature shifts, may result in pronounced differences in stream food webs.

Hågvar (2010) posed the important question of whether insects that emerge from open streams during winter, such as Chironomidae, would adapt to the absence of snow. This is worth consideration as consistent snow cover throughout the winter months is becoming less reliable due to climate change. Recent models for Minnesota, U.S.A., for example, suggest that there will be significantly less snow cover, with 55 fewer days per year with over 2.54 cm of snow (Liess et al. 2022); similarly, temperatures may be 6 °C warmer by the end of the 21st century (Notaro et al. 2014, Liess et al. 2022). This is significant as areas such as the Driftless Region in southeast Minnesota harbor a diverse network of spring-fed streams with at least 60 winter-emerging chironomid taxa. Winter-active chironomids seek refuge within crevices or under the snowpack to avoid and survive adverse winter conditions, and longevity studies suggest some taxa can survive for prolonged periods in these conditions (e.g. Ferrington et al. 2010, Anderson et al. 2013). Mid-winter periods of minimal or non-existent snow cover could be detrimental for insects that would otherwise seek cover from harsh conditions. Species that currently emerge in early-spring are favored under climate change scenarios; however, periodic cold snaps may affect their survival, especially if snow cover is unavailable.

Future Directions and Conclusion

Soszyńska-Maj et al. (2016) stated that winter emergence of Chironomidae should not be viewed as a curiosity, but instead a "strategy that allows these insects to live actively and to disperse widely." The studies we describe here support this claim. None-the-less, research detailing winter-emerging chironomids is limited, and as we demonstrate (Fig 1), research is largely restricted to only a handful of localities and detailed autecology studies of only select species. Expanding research to include a broader geographical range to better gauge species accounts is important, especially to document shifts in species composition under changing climate regimes. Studies documenting cold hardiness, longevity, behavior, and other life-history parameters are largely restricted to only a few taxa, leaving much room for additional research.

Emphasis on extending field work into the winter season is critical to better understand the distribution, diversity, and life history of winter-active insects. As suggested by Figure 1, the presence of winter-active species is simply unknown in many regions because of a lack of winter field surveys. It is also unknown where and in what life stage many winter-emerging species aestivate during warmer months. Furthermore, while we have an understanding of cold hardiness and select life history parameters, such as growth, emergence, and longevity for certain species (e.g. *D. mendotae*), little research documents these parameters in other taxa. In short, there are an endless number of basic biological questions yet untapped when discussing winter-active species.

Although the freeze tolerance and freeze avoidance of some chironomid taxa have been tested (e.g. Lencioni 2004, Bouchard et al. 2009), little work has been conducted on critical thermal maxima (CT_{max}). Additional work in this area would complement studies on thermal stress and reduced longevity by providing a physiological endpoint for testing ambient temperatures and for creating more accurate models of thermal acclimatization. Testing CT_{max} could also provide data on adaptive plasticity since studies on Diptera utilizing acclimatization have found some plasticity in this endpoint measurement and, in combination with the size of the fly, could affect the insect's ability to cope with a warming climate (Weaving et al. 2023). Additionally, obtaining thermal performance curves (TPCs) from laboratory tests and field investigations would also deepen understanding of how temperatures might affect cold-adapted Chironomidae. These studies could be used to identify local adaptation in different ranges and populations of various taxa and for launching further investigations on fitness, plasticity, and acclimatization (Sinclair et al. 2016).

Enhancing the awareness of the winter-emerging insect community is also important. For example, few studies documented in introductory ecology textbooks highlight research conducted during winter and fewer yet focus on invertebrates. Similarly, ecological or environmental-focused community science programs are typically conducted during the summer or growing season. While winter programs can present more logistical challenges considering low temperatures and icy conditions, winter field opportunities can offer profound hands-on learning opportunities for classrooms with various science learning objectives (Swenson and Nyquist 2024). Programs such as *Bugs Below Zero* (Anderson et al. 2025) which is directed at educators and community scientists can help create awareness about winter-active aquatic insects and their value in stream ecosystems and can assist scientists in terms of documenting winter-emerging insects.

As shown here, winter-emerging Chironomidae are not simply a novel occurrence, but an integral and surprisingly diverse component of stream ecosystems worldwide that play important roles in both aquatic and terrestrial food webs. Hibernal species possess behavioral and physiological strategies that allow them to not simply survive but thrive throughout the coldest months of the year, with several species only known to develop, emerge, and reproduce during winter. The study of winter-active Chironomidae and other cold-hardy aquatic insects, while growing, is still in its infancy. Furthermore, what the future holds for many of these species is uncertain, especially considering our warming climate and the fact that research shows that some species are unable to survive in warmer conditions. We hope this review will both enhance the awareness of winter-emerging species and encourage other researchers to take on winter field work, continuing explorations of midges that are active below zero.

Acknowledgements

We are indebted to the late Dr. Len Ferrington Jr. for instilling in us a passion for winter Chironomidae research. Thanks also to other cold-hardy Chironomidae researchers, past and present, who have contributed to the growing base of winter midge research. We also thank Nathan Roberts who assisted in creating a figure for the manuscript.

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Article submitted 30. January 2025, accepted by Barbara Hayford 11. June 2025, published 15. November 2025.