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Article

Overwintering capacity of water boatmen (Hemiptera: Corixidae) and other invertebrates encased in the ice of shallow prairie wetlands

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Abstract

Overwintering in shallow habitats presents a serious obstacle for aquatic invertebrates. Here we investigated the little-known ability of water boatmen (Hemiptera: Corixidae), an aquatic insect, to survive the winter encased in air pockets within the ice of shallow wetlands. We extracted and experimentally thawed large blocks of ice from prairie wetlands in Saskatchewan, Canada, from which we examined the species composition and revival of corixids. While multiple corixid species were present in wetlands prior to freeze-up, a single species, *Cymatia americana* Hussey, 1920, comprised the vast majority of corixids that were found within the ice later in winter. Only 4%–9% of corixids, all *Cymatia americana*, revived after ice thawing over both study years. Being encased within an air pocket appeared to be necessary for the survival of corixids in the ice, with up to 300 individuals grouped together. Other invertebrate taxa also revived after thawing, including Haliplidae and Dytiscidae (Coleoptera) encased within air pockets both alongside corixids and on their own, as well as Coenagrionidae (Odonata), Phryganeidae and Leptoceridae (Trichoptera), Chironomidae (Diptera), and Physidae and Planorbidae (Basommatophora), which appeared to be encased in solid ice. The ability to overwinter inside ice represents a little understood survival mechanism of aquatic invertebrates in shallow wetlands, which could confer energetic and reproductive advantages to those that endure until spring.

Key words: overwintering, winter ecology, aquatic insect, wetland, ice, Corixidae

Introduction

Winter is a challenging time for animals in regions that experience sub-zero temperatures. Aquatic invertebrates face a number of chemical and physical stressors resulting from seasonal changes in temperature and the formation of ice. In addition to changes in habitat quality, the risk of freezing may pose a serious threat, as internal ice formation can cause mechanical damage, osmotic shock, lethal damage to cell membranes, and rupturing of organs (Duman et al. 1991; Walters et al. 2009), while exposure to cold temperatures above the freezing point can still result in chilling injuries, such as the disruption of enzymatic systems or membrane functioning (Danks 2007; Bale and Hayward 2009). Aquatic insects have evolved a range of physiological and behavioural adaptations to deal with such challenges. Two approaches used by insects to deal with the problem of freezing are freeze avoidance and freeze tolerance. Freeze-avoidant insects generally cannot survive internal freezing, and are able to withstand sub-zero temperatures by supercooling, i.e., the ability to remain unfrozen at temperatures below the freezing point of body fluids, while freeze-tolerant insects have adapted to withstand internal freezing (Salt 1961; Frisbie and Lee 1997; Danks 2007).

Many aquatic insects that cannot tolerate internal freezing prepare for winter by moving to deeper waters or to new waterbodies that are less likely to freeze, where they will remain throughout the winter in the water beneath the ice (Moore and Lee 1991; Irons et al. 1993; Lencioni 2004). Such appears to be the case for many species of water boatmen (Hemiptera: Corixidae) that breed and develop in shallow wetlands across the Canadian Prairie Pothole Region (PPR). In fall, these species mass migrate to deeper bodies of water, such as large rivers, where they spend the winter beneath the ice (Hungerford 1919; Hilsenhoff 1970; Srayko et al. 2022). Adults later disperse back to newly filled or melted wetlands in spring (Fernando and Galbraith 1973; Batzer and Wissinger 1996). Failing to escape to deeper waterbodies for the winter, which are generally buffered against temperature changes and less likely to freeze through, can lead to considerable mortality in corixid populations (Pajunen and Jansson 1969; Pajunen and Salmi 1988).

Most of the existing literature on corixids indicates that these insects overwinter primarily in the water beneath the ice (e.g., Hungerford 1948; Menke 1979; Stonedahl and Lattin 1986; Suchá and Papáček 2008). However, there is evidence that one species of corixid, *Cymatia americana* Hussey 1920, common to prairie wetlands in North America (Brooks and Kelton 1967; Scudder et al. 2010), is able to survive the winter encased inside wetland ice. To our knowledge, this behaviour of *Cymatia americana* has only been examined twice in the literature, first by Hussey (1921) from a pond in Minnesota, USA, and again by Mihalicz (2015) in a prairie wetland in Saskatchewan, Canada. Both witnessed numerous individuals of *Cymatia americana* encased in clusters within air pockets inside the ice, the vast majority of which revived when the ice was thawed in a lab setting. Another species of *Cymatia* from Europe, *Cymatia bonsdorffii* (Sahlberg, 1819), has also been recorded overwintering encased in ice (Danell 1981). To our knowledge, there are no records of any corixid species other than those in the genus *Cymatia* that can tolerate encasement in ice over the winter. Unlike most corixid occupants of shallow PPR wetlands, *Cymatia americana* does not appear to migrate in large numbers to deeper habitats in fall (Srayko et al. 2022), which may be explained by its ability to withstand freezing conditions in wetlands. However, in previous research, we have found that a number of corixid species may be found in shallow prairie wetlands at the time of ice-over, including individuals of species that are known to migrate en masse out of such habitats to deeper overwintering sites in fall (Srayko et al. 2022). If these species are actually able to survive within the ice in a similar fashion as *Cymatia americana*, it could indicate that factors other than overwintering tolerances drive the seasonal corixid migration out of shallow habitats.

Little is known about the influences of overwintering conditions on the survival of aquatic invertebrates in prairie wetlands (Daborn 1971) or the overwintering strategies of aquatic insects in general (Danks 2007; Ditrich and Koštál 2011). Here we examine the ability of corixids to overwinter within pond ice, a phenomenon that has received little attention since it was first described a century ago by Hussey (1921). In this study, we attempt to determine if any corixid species other than *Cymatia americana* can survive encasement within wetland ice, and to assess the mortality that may be associated with overwintering in this manner. We also provide further documentation of overwintering within ice for a variety of other aquatic invertebrate taxa. We examined the species composition of corixids that are present in wetlands prior to freeze-up, followed by the extraction and thawing of wetland ice later in winter, to see which corixids and other invertebrates that were encased inside the ice revived. This information could increase our understanding of the mechanisms behind the survival of invertebrates that overwinter in shallow wetlands, and allow for predictions as to how the corixid-mediated linkage between wetland and river ecosystems may be affected by changing winter conditions in the future.

Materials and methods

Study area

Overwintering of corixids was examined at three wetland sites near Saskatoon, Saskatchewan (Fig. 1). A single site, ES7, was visited once in November 2016 to collect corixids from the water beneath a thin layer of recently formed ice, and again in March 2017, to extract ice samples from the solidly frozen wetland. In November 2017, corixids were again collected from beneath the ice at this site, as well as two additional wetlands, site RR3074 and the Saskatoon Swale. These sites were then visited later in winter in 2018 to extract ice samples. Ice was extracted from the site RR3074 on 24 and 27 February, from the Swale on 6 March, and from site ES7 on 12 and 17 February and 13 and 19 March. Water beneath the ice was sampled for corixids from the Swale on 9 March. All these sites were later visited from 19 to 21 April 2018 for observations of the spring thaw. Sites ES7 and RR3074 were class 4 wetlands bordered by gravel roads and agricultural activity, ranging in area from ~0.25 to 3.0 ha, with maximum depths from ~0.5 to 1.0 m. The Swale is a larger class 5 wetland, ~7.35 ha in area with a depth at center of ~2.0 m (wetlands classified using the system by Stewart and Kantrud 1971).

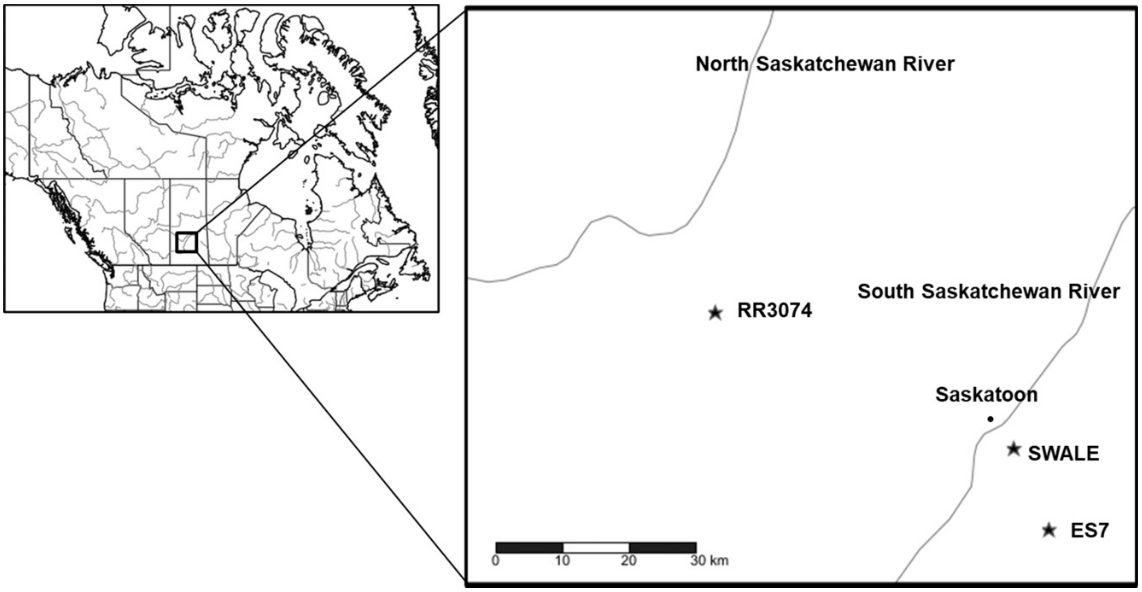
Temperature logger setup

In November 2017, HOBO Onset temperature loggers were deployed at the two shallowest wetland sites, ES7 and RR3074. Three loggers were deployed at each site on a single rebar post that was driven into the substrate, such that one logger was positioned near the surface of the ice, 0–5 cm down, a second logger was located 30–35 cm from the surface, and a third logger was positioned close to the sediment at 40–45 cm (loggers were placed at locations in the wetlands with a depth of ~0.5 m; Fig. S7). The loggers took temperature readings every 4 h and were retrieved in spring to examine temperature profiles at the varying depths for each site.

Early winter sample collection

In November of 2016 and 2017, wetland sites were sampled for corixids when a solid layer of ice just thick enough to walk on had formed, ranging from ~3 to 9 cm thick. Corixids were collected by performing sweeps with a D-frame net (mesh size = 500 μm, mouth = 30.5 × 25.4 cm) under the ice. To do this, a line of variable length was broken in the ice surface with a sledgehammer or axe, with widened openings at either end for the insertion and removal of the net. After waiting several minutes for the water beneath the ice to settle, corixids were collected by shuffling along the length of the transect once, while undulating the net between the substrate and the surface of the ice at random. Corixids were frozen and later identified to species. These were compared to those found within the ice later in winter to determine, of the species that could potentially be present, which were overwintering within the ice.

Fig. 1. Map of the study area in central Saskatchewan, Canada, with wetland sampling locations (stars). Map created with SimpleMappr (https://www.simplemappr.net/).



Late winter sample collection and ice thawing procedure

Ice extraction

In March 2017 and February–March 2018, ice was extracted from the wetlands to be thawed out in the lab. Ice blocks were extracted from throughout the two shallowest wetland sites, having roughly uniform depths, and closer to the edge of the deeper Swale site where freezing had occurred down to the sediment layer. During preliminary sampling, a randomized approach to collecting ice was attempted; however, this proved to yield very few corixids for the effort involved in removing large enough pieces of ice to have intact corixid clusters. Collections were later biased in that the majority of ice blocks were instead cut out from areas where air pockets could be seen in abundance when looking down into the ice, which was easiest in sections with little to no snow cover. In both years, snow cover on the surface of the wetlands was variable at the times when ice samples were extracted, with each site having large patches with little to no snow cover, and with that snow rarely exceeding 30 cm deep where present (Fig. S1).

Ice blocks of similar dimensions were extracted using a standardized procedure at each site. First, a square of approximately 30 × 30 cm was drawn in the ice, around which a series of holes was created with an ice auger. The divides between these holes were then broken down with axes and hammers, creating a column of ice extending down into the frozen sediment. These columns of ice were then loosened from the bottom and leveraged out with ice chisels (Fig. S2). Once ice columns were extracted, these were cut apart for transport to the lab. Two large ice blocks were extracted from ES7 in 2017, ~35 and 47 cm deep, and ~18 and 29 kg in weight. In 2018, the greatest sampling effort was carried out at site ES7, with ice blocks ranging from ~17 to 53 cm in depth and weighing ~10 to 70 kg, with ~576 kg of ice extracted from that site in total. This represented approximately 70% of the 840 kg of ice that was extracted from all three wetlands. This site was targeted as it appeared to yield the highest abundance of corixids within the ice, with an overall density of four corixids per kg of ice, as opposed to roughly one corixid per kg at the other two sites. Ice blocks extracted from site RR3074 ranged from ~10 to 30 cm in depth and weighed ~10 to 36 kg, with a total of ~156 kg extracted, while those taken in 2018 from the Swale ranged from ~18 to 30 cm in depth and weighed ~23 to 32 kg, with ~109 kg of ice extracted in total (Table S1).

Ice thawing procedure

In the lab, corixids were located within ice blocks and, where possible, the depth from the surface was recorded. The presence of air bubbles around corixids was also noted. However, in some cases the presence of corixids was only made apparent after considerable thawing due to the size and opaqueness of some of the pieces of ice, making the measurement of depth and the determination of the presence of an air pocket impossible. After noting these details, the large columns were cut apart into smaller pieces with chisels and an ice saw.

Following the general procedure outlined by Mihalicz (2015), ice pieces were thawed out in a fridge or walk-in cooler at 4 °C to 6 °C for several hours to several days, depending on the size of the piece of ice. Some pieces were left larger to prevent cutting through corixids inside. Once free to the open air or meltwater around each piece of ice, corixids were then placed in meltwater and transferred to room temperatures of 12 °C to 21 °C and monitored for signs of life for up to 1 week, indicated by any sign of movement, which was sometimes found to be stimulated by light or touch (Hussey 1921). While previous ice thawing studies have indicated that insects that do not resume activity after several hours may be considered dead (Hussey 1921; Daborn 1971; Mihalicz 2015), some of the corixids found in the first samples from our study only resumed activity 24–48 h or longer after being transferred to room temperature. It was observed that corixids that would eventually show signs of activity always appeared to float in a rigid stance with legs positioned outwards, while those that immediately sank or appeared curled up never revived, prompting wait times that were longer for some specimens than others. In 2017, the time that surviving corixids spent at room temperature (12 °C to 21 °C) until the first signs of activity were noted ranged from 0 (corixids became active at refrigeration temperatures of 4 °C to 6 °C as soon as they were exposed to meltwater or open air) to approximately 72 h, and up to 8 days in 2018.

The presence and mortality of other invertebrate taxa within the ice was noted. Corixids were identified to species using Brooks and Kelton (1967), while other invertebrates were identified to the family or genus level using Clifford (1991) and Merritt et al. (2008).

Late winter sampling from water beneath the ice

In March 2018, water beneath the ice was sampled at the Swale, the only site deep enough not to freeze to the bottom at the center, to examine if corixids were preferentially overwintering in the water instead of inside the ice. Two holes were drilled in the ice with a 15 cm (diameter) ice auger, into which a small dip net on a long pole was extended to the substrate and moved in a figure eight motion for approximately 1 min for each sample to collect invertebrates. Sampling was performed at locations with ice thickness of approximately 1.0 m, with 0.2–1.0 m of water underneath.

Spring observations

In April 2018, after considerable melting had occurred, but early enough that substantial corixid migration from permanent overwintering habitats had likely not occurred, wetlands were revisited to examine if corixids and other invertebrates had survived the winter under natural conditions.

Data analysis

Preliminary observations indicated that only *Cymatia americana* that were enclosed within air pockets survived encasement in the ice. As such, only individuals of *Cymatia americana*, or pairs or groups of corixids containing *Cymatia americana*, that were confirmed to be within air pockets and for which a depth measurement was obtainable, were used for statistical tests. Spearman's rank correlations were used to examine relationships between depth, the number of corixids encased together, and the percentage of corixids that revived after being thawed from the ice. Percent revival of corixids encased alone versus those encased in pairs or groups was examined using an independent samples *t*–test. Statistical analyses were conducted in SPSS 28 (SPSS Inc., IBM) with $\alpha = 0.05$.

Results

Temperature profiles

Temperature loggers positioned within 5 cm of the surface of the ice recorded mean temperatures (±SD) from −10.7 ± 6.0 °C to −11.3 ± 5.6 °C from 21 December 2017 to 20 March 2018, approximately 3 °C to 5 °C colder than those 30–45 cm deep, and with greater and more frequent temperature fluctuations. Recorded temperatures ranged from ∼0 °C to −26 °C at 0–5 cm depth, −1 °C to −16 °C at 30–35 cm depth, and ∼0 °C to −13 °C at 40–45 cm depth (Fig. 2; Table S2). Snow cover over the areas immediately above the temperature loggers ranged from 1 to 3 cm at the times when wetlands were visited for ice extraction.

Species composition

At the time of sampling in November, as a thin but complete layer of ice had covered the wetlands, corixids could be observed already trapped inside air pockets that were forming in the ice, with some still being partially open to the water below (Fig. S3). Three species of corixids (175 individuals) were collected in D-frame net sweeps taken from beneath the thin layer of ice on the wetland that had formed in November 2016, 98% of which were *Cymatia americana*. Nine species were found beneath the ice in November 2017 (503 individuals), 63% of which were *Cymatia americana*, followed by *Dasycorixa hybrida* (Hungerford, 1926) (28%), with only 1–20 individuals of the remaining species collected (Fig. 3).

In March 2017, only *Cymatia americana* was found from inside ice blocks. In February and March 2018, 98% of the 2703 corixids found within the ice were also *Cymatia americana*, with *Dasycorixa hybrida* composing ∼2% of the total (Fig. 3). Single individuals of three other species (*Callicorixa audeni* Hungerford, 1928, *Cenocorixa expleta* (Uhler, 1895), and *Hesperocorixa vulgaris* (Hungerford, 1925)) were also found within the ice in 2018.

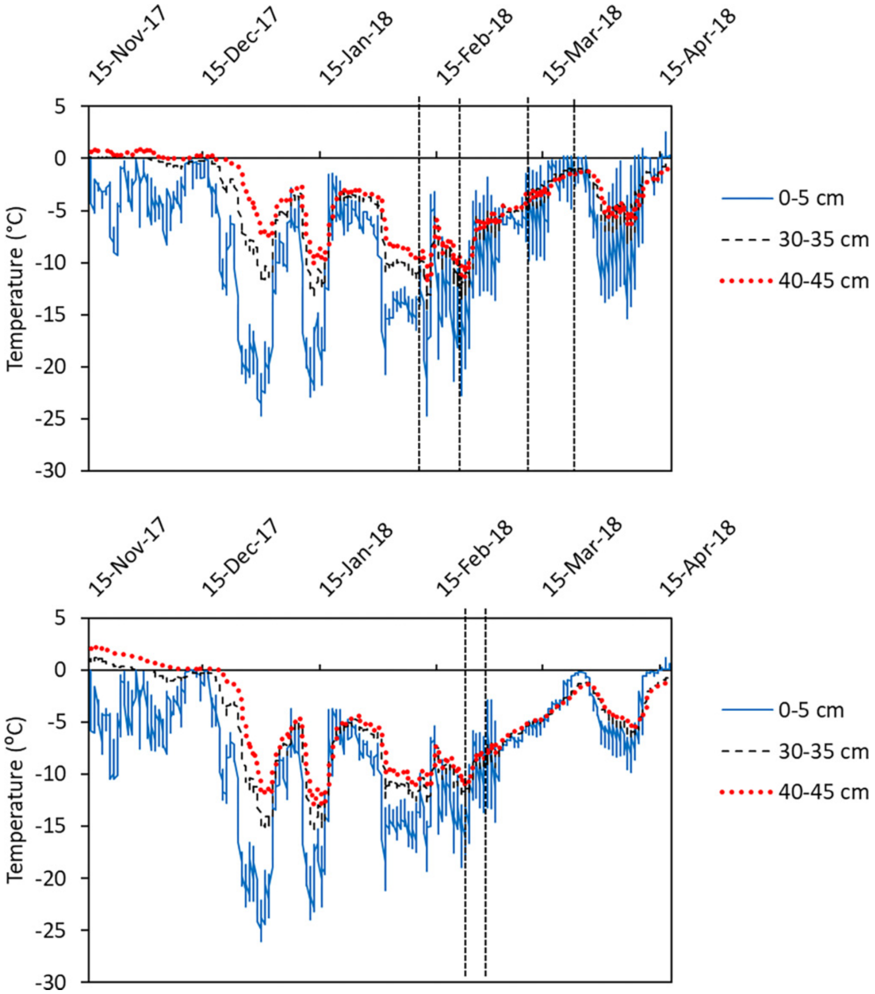
Mortality and position within the ice

Cymatia americana was the only corixid species to revive after being thawed from the ice. In 2017, 32 of 350 corixids (9.1%) revived after being thawed from the ice, while the revival from ice blocks in the winter of 2018 was lower, at 114 of 2703 corixids (4.2%) (Table 1).

Air pocket use, group size, and depth

In 2017 and 2018, all corixids that revived after being thawed from the ice had been clearly encased within air pockets, either alone (Fig. S4), in pairs, or in tightly packed groups of up to 298 individuals (Fig. S5). For those in pairs or groups, a mean number (±SD) of 31.6 ± 36.4 individuals were clustered together per group in 2017 ($n = 11$) and 24.6 ± 43.5 individuals per group in 2018 ($n = 102$). Corixids that were encased together in pairs or groups made up 99.0% of corixids from within the ice in 2017 and 92.8% of corixids in 2018.

Fig. 2. Temperature profiles of sites ES7 (top) and RR3074 (bottom), from 17 November 2017 to 17 April 2018, with readings taken every 4 h. Loggers in each wetland were positioned near the surface of the ice (0–5 cm depth, solid blue line), midway through the ice column (30–35 cm depth, black dashes), and just above the sediment layer (40–45 cm depth, red dots). Dashed vertical lines indicate dates when ice was extracted.



In 2017, all of the pairs or groups of corixids from within the ice were clearly encased in air pockets, while of the three corixids found on their own, only one was surrounded by an air pocket, with the other two frozen in solid ice. In 2018, the presence of an air pocket surrounding corixids could not be confirmed for 21 of 102 pairs or groups and 109 of the 194 lone corixids due to either opaqueness of the ice or detection within ice columns only after considerable melting had occurred. Of the lone 194 corixids, 50 were clearly inside air pockets, with these only just surrounding their bodies, and 35 were confirmed to be encased in solid ice.

In 2018, 94% of *Cymatia americana* were encased together in pairs or groups, with the remainder encased singly. Of the next most abundant species, *Dasycorixa hybrida*, 57% were encased in pairs or groups in air pockets either with *Cymatia americana* or on their own, while the remaining 43% were encased singly. The clear presence and absence of an air pocket around *Dasycorixa hybrida* that were encased singly could only be confirmed for two individuals. Of the three other corixid species located in the ice, all were encased singly, with only one that was clearly inside an air pocket.

In 2017, measurements of depth from the surface of the ice were possible for all 12 air pockets containing corixids (11 of which contained groups of corixids, with 1 encased singly), with a mean depth (±SD) of 8.3 ± 8.0 cm, and a mean depth of those pockets containing corixids that revived after thawing of 9.8 ± 10.4 cm ($n = 6$). In 2018, depth measurements were possible for 123 air pockets containing corixids, with a mean depth of 9.3 ± 9.0 cm. The mean depth of corixids encased in pairs or groups in air pockets was 4.8 ± 5.2 cm ($n = 75$), with a mean depth of corixids encased singly in air pockets of 16.5 ± 9.2 cm ($n = 48$). The mean depth of air pockets containing corixids that revived after thawing was 3.9 ± 4.8 cm ($n = 33$), two of which contained corixids that were encased singly, with the remaining containing pairs or groups.

In 2017, Spearman's correlations revealed no significant relationships between the percent of corixids that revived after thawing and the number grouped together ($r_s = 0.530$,

Fig. 3. Species composition of corixids collected from beneath the ice in (A) early winter (November) 2016, (B) from within the ice in late winter (March) 2017, (C) from beneath the ice in early winter (November) 2017, and (D) from within the ice in late winter (February–March) 2018. Species abbreviations: CAM, *Cymatia americana*; CAUD, *Callicorixa audeni*; CBIF, *Cenocorixa bifida*; CDAKO, *Cenocorixa dakotensis*; CEXPL, *Cenocorixa expleta*; CUTAH, *Cenocorixa utahensis*; DHYB, *Dasycorixa hybrida*; HVULG, *Hesperocorixa vulgaris*; SALT, *Sigara alternata*; SBIC, *Sigara bicoloripennis*; SDEC, *Sigara decoratella*.

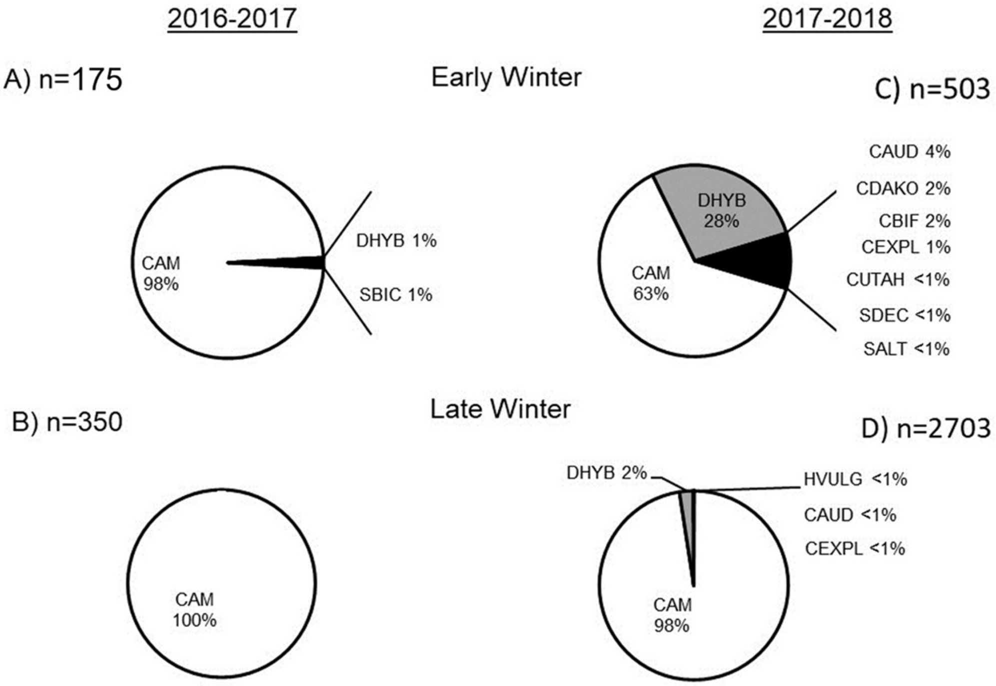


Table 1. Total and species-specific percent revival of corixids thawed out from ice blocks in the winters of 2017 and 2018.

Species	Year	Number Live	Number Dead	Total	Percent revival
Cymatia americana	2017	32	318	350	9.1%
	2018	114	2521	2635	4.3%
Dasycorixa hybrida	2017	0	0	0	–
	2018	0	65	65	0%
Callicorixa audeni	2018	0	1	1	0%
Cenocorixa expleta	2018	0	1	1	0%
Hesperocorixa vulgaris	2018	0	1	1	0%
Total	2017	32	318	350	9.1%
	2018	114	2589	2703	4.2%

$p = 0.072$, $n = 12$) or the depth at which they were encased ($r_s = 0.306$, $p = 0.334$, $n = 12$; Fig. 4). In 2017, depth and the number of corixids that were encased together was not significantly correlated ($r_s = -0.119$, $p = 0.714$, $n = 12$); however, these variables were negatively correlated in 2018 ($r_s = -0.734$, $p < 0.001$, $n = 121$), with smaller groups of corixids tending to be encased further down in the ice than larger groups, confounding the interpretation of the influence of either depth or group size on revival after thawing (Fig. 4).

In 2018, the revival rate of *Cymatia americana* encased in air pockets on their own did not differ significantly from the revival rate of those encased together in pairs or groups ($t_{119} = 1.182$, $p = 0.476$), with a mean (±SE) percent revival of lone corixids of 4.4 ± 3.1% ($n = 46$, two survivors total), and a mean percent revival of each pair or group of corixids of 8.0 ± 3.0% ($n = 75$ groups, 111 of 2132 corixids). The lone *Cymatia americana* in air pockets were encased at a mean depth (±SD) of 16.5 ± 9.1 cm, while those encased together in pairs or groups were located at a mean depth of 4.8 ± 5.2 cm.

Noncorixid invertebrates

In 2018, we recorded the presence, number, and revival of noncorixid taxa that thawed out from within the ice (Table 2). Predaceous diving beetle (Coleoptera: Dytiscidae) adults (*Coelambus* sp. and *Hygrotus* sp.) and larvae (*Ilybius*/*Agabus* sp.), and crawling water beetle adults (Coleoptera: Haliplidae:

Fig. 4. In the late winter of 2017 (left) and 2018 (right), the percentage of corixids that revived from each individual air pocket (percent revival) by the number of corixids encased together (A, B) and depth from the surface of the ice (C, D). Also shown is the number of corixids encased together by distance from the surface of the ice (E, F).

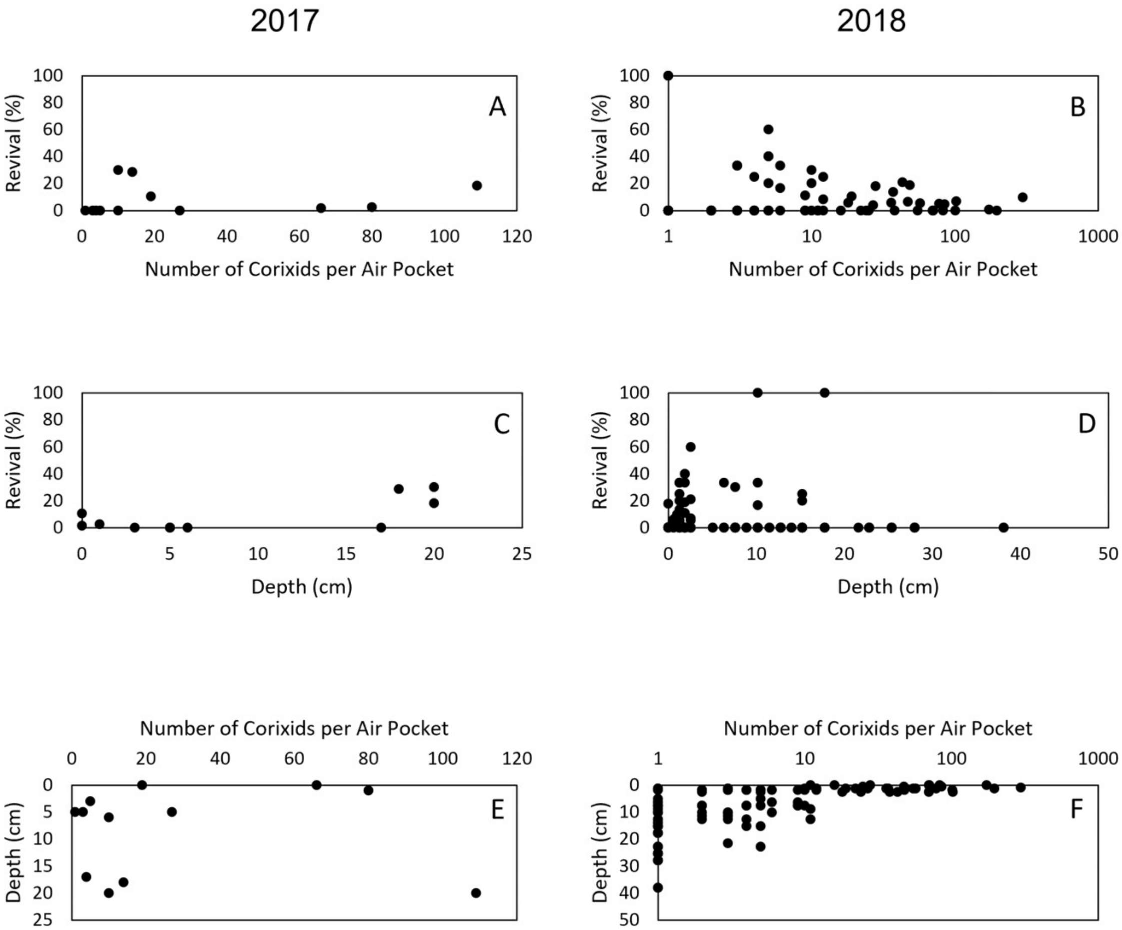


Table 2. Location in the ice and revival of noncorixid invertebrate taxa found within ice blocks thawed out in the winter of 2018.

Location in ice	Order	Family	Genus	Dev. stage	Total	Percent revival
Air pockets	Coleoptera	Haliplidae	*Haliplus*	Adult	155	60%
				Larvae	2	100%
		Dytiscidae	*Coelambus/Hygrotus*	Adult	71	7%
			Ilybius	Larvae	13	0%
		Gyrinidae	*Gyrinus*	Adult	1	0%
Solid ice	Odonata	Coenagrionidae	*Coenagrion/Enallagma*	Nymph	326	13%
		Aeshnidae		Nymph	5	0%
		Libellulidae		Nymph	4	0%
	Trichoptera	Phryganeidae	*Agrypnia/Phryganea*	Larvae	26	100%
		Leptoceridae		Larvae	3	100%
	Hemiptera	Notonectidae	*Notonecta*	Adult	1	0%
	Diptera	Chironomidae		Larvae	–	Live
	Basommatophora	Physidae	*Physa*	–	–	Live
		Planorbidae		–	–	Live

Note: "Live" indicates taxa that revived but were not counted in their entirety.

Haliplus sp.) were commonly found within air bubbles in the ice, either in groups on their own or mixed in with corixids (Fig. S6). Fewer than 10% of the dytiscid adults revived, all of which were *Coelambus* sp., and none of the larvae, while the majority of the haliplid adults (60%) revived. Also found with corixid clusters were two haliplid larvae (*Haliplus* sp.), both of which revived, and a single whirligig beetle adult (Coleoptera: Gyrinidae: *Gyrinus* sp.) which did not.

Over 300 damselfly nymphs (Odonata: Coenagrionidae: *Coenagrion*/*Enallagma* sp.) were found encased solidly in the ice, which had a 13% revival rate after thawing. All of the caddisfly larvae, which were also found encased in solid ice, revived after thawing (Trichoptera: Phryganeidae: *Agrypnia*/*Phryganea* sp., Leptoceridae). Other taxa, many of which revived on thawing but were not enumerated in their entirety, included midge larvae (Diptera: Chironomidae) and snails (Basommatophora: Physidae: *Physa* sp., and Planorbidae). Other taxa frozen solidly in the ice which did not revive included dragonfly nymphs (Odonata: Aeshnidae, Libellulidae), and a single backswimmer adult (Hemiptera: Notonectidae: *Notonecta* sp.).

In 2018, taxa collected from the water beneath the ice in the larger Swale site in March included scuds (Amphipoda), chironomid larvae, and snails. No corixids were collected from the water beneath the ice at this site.

Spring observations

From 19 to 21 April 2018, shortly after the spring thaw had begun, wetlands were revisited to see if any corixids or other invertebrates had survived the winter within the ice under natural conditions. Warming had occurred rapidly within the past few days, leading to a large amount of meltwater from the surrounding landscape flooding over the ice in the two smaller wetland sites, while the larger wetland site was not flooded, but had begun to melt at the edges.

At site ES7, a large number of corixids, likely numbering >100 000, were found floating in meltwater that had flooded the ice, likely having been freed from surface clusters in the ice below, with strong winds on the day of sampling gradually blowing these to one side of the wetland, the vast majority of which appeared to be dead. A random sampling of approximately 2000–3000 corixids was taken from this amalgamation, of which 370 corixids were found to be alive, all *Cymatia americana*. Of those that were dead, a random sampling of 500 were identified, of which 98% were *Cymatia americana*, and the remainder *Dasycorixa hybrida*. At the smaller site RR3074, only two live *Cymatia americana* were collected from random sweeps made throughout the meltwater on the surface of the ice, with another four found dead. Other live taxa that were noted from these wetlands included dytiscid adults (Dytiscinae: *Graphoderus* sp.; Colymbetinae, Hydroporinae), and larvae (*Ilybius*/*Agabus* sp.), haliplid adults (*Haliplus* sp.), water scavenger beetle larvae (Coleoptera: Hydrophillidae), phryganeid larvae, amphipods (*Hyallela* sp.), coenagrionid nymphs, and cranefly (Diptera: Tipulidae) and hoverfly larvae (Diptera: Syrphidae). The presence of these taxa alive likely indicated successful overwintering either within the ice, or possibly within or beneath the frozen sediment layer, as both ponds had frozen solid throughout. At site RR3074, large numbers of dragonfly nymphs (Odonata: Aeshnidae, Libellulidae) were found floating dead on the wetland surface, with none living.

At the larger Swale site, which was not completely flooded over by meltwater, two *Cymatia americana* and three *Dasycorixa hybrida* individuals were found live and isolated within melted depressions on the surface of the ice. This contrasts with the mortality that we observed in our ice extraction and thawing experiment mid-winter, in which none of the *Dasycorixa hybrida* that we found in the ice revived on thawing. These species were also found swimming freely at the periphery of the wetland, where considerable melting had occurred.

Discussion

This study has provided further evidence that corixids and a variety of other wetland invertebrates are able to survive winter encased in ice. While multiple species of corixids may be present in prairie wetlands at the onset of freezing, we found that only a single species, *Cymatia americana*, appears to be able to survive the winter in this manner, according to thawing experiments in the lab. However, there is some evidence to suggest that a second species, *Dasycorixa hybrida*, may also be capable of overwintering within ice. For corixids, this appears to be a risky way to spend the winter, with mortality rates that could exceed 95%. Other taxa were also found encased in air pockets with or without corixids, and within solid ice. Additional experimentation is warranted to understand the significance of overwintering within ice for aquatic invertebrates in shallow wetlands.

Overwintering abilities of different corixid species

Despite multiple corixid species being present in study wetlands at the time of ice-over, almost all that we found within the ice were *Cymatia americana* and *Dasycorixa hybrida*, of which only the former revived after being experimentally thawed. This species is the only corixid that we are aware of that can survive the winter encased in ice (Hussey 1921; Danell 1981; Mihalicz 2015). Of those species noted in wetlands both at the time of ice-over and within the ice, *Callicorixa audeni*, *Cenocorixa bifida* (Hungerford, 1926), *Cenocorixa dakotensis* (Hungerford, 1928), *Cenocorixa expleta*, *Hesperocorixa vulgaris*, *Sigara alternata* (Say, 1825), *Sigara bicoloripennis* (Walley, 1936), and *Sigara decoratella* (Hungerford, 1926) appear to be migratory, with large numbers of these species leaving wetlands in fall and flying into larger bodies of water, such as rivers, to overwinter (Srayko et al. 2022). The small numbers of these species that were present in wetlands at the time of ice-over and the complete mortality of the few that were found within the ice indicates that their presence in these wetlands over the winter was likely accidental, and that they are not capable of survival in shallow wetlands that freeze through. These may be individuals that simply did not manage to migrate before conditions rendered flight impossible (as corixids appear to require relatively warm and sunny weather for flight and navigation; Popham 1964). They could also be individuals that are simply incapable of flight, due to either a reduction in flight muscles or wing structure. This is a common feature in many corixid species, as it could convey reproductive and metabolic advantages in permanent habitats (Popham 1964; Young 1965; Reynolds et al. 2013).

Previous research indicates that *Cymatia americana* and *Dasycorixa hybrida*, the dominant species from within the ice, are largely nonmigratory (Srayko et al. 2022). For these species, the avoidance of seasonal migrations may be made possible by their ability to survive the winter even in shallow wetlands that freeze down to the bottom. Populations of species of *Cymatia* in Europe are known to be largely incapable of flight (Brown 1951; Reilly and McCarthy 1991; Papáček and Tříska 1992) which may be the case for *Cymatia americana* in North America. While none of the *Dasycorixa hybrida* in our study revived after thawing in the lab, the large numbers of this species that were present in air pockets alongside *Cymatia americana*, coupled with the observation that *Dasycorixa hybrida* does not appear to mass migrate into rivers in Saskatchewan to overwinter (Srayko et al. 2022) but is still present in shallow wetlands that are likely to freeze through, indicates that this species may be able to survive within the ice. It is possible that this ability was missed in the current study due to the overall high mortality of corixids and the relatively low numbers of *Dasycorixa hybrida* that were found compared to *Cymatia americana*. In spring, no live individuals of *Dasycorixa hybrida* were found among the meltwater that had flooded the shallower ponds ES7 and RR3074. However, the larger Swale site was not flooded over by meltwater, where live *Dasycorixa hybrida* were found singly in meltwater depressions on the surface of the ice, as well as in meltwater on the periphery of the wetland. It is possible that those on the ice surface had spent the winter encased inside the ice, and were warmed by the sun, creating meltwater depressions around them.

Corixid mortality, position in the ice, and overwintering adaptations

The majority of corixids from ice blocks that were thawed out in the lab did not survive, with 4%–9% reviving in both winters. These values were much lower than the survivability of *Cymatia americana* reported in previous studies from wetlands in Minnesota by Hussey (1921) and Saskatchewan by Mihalicz (2015). Both observed numerous individuals of *Cymatia americana* encased in clusters within air pockets in the ice, of which over 75% showed signs of life after thawing.

Clusters within air pockets

Insects commonly survive exposure to sub-zero temperatures either by being able to tolerate internal freezing, or by avoiding internal freezing altogether through supercooling and the use of antifreeze compounds (Duman et al. 1991; Bale 2002; Bale and Hayward 2009). The supercooling point, the temperature at which spontaneous freezing of fluids occurs, represents the lower lethal temperature limit for freeze-avoiding insects (Salt 1961; Duman et al. 1991; Ditrich and Košťál 2011). Overwintering in a dehydrated state may also convey resistance to freezing (Holmstrup et al. 2002; Danks 2007; Elnitsky et al. 2008). Additional experiments are needed to determine whether *Cymatia americana* and other corixid species are freeze tolerant or freeze avoidant. Several other species of aquatic and semi-aquatic Hemiptera are known to be freeze avoidant, relying on supercooling abilities (Frisbie and Lee 1997; Ditrich and Košťál 2011). However, for *Cymatia americana* to survive as it did without freezing internally, the supercooling abilities of this species must be extensive. In the winter of December 2017–March 2018, temperatures within the top 35 cm of ice averaged −7 °C to −11 °C, and reached as low as −26 °C in the top 5 cm of ice, where most of the corixids that revived after thawing were located. These temperatures are well below the supercooling point of most aquatic insects, which has been estimated at approximately −5 °C (Irons et al. 1993). For example, exposure to temperatures of −2 °C to −8 °C has been shown to result in high mortality of damselfly nymphs (Coenagrionidae) within ice (Daborn 1971; Sawchyn 1971; Duffy and Liston 1985). Brief exposure to cold stress can be endured by most species that have been adequately acclimatized; however, contact with ice poses an additional danger (Frisbie and Lee 1997). Despite efforts to supercool, ice itself is a very efficient nucleator (a structure around which ice will form), so if contact with external ice penetrates an insect's cuticle, this could initiate internal freezing at a much higher temperature than if cooled dry, negating the full extent of an insect's supercooling abilities (Salt 1961; Frisbie and Lee 1997; Danks 2007). For example, Frisbie and Lee (1997) found that the supercooling point of the aquatic Heteropteran *Belostoma flumineum* Say, 1832 (Hemiptera: Belostomatidae) increased from −7.9 °C when cooled dry to −1.2 °C when cooled in contact with ice.

It is possible that becoming trapped within air pockets, especially in groups, could protect corixids from the danger of inoculative freezing by reducing direct contact with the surrounding ice. Mihalicz (2015) and Hussey (1921) both reported groups of 3–50 *Cymatia americana* encased together in the ice, always within air pockets. Hussey (1921) observed that there was often a space of 2–3 mm between the dense corixid clusters and the edge of air pockets. Corixids carry air stores with them in the water (Popham 1960), and when grouped together may collectively merge those air stores (Mihalicz 2015), potentially reducing ice contact. It is possible that corixids positioned in the center of groups may be better shielded from ice contact by their conspecifics. In both years of this study, the largest numbers of corixids that revived after thawing came from the largest two clusters, 20 of 109 individuals from an air pocket 20 cm below the surface of the ice in 2017, and 29 of 298 individuals from an air pocket 1 cm down in 2018. However, the percentage of *Cymatia americana* per air pocket that revived after thawing was the same for both groups and corixids encased alone, with no apparent proportional increase in survival with group size. In 2018, the largest groups tended to be located closer to the surface of the ice, which may have negated any potential benefits conveyed by increased shielding from the surrounding ice due to increased exposure to more extreme temperatures than those encased in smaller numbers further down. It is possible that group size and depth is simply a function of where the largest air pockets are distributed throughout the ice. The overall distribution of air pockets throughout the ice was not examined in this study, just those containing corixids, so it is unknown if large air pockets were available to corixids further down in the ice.

Effect of depth and temperature

Mortality rates of corixids in the ice could be related to the depth at which they were positioned. Shallower depths could increase exposure to extreme temperatures. While Hussey (1921) and Mihalicz (2015) found groups of *Cymatia americana* in the ice at depths of 8–20 cm below the surface, most of the corixids examined in this study were positioned higher in the water column, with the mean depth at which groups and pairs in air pockets were encased at ∼5–8 cm down. Temperature loggers in the wetlands revealed that the top 5 cm of ice was exposed to lower temperatures, with more frequent and drastic fluctuations throughout the winter, than further down. It is likely that these temperatures were more extreme than those examined by Hussey (1921), as the pond in that study still contained unfrozen water beneath the ice in January, despite being only ∼50 cm deep, similar to our wetland sites. Mihalicz (2015) also reported consistent snow cover of 40–70 cm depth across the study wetland, which would have provided better insulation for the underlying ice (Danks 1971; Sawchyn and Gillot 1975), as opposed to the uneven cover that we observed in both study years. For example, Sawchyn (1971) reported that snow cover was crucial for the survival of damselfly nymphs overwintering in the ice of a shallow pond in Alberta, Canada. Most of the sampling in our study was also carried out later in winter, from 10 February to 19 March, as opposed to 15 January (Hussey 1921) and 17 February (Mihalicz 2015). Increased time in the ice, with greater chance of being exposed to extreme and highly fluctuating temperatures, may lead to higher mortality (Daborn 1971). However, there was no difference in the proportion of corixids that revived from February to March in our study (Fig. S8). In addition to lower temperatures overall, temperature fluctuations add additional danger for insects that overwinter in ice, as freezing tolerance and abilities to resist internal freezing can be reduced with increased freezing and thawing (Duman et al. 1991; Irons et al. 1993; Marshall et al. 2014). These factors may have acted in concert with the shallower depths at which corixids were encased to produce greater mortality rates than these previous studies.

The depth in the ice at which corixids become encased could represent a trade-off between increased thermal buffering and having to endure harsh conditions beneath the ice in fall for longer, such as low oxygen and increased solute concentrations (Danks 2007). Hypoxic conditions under ice may prevail when deep snow cover inhibits photosynthesis (Huang et al. 2021) and can result in mortality even among taxa that are capable of anaerobic metabolism (Nagell 1977; Lillie 1991; Hoback and Stanley 2001). Hypoxic conditions under the ice can result in extensive winterkill of corixids (J. Acorn, personal communication, 2022). No corixids were collected from the water beneath the ice during March at the deeper Swale site; however, efforts at collecting corixids from beneath the ice at this site were very limited, consisting only of 2 min of sampling with a small net. Earlier on in November, it was observed that corixids were becoming encased in newly formed air bubbles in the ice almost as soon as a solid layer had begun to form over the wetlands (Fig. S3). Dormancy within the ice for a longer period of time may allow corixids to better conserve energy stores throughout the winter (Danks 2007). Becoming encased closer to the surface may also allow for earlier release into meltwater on the surface of the ice in spring, with dark corixid clusters melting the ice around them faster due to increased heat absorption from sunlight (Mihalicz 2015).

Whether corixids enter air bubbles in the ice as an adaptive strategy for overwintering or are trapped within them due to other means is unclear. It is possible that the advancing ice front concentrates corixids from the water column, both living and dead, together into clumps. Corixids may also become trapped in air pockets accidentally while skimming along the underside of the ice or actively seeking out air stores. During the winter, aquatic insects that use a physical gill for respiration may be able to rely strictly on the absorption of oxygen into air stores when temperatures are cold and the concentration of dissolved oxygen in the surrounding water is high (Gittelman 1975; Balmert et al. 2011; Seymour and Matthews 2013). However, corixids are also able to trap small gas bubbles and use them to augment their own air supply when brushing along plants or the underside of ice (Ege 1915; Popham 1960). It is possible that this could lead corixids to seek out air bubbles during low oxygen conditions. For example, mudminnows (*Umbra limi* (Kirtland, 1841)) have been shown to breathe oxygen directly from gas bubbles trapped under the ice in a shallow lake that becomes anoxic in winter in Wisconsin, USA (Klinger et al. 1982; Magnuson et al. 1983). These bubbles were composed of varying mixtures of oxygen, methane, and nitrogen (Klinger et al. 1982). We also do not know exactly how the bubbles in our study wetlands were formed or how their gaseous composition could affect the survival of corixids trapped inside.

Fitness consequences of migration vs. overwintering in ice

Remaining dormant in ice over winter could have benefits to energy storage. Overwintering within ice may require the storage of lipids and the production of compounds that confer freeze tolerance or resistance, such as glycerol (Somme 1982; Duman et al. 1991; Marshall et al. 2014). However, when these cryoprotectant compounds are no longer needed, they may be converted into compounds such as glycogen, to be used for other functions such as reproduction (Storey and Storey 1996; Hahn and Denlinger 2007). Meanwhile, for migratory species of corixids, lipid reserves are shared by both flight muscle and ovarian development (Young 1965; Reilly and McCarthy 1991), and in at least one species of corixid, *Cenocorixa bifida*, it has been demonstrated that once flight muscles are formed, they are not degenerated in ovipositing females or over the course of the winter (Scudder 1971). Unlike corixids that invest energy into cold hardiness, those that invest energy into wing muscle development may be unable to later reclaim that energy for reproduction. In addition to these energetic advantages, corixids that overwinter in habitats that freeze solid may find themselves in an environment that is relatively free of predators and competitors when spring arrives, compared to bodies of water that do not freeze through. For predatory species like *Cymatia americana*

(Reilly and McCarthy 1990), they may also find a ready food source in the form of chironomids and other small invertebrates that are released from the ice in early spring.

The trade-off to any advantages conveyed by overwintering in wetland ice may be the potential for high mortality. In the spring of 2018, snowmelt created by rapidly increasing temperatures in April flooded the ice in the smaller wetland sites, liberating thousands of corixids from the surface of the ice in site ES7. Out of the several thousand that were randomly collected from this site, approximately 10%–20% appeared to be alive, a slightly higher revival percentage than we observed in the lab. However, the mortality associated with migration may also be high, such as from predation (Srayko et al. 2022), failing to find suitable overwintering sites, and being crushed by ice scouring in rivers in spring (S. Srayko, personal observation). The relative advantages of the two strategies for corixids may ultimately depend on winter conditions.

Noncorixid invertebrates

Invertebrates other than corixids were also found overwintering in the ice, encased in air bubbles with or without corixids, or encased solidly. Relatively little information exists on the overwintering abilities of many aquatic taxa that inhabit shallow waterbodies (Daborn 1971; Olsson 1981; Danks 2007). Haliplid adults and larvae were found inside air bubbles alongside corixids, with haliplid adults exhibiting a much higher revival percentage than the corixids. To our knowledge, no records exist of this taxon overwintering within ice, save for two individuals found live by Mihalicz (2015) having overwintered in frozen sediment. Some live dytiscid adults were also found sharing air pockets with corixids. In shallow wetlands, dytiscid adults may also overwinter at the base of emergent or shoreline vegetation at the pond edge (D. Larson, personal communication, 2022). While none of the dytiscid larvae revived when thawed from the ice in the lab, live larvae were seen in the meltwater that had flooded the ice in one of the shallow wetland sites in spring, which had frozen solid in winter. We are aware of few other records of dytiscid adults overwintering encased in ice (Danell 1981; DeBruyn and Ring 1999), and no records for dytiscid larvae.

Other taxa that did not appear to be encased in air pockets, but which revived after thawing, included multiple caddisfly taxa, as well as damselfly nymphs, chironomids, and snails. These were either encased solidly in the ice, or may have been positioned next to frozen macrophytes or in frozen sediment at the bottom of ice blocks. Phryganeid and leptocerid caddisfly larvae that were found frozen solidly within the ice in 2018 all revived once thawed. The larvae of several caddisfly species are known to be freeze tolerant, and are able to endure being frozen into ice and sediment (Olsson 1981; Wiggins and Winchester 1984; Danks 2007). The ability of coenagrionid damselfly nymphs to survive freezing into pond ice appears to be well known (Daborn 1971; Sawchyn 1971; Sawchyn and Gillot 1975; Duffy and Liston 1985). While most of the specimens in our study did not revive after thawing, the revival rate of ∼13% was similar to the recovery of specimens observed by Daborn (1971) from a shallow wetland in Alberta. We have found no records of dragonfly nymphs (Anisoptera) successfully overwintering encased in ice, while the ability of chironomids and snails to survive within ice appears to be well recorded (Daborn 1974; Olsson 1981; Danks 2007). While the single notonectid that we found within the ice did not revive, *Notonecta undulata* Say, 1832, has been found to successfully overwinter buried ∼10 cm deep in the mud at the bottom of pools that freeze solid in Manitoba, Canada (Clark 1928). The possibility that corixids may also overwinter deep within mud beneath the ice was not explored in this study.

Implications under climate change

Climate change could have implications for the survival of taxa that overwinter in ice. Global increases in overall temperature are predicted to endure until the end of the 21st century, with temperatures in the Northern Great Plains of the United States potentially increasing by 4 °C (USGRCP 2017; McKenna et al. 2021). For species that experience cold stress, warming could increase survival rates, as the annual abundance of some insect species are heavily regulated by winter conditions (Moore and Lee 1991; Bale 2002). For example, during a mild winter in the Czech Republic, with temperatures averaging around 5 °C, Suchá and Papáček (2008) found more diverse corixid assemblages when compared to a normal winter averaging around −0.8 °C to −0.1 °C. However, a number of stressors are likely to occur with climate change that could also have extensive negative impacts on overwintering survival. Changes in temperature and precipitation could reduce winter snow cover, an important source of insulation for overwintering aquatic insects (Bale and Hayward 2009). Fluctuations in temperature can also be dangerous to overwintering insects, as freezing tolerance and abilities to resist internal freezing can be reduced with increased freezing and thawing, and repeated freezing stress can result in the need to produce higher concentrations of antifreeze compounds (Duman et al. 1991; Irons et al. 1993; Marshall et al. 2014).

Periods of winter dormancy or diapause in insects may be affected by climate change, with entry into these states being delayed or disrupted, avoided completely, or altered such that a return to activity may not be synchronized with optimal conditions (Bale and Hayward 2009). Warming may also have effects on aquatic insect development. For example, Suchá and Papáček (2008) found that different species of *Sigara* were able to accelerate ovarian development by approximately 2 months during a mild winter. Climate change induced alterations to the life histories and survivability of different corixid species that either migrate or reside permanently in breeding habitats could shift the prevalence of different species across the landscape. Many natural wetlands in the PPR have been lost due to anthropogenic activity and drying, particularly small, shallow wetlands (Dale-Burnett and Anderson 2003; Dahl 2014; McCauley et al. 2015) which may be driving much of the seasonal corixid migration into larger habitats (Srayko et al. 2022) due to their unsuitability as overwintering sites for many species. If more of the remaining wetland area across the landscape consists of deeper habitats, in which corixids may overwinter beneath the ice, it is possible that this could increase the prevalence of flightless morphs in different corixid species while diminishing the need to migrate in others (Brown 1951; Young 1961; Popham 1964; Stonedahl and Lattin 1986), reducing the intensity of this seasonal transfer of insect material across the landscape.

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Data availability

Data are available from Srayko et al. (2022), Overwintering of water boatmen (Hemiptera: Corixidae) Federated Research Data Repository; https://doi.org/10.20383/102.0668. Data can also be provided by the corresponding author upon reasonable request.

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The authors declare there are no competing interests.

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Supplementary material

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