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Notes

Observations of cocooned *Hydrobaenus* (Diptera: Chironomidae) larvae in Lake Michigan

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ABSTRACT

Larvae of the family Chironomidae have developed a variety of ways to tolerate environmental stress, including the formation of cocoons, which allows larvae to avoid unfavorable temperature conditions, drought, or competition with other chironomids. Summer cocoon formation by younger instars of the genus *Hydrobaenus* Fries allows persistence through increased temperatures and/or intermittent dry periods in arid regions or temporary habitats, but this behavior was not observed in the Great Lakes until the current study. Cocoon-aestivating *Hydrobaenus* sp. larvae were found in benthic grab samples collected in 2010–2013 near Sleeping Bear Dunes National Lakeshore in northern Lake Michigan with densities up to 7329/m^2. The aestivating species was identified as *Hydrobaenus johannseni* (Sublette, 1967), and the associated chironomid community was typical for an oligotrophic nearshore system. *Hydrobaenus* cocoon formation in the Great Lakes was likely previously unnoticed due to the discrepancies between the genus' life history and typical benthos sampling procedures which has consequences for describing chironomid communities where *Hydrobaenus* is present.

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Introduction

The development of different life history strategies allows aquatic organisms to persist in the face of environmental challenges (Verberk et al., 2008). Members of the family Chironomidae can tolerate a wide variety of adverse environmental conditions including pollution, hypoxia, drought, and extreme cold (Danell, 1981; Irons et al., 1993). Some chironomids survive inhospitable circumstances by simply leaving the area or by burrowing deeper into the sediment (Kornijów, 1992; Yamagishi and Fukuhara, 1972). Other chironomids aestivate/enter diapause, which has been observed in many other aquatic invertebrates including cladocerans, cyclopoid copepods, and asellid isopods (Dietz-Brantley et al., 2002). When entering diapause, some chironomids fashion silk cocoons with their salivary glands (Frouz et al., 2003; Tokeshi, 1995). Onset of winter cocoon formation may be due to lack of food or depleted oxygen (Sæther, 1962), and while the cocoon does not necessarily prevent the chironomid from freezing, it acts as protection against mechanical stress caused by freezing (Danks, 1971, 2004; Olsson, 1981). Drought-resistant species form cocoons to reduce water loss during dry spells and re-emerge when the soil is rehydrated (Benigno and Sommer, 2008; Grodhaus, 1980; Jones, 1975; Steinhart, 2000; Tronstad et al., 2005). Upon emergence, cocoon-aestivating chironomids gain earlier access to food resources and improved conditions, thereby potentially outcompeting their counterparts unable to survive drought (Frouz et al., 2003; Steinhart, 2000).

Cocoon-forming chironomids in the genus *Hydrobaenus* Fries are found in littoral areas of oligotrophic lotic and lentic northern waters (Sæther, 1976). Cocoon aestivation by *Hydrobaenus* has been observed in both temporary habitats (vernal pools and floodplains; Grodhaus, 1980; Steinhart, 2000) and permanent waterbodies (lakes and rivers; Hudson, 1971; Kondo, 1996). In the United States, cocoon aestivation has been observed in South Dakota (Hudson, 1971) and California (Grodhaus, 1980) with suspected aestivation reported near San Francisco Bay (Benigno and Sommer, 2008). Outside of the United States *Hydrobaenus* cocoons have been documented in Japan (Kondo, 1996), Europe (Steinhart, 2000), northern Germany (Mozley, 1970) and in the Northwest Territories, Canada (Sæther, 1976).

Cocoon formation in *Hydrobaenus* typically occurs in the summer during the second or third instar and diapause is terminated when temperatures begin to fall as winter approaches (Grodhaus, 1980; Hudson, 1971; Kondo, 1996; Steinhart, 2000). Hudson (1971) broke diapause by experimentally decreasing temperature from 23 °C to 3 °C and reducing daylight hours from 15.5 to 10.5. Grodhaus (1980) suggested that the summer cocoon may be an obligatory phase for early instars, but Steinhart (2000) found that 28% of *Hydrobaenus lugubris* larvae did not form cocoons under experimental temperature regimes (ranging from 5 to 20 °C) used to simulate seasonal changes. Delaying development until autumn has been hypothesized to reduce competition with

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and predation from other chironomids (Mozley, 1970), and may allow for multivoltinism (Kondo, 1996; Sæther, 1976; but see Steinhart, 2000).

Hydrobaenus has been found in most of the Laurentian Great Lakes (Winnell and White, 1985), but may be more common in rivers, wetlands, and inland ponds than in the lakes proper (Judd, 1964; Krieger and Klarer, 1992; Walther et al., 2006). Here we present the first known observation of aestivation and cocoon formation by *Hydrobaenus* in the Great Lakes with a review of its life history.

Methods

Sample collection

Benthic sediment samples were collected from offshore sites in northern Lake Michigan near Sleeping Bear Dunes National Lakeshore (hereafter, SLBE) from July–October 2010, July–November 2011, May–November 2012, and July–November 2013 at 36 sites (changing yearly) with depths of 10, 20, and 30 m (Fig. 1). At these depths, we targeted sites from three broad substrate categories determined by underwater camera surveys: bare sand, live invasive dreissenid mussel beds with *Cladophora* algae growth, and depositional areas with sloughed, decaying algae, diatoms, and other organic matter. Benthic samples were collected with a standard 523-cm^2 Ponar grab. The sample grab was rinsed of fine sediment in a 5-gallon bucket with 500-μm mesh openings. The sample was then rinsed into a collection jar and placed on ice until returning to shore (~6 h on average), when it was fixed with a 10% buffered formalin solution. Surface water temperatures were recorded from an onboard GPS/depth sounder (Garmin GPSMAP; Garmin International, Olathe, KS), and in 2013 a bathythermograph (SBE 19plusV2 Seacat Profiler; Sea-Bird Electronics, Inc., Bellevue, WA) was used to measure water temperature from approximately 1 m above the lake bottom at each site.

Chironomid identification and analysis

In the lab, samples were stained with rose bengal for at least 24 h to facilitate sorting. All invertebrates from 133 samples were removed, identified to the lowest practical taxonomic unit (usually family; Merritt et al., 2008; Smith, 2001; Thorp and Covich, 2009), enumerated, and stored in 80% ethanol. *Hydrobaenus* cocoons, the encased larvae, and the sand grains to which a cocoon was attached were photographed and measured in Image-Pro Plus 7.0 (Media Cybernetics, 2009). The number of cocoons per sample was correlated with daylight hours, surface water temperature, and lake bottom water temperature in R v3.2.2 (R Core Development Team, 2015). The number of cocoons was log-transformed to achieve normality prior to analysis.

From a subset of 19 samples, six of which contained *Hydrobaenus* cocoons or larvae, we identified Chironomidae larvae and pupae to genus or species. These samples were collected at 10 and 20 m sites at Good Harbor and South Manitou from June–November 2012 and July–November 2013. Larval specimens in each sample were first sorted by size, color, and shape, and then representative individuals (~10%) from each group were mounted in lactic acid on a glass slide with a coverslip. If the individuals mounted were identified as belonging to the same taxon, the rest of the group was counted and recorded as being that taxon as well. Individuals were identified to genus using Andersen et al. (2013). Species identifications, when possible, were determined using Epler (1988); Maschwitz and Cook (2000); Proulx et al. (2013); Roback (1985), and Sæther (2009).

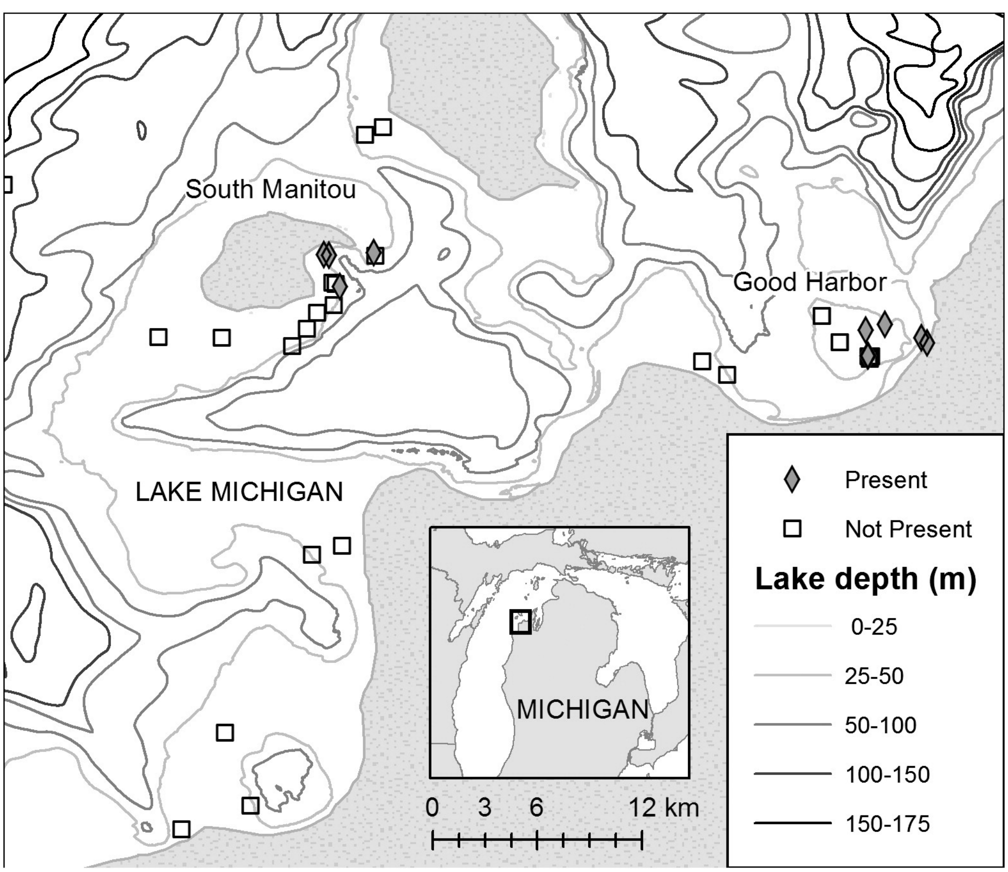

Fig. 1. Benthic sampling locations near Sleeping Bear Dunes National Lakeshore, northern Lake Michigan. "Present"/"Not present" indicate whether *Hydrobaenus* cocoons were found at a given sampling site. Bathymetry contours were derived from Michigan Technological Research Institute et al. (2015).

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Identification of Hydrobaenus sp.

In his revisionary work on the genus *Hydrobaenus*, Sæther (1976) identified 11 species of adult males that occurred in North America. Of those 11 species, eight were associated with their pupal stage and seven with their larval stage. These incomplete larval keys, and the fact that many characteristics used in these keys are not fully developed in the first three instars, limit identification of aestivating second-instar *Hydrobaenus* larvae found in our samples. Because fourth instars, pupae, or adults were not collected in this study, we reviewed which *Hydrobaenus* species were present in the Great Lakes using specimens found in the US Geological Survey Great Lakes Science Center (USGS GLSC) Great Lakes reference collection (identified using Sæther, 1976) to aid in tentatively identifying this species.

Results

Hydrobaenus cocoons were not observed until the 103rd sample processed (of 133 total samples), while processing the 2012 and 2013 samples without order, having already finished those from 2010 and 2011. After their initial discovery, cocoons were found in another 17 of 30 subsequent samples processed since that time, indicating possible error in recognizing cocoons. Samples containing *Hydrobaenus* came from Good Harbor and South Manitou 10 and 20-m deep sites near SLBE (Table 1; Fig. 1). These samples typically came from sites with sand and silt substrate, with some live and dead dreissenid mussels, and low amounts of decomposing material or algae. *Hydrobaenus* cocoons were translucent, flattened cylinders, and the enclosed chironomids were folded into a spiral (Fig. 2). Most cocoons were found attached to coarse sand grains, much like those observed by Kondo (1996); but a few were attached to dead dreissenid mussel shells or fragments. Mean cocoon area was 0.12 mm^2 ($\pm$0.02 s.d., n = 19) with an approximate diameter of 0.4 mm, and the sand grains to which they were attached had a mean area of 1.73 mm^2 ($\pm$1.92 s.d., n = 19) with an approximate diameter of 1.48 mm, indicating very coarse sand (Wentworth, 1922). All encysted *Hydrobaenus* appeared to be in the second instar and were typically 1.05 mm in length ($\pm$0.10 s.d., n = 8) with head capsule widths ranging from 96 to 112 µm.

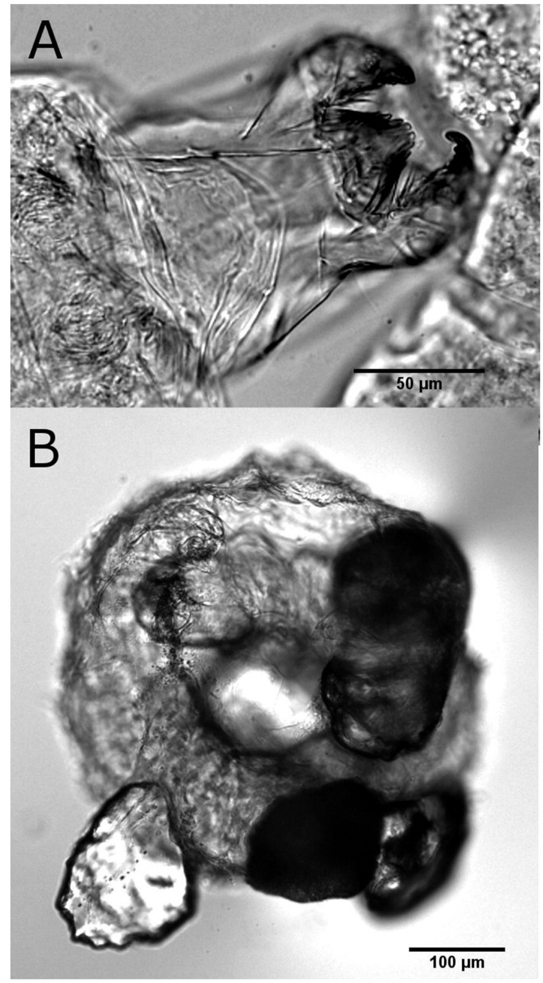

Fig. 2. (A) *Hydrobaenus johannseni* head capsule, ventral view; (B) *H. johannseni* cocoon with small sand grains attached.

Table 1
Site descriptions and density of *Hydrobaenus* cocoons (No./m^2) from Ponar grab samples collected 2010–2013 at Sleeping Bear Dunes National Lakeshore, MI. Surface water temperatures were collected with an onboard GPS/depth sounder and in 2013 lake bottom temperatures (within 1 m of the substrate) were collected with a bathythermograph.

Date	Cocoons/m^2	Water temperature (°C)		Substrate in Ponar grab
		Surface	Bottom	
Good Harbor, 10 m sites				
June 30, 2012	364	19.2	–	Sand, some *Cladophora*, dreissenid mussel shells
September 25, 2012	96	15.6	–	Sand
September 25, 2012	115	15.6	–	Sand, some dreissenid mussels
July 16, 2013[a]	1971	22.2	17.9	Sand, some *Cladophora*, few dreissenid mussel shells
July 21, 2013	1320	21.1	22.2	Mostly sand, some dreissenid mussel shells
August 11, 2013[a]	459	19.4	20.1	Sand and silt, few dreissenid mussel shells, some *Chara* algae
September 11, 2013	1875	19.4	19.2	Sand, few dreissenid mussel shells
September 13, 2013[a]	7329	18.3	20.0	Sand and silt
Good Harbor, 20 m sites				
July 29, 2012[a]	38	22.9	–	75% sand, 25% organic matter, some live dreissenid mussels
September 25, 2012	77	15.6	–	Sand with some dreissenid mussels, *Chara* algae
July 16, 2013[a]	2201	24.6	12.3	Bare sand, few shells
South Manitou, 10 m sites				
June 28, 2012	19	17.1	–	Sand and silt mix, diatom debris, some dreissenid mussel shells
November 5, 2012	38	9.9	–	60% sand, 40% organic matter, live dreissenid mussels and shells
September 17, 2013	287	16.2	17.5	Sand, silt, and *Chara* algae
South Manitou, 20 m sites				
June 29, 2012[a]	19	17.6	–	Thick black sediment
July 15, 2013	325	20.2	15.0	Dark clay, some silt, dreissenid mussels, brown microbial layer
August 15, 2013	115	17.9	10.6	Dark clay, some silt, dreissenid mussels and shells, brown microbial layer

[a] Samples processed for community analysis (Table 2).

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A significant positive correlation between the number of cocoons and surface water temperature was observed ($r = 0.5$, df $= 15$, $p = 0.04$; Fig. 3), while a positive, yet insignificant relationship was observed between the number of cocoons and lake bottom temperature ($r = 0.47$, df $= 7$, $p = 0.2$). A Spearman rank correlation found no relationship between the number of cocoons and the number of daylight hours ($\rho = 0.04$, $p = 0.89$).

A total of 32 chironomid taxa were identified from the 19 Ponar grabs designated for community analysis; each sample contained 8.6 taxa on average (±3.4 s.d.; Table 2). Most of these chironomids identified were third or fourth instars (260–320-μm head capsule width). Despite the fact that cocooned *Hydrobaenus* were only found in 6 of the 19 samples selected for community analysis, they were still the most numerous chironomids identified in July–September. Only three specimens of second-instar *Hydrobaenus*, one found in June, one in October, and the last in November, were not encysted. Common chironomid larvae and pupae of summer included *Micropsectra*, *Paratendipes*, *Orthocladius*, *Parakiefferiella*, and *Phaenopsectra*. Common chironomids of the fall included *Chironomus*, *Microtendipes*, and *Thienemannimyia norena*. *Dicrotendipes fumidus* and *Stictochironomus* were found throughout the sampling period. The chironomid communities were similar between samples containing *Hydrobaenus* cocoons and samples missing cocoons, with a few minor differences. When comparing sample averages from June, August, and September (the months when sample coverage overlapped), we found that those samples containing cocoons had more *Dicrotendipes*, *Monodiamesa*, and *Parakiefferiella bathophila*, while those without cocoons had more *Chironomus*, *Micropsectra*, *Orthocladius*, *Paratendipes*, *Phaenopsectra*, and *Ablabesmyia mallochi*.

By using the USGS GLSC reference collection and narrowing down which *Hydrobaenus* species were found in the Great Lakes, we determined that the aestivating chironomids found at SLBE are likely *Hydrobaenus johannseni* (Sublette, 1967). We found 32 reference slides containing larval, pupal, and adult *Hydrobaenus* specimens from Lake Superior, St. Marys River, Lake Michigan, Lake Huron, St. Clair River, Lake St. Clair, and the Detroit River. Four of the slides had been positively identified by Sæther as *H. johannseni*. We found the specimens on the remaining *Hydrobaenus* slides in the collection to conform to the description of *H. johannseni*, particularly the rugulosity of small papillae on the pupal anal lobe and the position of the ring organ on the larval antennae. Sæther (1976) noted that *H. johannseni* and *Hydrobaenus pilipes* are the most common species of *Hydrobaenus* in temperate North America and that the ring organ position and anal lobe papillae clearly delineate the two species.

Discussion

Cocooned *Hydrobaenus* larvae have not previously been documented in the Laurentian Great Lakes, but 57% of the Ponar grab samples from

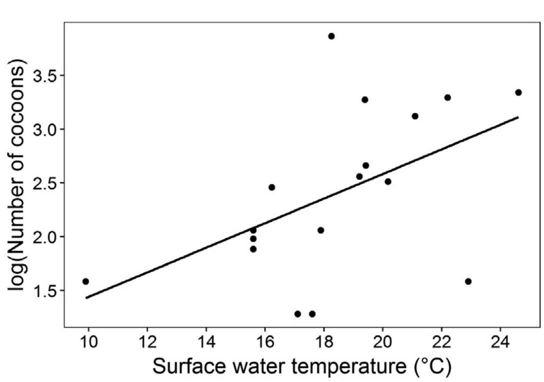

Fig. 3. Correlation between the number of *Hydrobaenus* cocoons per sample (log-transformed) and surface water temperature (°C).

Table 2
Mean densities of chironomid larvae and pupa taxa (No./m^2) per month from a subsample of Ponar grab samples collected 2012–2013 (n = 19) at Sleeping Bear Dunes National Lakeshore in northern Michigan.

Taxon	June	July	Aug.	Sept.	Oct.	Nov.
	n = 4	n = 3	n = 3	n = 5	n = 1	n = 3
Chironominae						
Chironomini	19	13	0	0	0	0
Chironomus anthracinus gr.	81	26	153	1359	670	555
Cladotanytarsus	0	0	13	4	0	0
Cryptochironomus blarina	10	19	0	0	0	0
Cryptochironomus	0	0	0	0	0	13
Dicrotendipes fumidus	340	57	38	367	746	70
Dicrotendipes modestus	43	0	0	4	0	0
Micropsectra	1258	166	13	0	0	45
Microtendipes	0	0	0	8	785	0
Paratanytarsus	0	0	0	11	0	0
Paratendipes	488	6	0	0	0	19
Phaenopsectra	268	38	32	27	38	13
Polypedilum scalaenum	14	89	6	19	0	70
Polypedilum simulans	0	6	0	11	0	0
Pseudochironomus	5	0	0	8	0	6
Stictochironomus	10	147	51	214	115	51
Tanytarsus	5	0	0	4	0	0
Diamesinae						
Potthastia	19	0	0	0	0	0
Potthastia longimanus gr.	5	6	13	8	0	0
Orthocladiinae						
Cricotopus	19	13	0	4	19	0
Cricotopus bicinctus gr.	0	0	0	4	0	0
Cricotopus laricomalis gr.	0	0	0	4	0	0
Heterotrissocladius oliveri	0	26	0	0	0	0
Hydrobaenus johannseni	5	1391[a]	153[a]	1466[a]	19	6
Hydrosmittia ruttneri	14	0	0	31	0	0
Orthocladius	349	6	0	15	19	0
Parakiefferiella bathophila	19	287	0	0	0	0
Psectrocladius	10	0	6	11	19	0
Prodiamesinae						
Monodiamesa	5	32	0	4	0	0
Tanypodinae						
Ablabesmyia mallochi	81	32	6	0	0	0
Procladius (*Holotanypus*)	0	0	6	0	19	0
Thienemannimyia norena	10	0	6	15	96	0

[a] Cocooned.

SLBE that were actively searched for cocoons contained large numbers of aestivating second-instar *H. johannseni* that dominated the observed chironomid communities. Potential reasons why this behavior has not been previously observed in the Great Lakes include the scarcity of *Hydrobaenus* observations, a mismatch between typical sampling gear and sampling seasons and the life history of *Hydrobaenus*, or error in washing or processing samples.

Observations of *Hydrobaenus* spp. are sporadic in the Great Lakes proper (Fig. 4). During large-scale benthic sampling surveys of Lake Huron (1972, 2000–2003; Nalepa et al., 2007), and Saginaw Bay (1987–1996; Nalepa et al., 2002), only two *Hydrobaenus* were found out of >1400 total Ponar grabs. The first was found in 1987 at a 12.5-m site with "silty sand" in Saginaw Bay (Nalepa et al., 2002), and the other was found in 2002 at an 89-m site in Georgian Bay (Nalepa et al., 2007). In eastern Lake Michigan, a survey offshore from the J. H. Campbell Power Plant at 3–15-m depths found *Hydrobaenus* most often at 15 m (116/m^2) in a combination of coarse and fine sediments (Winnell and Jude, 1984). The highest densities of *Hydrobaenus* near the Great Lakes were recorded in connected shallow rivers and inland lakes, while fewer were found in larger systems. High densities (226–12,514/m^2) were found in Old Woman Creek, an Ohio tributary of Lake Erie, with highest densities in the winter and spring (Krieger and Klarer, 1992). Muskegon Lake near eastern Lake Michigan yielded 43–3273/m^2 at 0.03–2-m sites in August 2011 (Rediske and Nelson, 2013). *Hydrobaenus* in Lake St. Clair were rare (~1/Ponar grab) at 4 and 6-m sites with fine sand and silt, and listed as 'present' in the St. Clair River (Griffiths, 1987; Hudson et al., 1986).

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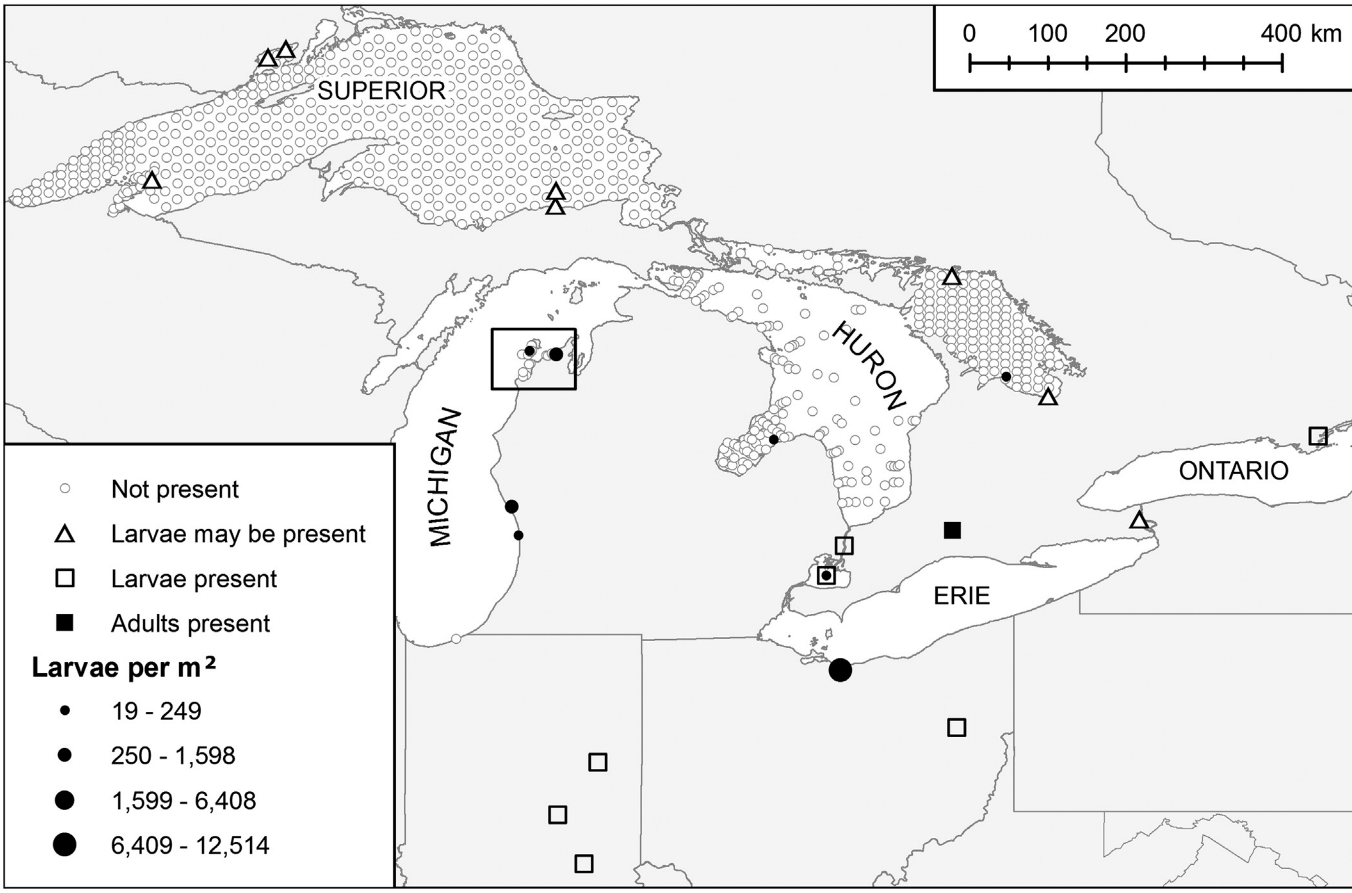

Fig. 4. Locations and densities of *Hydrobaenus* spp. larvae and adults in the Great Lakes region drawn from Cook (1975); Garza and Whitman (2004); Griffiths (1987); Hiltunen (1969); Hudson et al. (1986); Johnson and Brinkhurst (1971); Judd (1964); Krieger and Klarer (1992); Loveridge and Cook (1976); McMurry and Newhouse (2006); McShaffrey and Olive (1985); Nalepa et al. (2007, 2002); Rediske and Nelson (2013); Warwick (1980); Winnell and Jude (1984), and Winnell and White (1985). Empty grey dots ("Not present") indicate a location sampled where no *Hydrobaenus* spp. were observed. Empty triangles ("Larvae may be present") indicate locations where *Hydrobaenus* spp. may have been found but identification is in doubt. Black dots indicate the total number of *Hydrobaenus* spp. larvae found (standardized to No./m^2).

Older records regarding *Hydrobaenus* spp. are difficult to parse: distribution maps and counts may reflect potentially inaccurate identifications of the genus and related genera prior to taxonomic revision by Sæther in 1976. In a review of Lake Michigan benthos written prior to this revision, Mozley and Howmiller (1977) stated that "…comparison of [chironomid] records is difficult or impossible" and that the "typical larva of the profundal zone … has been listed as *Spaniotoma*, *Hydrobaenus*, and *Metriocnemus*." Further, *Hydrobaenus* spp. and *H. pilipes* have also been referred to as *Orthocladius* or *Trissocladius* (ITIS, 2015). Thus, it is possible that some instances of *Orthocladius* found in large-scale benthic surveys of 1973 in Georgian Bay (Loveridge and Cook, 1976) and in Lake Superior (Cook, 1975) may actually represent *Hydrobaenus* (Winnell and White, 1985).

Given that records of *Hydrobaenus* are uncommon, little is known about its life history in the Great Lakes. Elsewhere, *Hydrobaenus* commonly aestivates in cocoons during the summer months and emerges when temperatures cool or when the habitat is rehydrated (Benigno and Sommer, 2008; Grodhaus, 1980; Hudson, 1971; Kondo, 1996; Steinhart, 2000). Adult emergence occurs in the early spring (Raunio et al., 2007; Tokeshi, 1995), the timing of which changes by locale: early February in Japan (Kondo, 1996), February–April in eastern Europe (Steinhart, 2000), February–May in Ontario (Judd, 1964), March in Ohio (McShaffrey and McCafferty, 1991), and April–May in Kansas (Ferrington et al., 1994). The USGS GLSC reference collection also provided additional information regarding development and emergence of *H. johannseni* in the Great Lakes from 1983 to 1996. A third-instar larva was collected in Lake Superior on April 20, and 11 fourth-instar larvae between May 5–25 in the St. Marys River and Lake St. Clair. Twenty adults were collected at all the sites listed above from April 29 to May 25. In the present study, so few free-living *Hydrobaenus* larvae were found that it is impossible to infer at which temperatures larvae begin to form cocoons or emerge from them, but the positive relationship between the number of cocoons and surface water temperatures suggests that water temperature may be a potential trigger for aestivation. Whether the cocoon phase of early instars is obligatory or occurs only in some generations or individuals remains unknown due to the limited scope of our study.

Standard benthic sampling techniques and sampling dates may have further reduced the probability of *Hydrobaenus* larvae detection. Most of the large-scale benthic surveys that were reviewed used sieves or elutriation sleeves with 500–600-μm mesh to decrease processing time, but smaller invertebrates and early-instar chironomids are lost (Hudson and Adams, 1998; Nalepa and Robertson, 1981). Since *Hydrobaenus* exhibits early spring emergence, the larger third- or fourth-instar larvae that are more likely to be captured by 500–600-μm meshes are not present until late fall through early spring. The high densities of *Hydrobaenus* found in Old Woman Creek, Ohio, occurred in February and March (Krieger and Klarer, 1992). In eastern Europe, Steinhart (2000) found up to 20,592/m^2 in February and March 1995. In a California floodplain sampled from November 2004 to January 2005, *Hydrobaenus saetheri* made up 74% of chironomids in sediment and 99% of chironomids in floodplain drift samples (Benigno and Sommer, 2008). Sampling by Nalepa et al. yielded little to no *Hydrobaenus*, and took place between late April to early November in Saginaw Bay (2002) and in July and September in the whole of Lake Huron (2007). Interestingly, those observed by Rediske and Nelson

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(2013) in Muskegon Lake were found in August, but information regarding instar was not presented.

Standard mesh sizes ≥500 μm could also allow the passing of *Hydrobaenus* cocoons, which were only 80% of that size. While the cocoons found in the present study were attached to sand grains that were larger than 500 μm, those found by Grodhaus (1980) seem to have been freely distributed in sediments which may have been too small for attachment. The average *H. johannseni* cocoon we found had a diameter ~400 μm and could have been washed through standard mesh if unattached or if forcibly dislodged from substrates during washing. In the current study, we found cocoon residue or ripped remains on some sand grains, which could have been caused by the washing process or could also be evidence of past emergence. Rose bengal stain augmented the detection of cocoons in this study, which clearly distinguished cocoons from the craggy surface of some large sand grains. Detection of cocoons did not occur until after the 2010 and 2011 samples had already been processed, and whether this is due to technician error or differences in *Hydrobaenus* abundances between years or locations is unknown.

Due to the coarse mesh size employed here, most early instar chironomids were filtered out of the samples; subsequently, comparisons between the numbers of aestivating *H. johannseni* and the densities of other chironomid genera cannot be drawn because they do not accurately reflect relative abundance of the entire chironomid community. However, the taxa composition of the observed chironomid community at Sleeping Bear Dunes appears similar to those in comparable Great Lakes habitats. In southeastern Lake Michigan, nearshore habitats (4–20 m deep) were similarly occupied by *Cryptochironomus*, *Psectrocladius*, *Cladotanytarsus*, *Polypedilum*, *Potthastia*, *Chironomus anthracinus* gr., *Monodiamesa*, *Procladius*, and *Micropsectra*; however, these areas hosted some genera not found at SLBE: *Robackia*, *Saetheria*, *Paracladopelma winnelli*, and *Paracladopelma camptolabis* gr. (Winnell and White, 1985). These missing genera, with the exception of *Paracladopelma winnelli*, are most abundant in shallower waters (<10 m; Winnell and White, 1985) not sampled in the current study.

Common benthos sampling techniques used in the Great Lakes may not be suitable for detection of small cocoons or early-instar chironomids, which may skew characterizations of chironomid communities toward larger genera that emerge in late spring or summer. Cocoon building for protection appears to be widespread in Chironomidae, but whether the cocoon stage of *Hydrobaenus* early instars is obligatory or only used by some generations in the Great Lakes remains undetermined.

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