Hydrobiologia (2023) 850:1091–1108
https://doi.org/10.1007/s10750-023-05145-2

PRIMARY RESEARCH PAPER

Movement and surrounding community of the understudied and endangered *Ligumia recta* (Mollusca, Unionidae)

Meghan E. Martinski · Daelyn A. Woolnough

Received: 10 February 2022 / Revised: 6 January 2023 / Accepted: 9 January 2023 / Published online: 31 January 2023

Abstract Native freshwater mussels (unionids) are indicators of water quality, with unique behaviors and movement patterns. Many of these species are endangered, yet basic movement and co-occurring community data are lacking for successful unionid conservation. In this study, movement, community, and habitat use among *Ligumia recta*, an endangered unionid in Michigan, were analyzed across four rivers in central Michigan. The effects of sex, community, substrate use, and other abiotic factors on the movement and occurrence of *L. recta* were quantified. 24 *L. recta* individuals were found with variable male:female ratios and were monitored bi-weekly. Over the recapture period, *L. recta* moved an average minimum convex polygon of 1.43 m^2 per day but was variable among rivers. 19 unionid species were found occurring with *L. recta*; ~13 species in the same river reach as *L. recta* and ~5 species in closer proximity to *L. recta*. The tribe Lampsilini most often occurred in close proximity to *L. recta*. This study identified basic movement and occurrence patterns of *L. recta* and provides a better understanding of the status of *L. recta* in Michigan. Our study highlights useful methods in understanding imperiled unionids, expanding the knowledge of their movement, behavior, community assemblages, and habitat use.

Keywords Habitat · Behavioral analyses · Burrowing · Community · Mussels · Mark-recapture

Handling editor: Manuel Lopes-Lima

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05145-2.

M. E. Martinski · D. A. Woolnough (✉)
Biology Department and Institute for Great Lakes Research, Central Michigan University, Mount Pleasant, MI, USA
e-mail: wooln1d@cmich.edu

M. E. Martinski
e-mail: martinskim7@gmail.com

M. E. Martinski
Honors Program, Central Michigan University, Mount Pleasant, MI, USA

Present Address:
M. E. Martinski
Texas State University, San Marcos, TX, USA

Introduction

There are 300 mussel species native to North America and over 40 mussel species native to Michigan (family Unionidae; hereafter unionid); all are indicators of water quality and have the ability to filter water (Graf & Cummings, 2007; Haag 2012). With various sizes, morphology, and life histories, each unionid species has its own unique characteristics and habitat requirements, even within a single watershed. As concern for environmental conservation increases due to increased landscape changes (e.g., urbanization, agricultural development), research efforts are needed for these understudied unionids. Knowledge gaps for many unionids often include basic life history data (FMCS, 2016). Unionids are important to a balanced freshwater system due to their role as filter feeders, making the conservation of this group of high importance. Further, the nutrients that unionids excrete and bio-deposit aid in the stimulation of stream production, cycling energy and nutrients (DuBose et al., 2019; Atkinson & Forshay, 2022). Conservation of unionids is highlighted on a state level in the Michigan Wildlife Action Plan—a framework that serves to conserve Michigan wildlife (Derosier et al., 2015). To promote the conservation of unionids on a national scale the 1998 National Strategy was created (NNMCC, 1998) and updated in 2016 (FMCS, 2016); these priorities, focusing on the United States, parallel international priorities for freshwater mollusks (Ferreira-Rodriguez et al., 2019). Little is known about species that are endangered in the Laurentian Great Lakes region, and this study contributes to the national and international conservation strategies by identifying and quantifying previously unknown characteristics of rare species and surrounding communities that are essential in conserving molluscan fauna (FMCS, 2016; Ferreira-Rodriguez et al., 2019).

One of these understudied and under-represented species is the Michigan state endangered *Ligumia recta* (Lamarck, 1819) (Black Sandshell). Other states have assessed *L. recta* as being a species of high risk in terms of localized extinction (Gangloff et al., 2013). *Ligumia recta* is listed as near threatened globally according to the International Union for Conservation of Nature (IUCN) Red List. Although the IUCN Red List ranking for *L. recta* has not been assessed since June of 2015 (IUCN, 2020), this species remains understudied, with much of the data collected prior to the twenty-first century. Current occurrence patterns within rivers are unknown in Michigan, and an absence of recent data of a State of Michigan endangered species within the Laurentian Great Lakes prompts updated research and conservational assessment of *L. recta* (MNFI, 2020). Due to lack of data, it is difficult to assess *L. recta* population patterns, distribution, behaviors, and habitat use, all of which are necessary for successful conservation.

The genus *Ligumia* historically had 3 species, including *L. recta*, *L. nasuta* (Say, 1817) (Eastern Pondmussel), and *L. subrostrata* (Say, 1831) (Black Pondmussel). Recently, the genus *Ligumia* has changed, with the classification of *L. nasuta* and *L. subrostrata* revised to the genus *Sagittunio* (Watters, 2018; Mulcrone & Rathbun, 2020). With only one species remaining in this genus, it is imperative that basic life history, including movement, is understood in Michigan to conserve species biodiversity. Measuring up to 25 cm in length, *L. recta* represent the largest, elongate species in Michigan (Mulcrone & Rathbun, 2020). *Ligumia recta* are also one of the few unionids that are sexually dimorphic (Mulcrone & Rathbun, 2020). Unlike other unionids that burrow in the bottom of rivers and lakes, *L. recta* are reported to stay on the surface of the riverbed laying on their sides, often having to do with their reproductive display methods (Corey et al., 2006) as a result of their large size. Further information on *L. recta* burrowing behavior, specifically what habitat *L. recta* use, is unquantified.

Movement in relation to abiotic and biotic factors, within an aquatic waterbody, is important for a full understanding and comparison among unionid populations. As more movement data becomes available, it appears that unionids may move more during adult stages than previously assumed, and these movement data are becoming important for conservation. While movement of adult unionids is known to be in small increments over time, it can be significant in their survival and reproduction (Amyot & Downing, 1997; Sullivan & Woolnough, 2021). Unionids are sperm casters, meaning that fertilization occurs via the males releasing their sperm into the water column, where downstream females then filter it into their gills to fertilize their eggs (Gates et al., 2015). Therefore, for unionids, relative adult movement (i.e., active movement) between sexes plays a role in reproductive success. Unionids have a unique life cycle with larval parasitism that involves attachment to freshwater fish gills during an obligate host fish life stage (Graf & Cummings, 2007). During this pre-adult life stage, the host fish may provide large movements. Following the drop-off of larval unionids from the fish gills, juvenile survivorship is dependent on whether they land in suitable habitat—this can include substrate type and temperature. Conditions must all be ideal for unionids to grow successfully, with varying thermal tolerances at different life stages (Pandolfo et al., 2010). Unionids are ectotherms, therefore, temperature can be a large determinant of adult behavior and movement as well, as observed during the cold winter months with burrowed unionids (Lurman et al., 2014). Not much is known about optimal depth, flow, and position within rivers for *L. recta*, and understanding their habitat use and hydraulic characteristics (e.g., ideal habitat for survival) can help in future conservation efforts. Species may disperse to move and expand population range into uninhabited areas or connect to other populations in an established range. Movement into new areas results in an increase in geographic range and establishment of new and/or larger populations (Strayer, 2008). Although the majority of unionid movement occurs via the host fish, adult unionids do have the capability to move around with their muscular foot or passively in flowing rivers. Studying movement, especially within and among species, can be helpful for understanding reproduction efforts and the effects of depth and flow on a species that has varying burrowing habits (Sullivan & Woolnough, 2021). In fact, community assemblages and the reproductive cycle of a unionid impacts burrowing behavior (Sansom et al., 2018). A loss of biodiversity can be detrimental to an ecosystem, making remaining organisms vulnerable and possibly resulting in the loss of imperiled fauna (Burlakova et al., 2011). Being aware of the surrounding unionid community can be important to understanding how to determine species-specific conservation actions for rare species like *L. recta*. While a multitude of surveys have been done across North America for unionids, including surveys in the Great Lakes region (Metcalfe-Smith et al., 2000; Sheldon et al., 2020; Goguen et al., 2022), little is known about which unionids are likely to occur together. Species community data can be helpful for future conservation efforts as well as provide an understanding of co-occurring unionids.

For this study, there were three questions: (1) What are the movement and behavioral trends among *L. recta* found in different Laurentian Great Lakes watersheds during the summer period when they are likely the most active? (2) What are the unionid community assemblages that are co-occurring with *L. recta* across and within different Laurentian Great Lakes watersheds and are assemblages consistent at different spatial scales? (3) What habitat does *L. recta* use? To answer these questions, we performed species-specific searches and a mark-recapture monitoring study for *L. recta*, as well as surveying the sites for other unionid species that may be co-occurring with *L. recta*. The answers to these questions will provide a comprehensive and quantitative overview of *L. recta* that can be used in national and international conservation actions.

Materials and methods

Study sites

Data mining of past records of *L. recta* from past Central Michigan University research within the Laurentian Great Lakes watersheds was performed. To effectively assess preferred habitat and distribution of *L. recta* sites were selected based on previous surveys done in the Grand River and Saginaw River watersheds located in Michigan, USA. These two watersheds represent two different Laurentian Great Lakes watersheds, with the Grand River watershed flowing into Lake Michigan and the Saginaw River watershed flowing into Lake Huron. Four sites were selected, two in each watershed, based on their presence of live *L. recta,* accessibility, and presence of healthy unionid community (Table 1; Fig. 1). Based on past tactile surveys done by Chambers & Woolnough (2016) in the Chippewa River and other monitoring surveys in the Grand River (Woolnough et al., 2020), sites were chosen if they had at least two ($n \geq 2$; low due to their endangered status) recorded *L. recta* adults found during surveys within the past five years. Reconnaissance trips were taken to the sites to determine if the selected sites were searchable and accessible (Table 1). The number of sites were limited to four due to the global COVID-19 pandemic and safety precautions taken by researchers.

The four sites in this study included the Maple River (MA) and Grand River (GR) that flow into Lake Michigan and the Chippewa River (CH) and Pine River (PI) that flow into Lake Huron all within the Laurentian Great Lakes watershed (Fig. 1). MA was located in a rural area of Elsie, MI with an agricultural field bordering the riverbank. The site was located downstream of a low head dam and was observed to be a narrow, shallow, and generally a slow-moving stretch of the Maple River. GR was located in Lyons, MI in a rural area that was downstream (> 1 km) of a

Table 1 Four sites surveyed for *Ligumia recta* in 2020, Michigan, USA. Each Great Lakes watershed has one upstream location and one downstream location. Number of species found includes *L. recta*

River Name	Site Code	Great Lakes Watershed	Upstream or Downstream	Latitude	Longitude	Number of visits	Person hours searched	Number of *L. recta* tagged* (male: female)	Unionid individuals pph (timed searches)	Number of Species found (# of dominant taxa)
Maple River	MA	Michigan	Upstream	43.090162	− 84.404745	6	13.83	7 (1:1)	29.14	15 (6)
Grand River	GR	Michigan	Downstream	42.985908	− 84.945311	6^	12.73	6 (1:2)	11.31	13 (4)
Chippewa River	CH	Huron	Upstream	43.625630	− 84.71635	6	13.92	5 (1:1.5)	23.49	11 (1)
Pine River**	PI	Huron	Downstream	43.602460	− 84.291687	6	12.28$^{\#}$	6 (1:0.2)	105.93$^{\#}$	12 (1)

*Number of added *L. recta* after visit one included in this total: MA = 2 (revisit 2), GR = 1 (revisit 2), CH = 1 (revisit 1), PI = 4 (revisit 1)

**Pine River site is confluence of Pine and Chippewa Rivers

^Two of the total six individuals were found prior to the start of the study, and therefore are not included in person hours searched

$^{\#}$*Actinonaias ligamentina* were found in high abundances (see methods and results)

large hydroelectric dam. The upstream reach of GR was characterized as a wide, fast-moving, and deep part of the Grand River that was just downstream of a low head dam removal. The downstream reach of GR, which is ~250 m downstream of the upstream reach, was characterized by being a wide, fast-moving, yet slightly shallower, riffle part of the Grand River. Surveys at this location were done along stretches of the bank, as the center of this stretch of the river was very deep (> 2 m) and swift. CH was just east of Mt. Pleasant, MI and located in a rural area just downstream of a local golf course. This site was in a residential area with houses along the riverbank. The river at CH was characterized as narrow and shallow with moderate flow. PI was located in Midland, MI at the Chippewa Nature Center. This site is immediately downstream of the confluence of the Chippewa and Pine River, but for this study was named the Pine River site for convenience. The site is located in a rural area with some development for a nature center, including a kayak and canoe launch just off the bank of this site. The river was generally wide, shallow, and had moderate flow.

Initial field surveys

Initial surveys were completed in the four selected areas via tactile hand searches beginning in June and ending in August during the summer of 2020. Timed searches using snorkeling and tactile techniques (Strayer & Smith, 2003) were used to collect live unionids by hand for ~12 person hours (ph) at each site; 4.5 ph is the suggested minimum effort used for detecting rare species (Metcalfe-Smith et al., 2000) in other Great Lakes watersheds. The number of ph at each site during the initial visit and timed survey was recorded. If any species were abundant (e.g., too many to hold in each surveyor's ~10 liter collection bag), that species could be excluded from a portion of the survey in order to properly assess all species; ph for each species was adjusted accordingly (see Results). The number of individuals per person hour (pph) was calculated for each species found at each site.

All individuals found were identified to species according to Mulcrone & Rathbun (2020), counted, and measured for length (mm) using calipers; this community is hereafter referred to as the river community (this could be considered time search survey

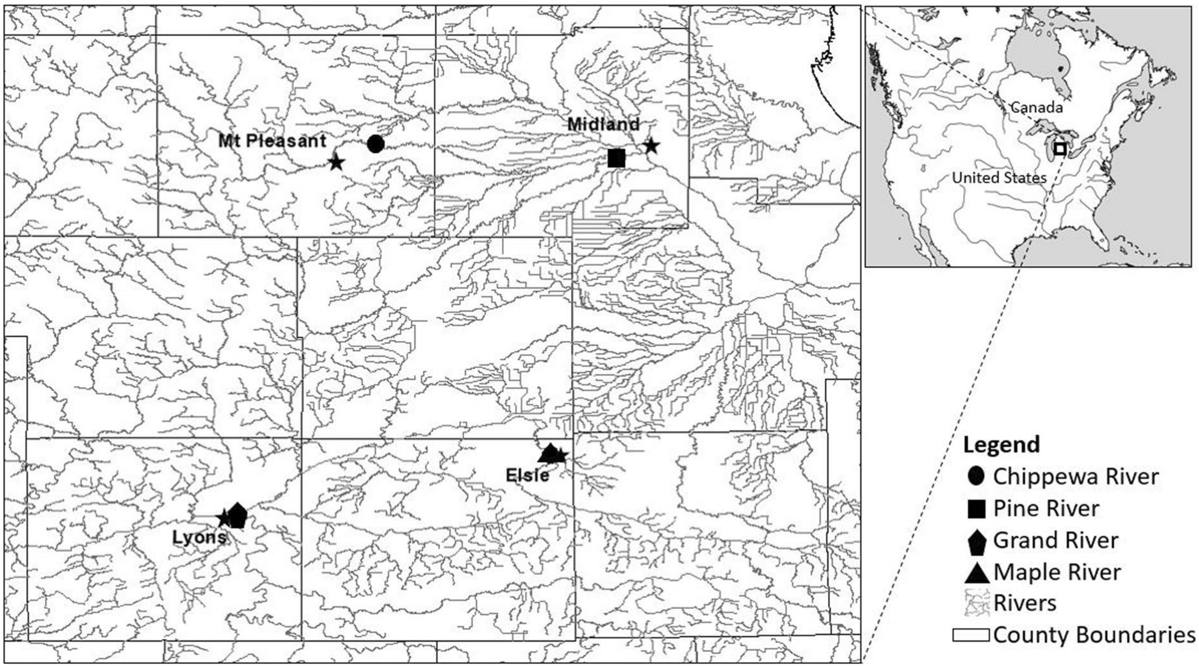

Fig. 1 Map of the four sites sampled for *Ligumia recta* in Michigan, USA during summer 2020. The Lake Michigan watershed was represented in this study by the Maple (MA) and Grand (GR) rivers, located in Elsie and Lyons, respectively. The Lake Huron watershed was represented in this study by the Chippewa (CH) and Pine (PI) rivers, located in Mt. Pleasant and Midland, respectively. The Grand River site included two sites ~ 250 m apart from one another. Stars represent centroid of closest town (named on Figure)

data). Additionally, all *L. recta* counts, sizes (length, width, and height), sex, gravidity (visual check of inflated gills in females by prying open valves slightly), and photos were taken during these surveys. To successfully track movement of all *L. recta* individuals, a Biomark® HPR Plus Handheld PIT Tag Reader (Biomark, Inc. Boise, ID) and compatible Passive Integrated Transponder (PIT) tags (12 mm APT12 tags) were used. Upon finding a *L. recta* individual marking flags were placed in the substrate at their exact location in order to allow for precise replacement. Hallprint® shellfish tags were glued to the outside of the left and right valves, and PIT tags were glued to the outside of the left valve only. Gluing of both tag types was done using Gorilla Glue™ Super Glue Gel and cyanoacrylate adhesive (Turbo Set 1; Palm Labs Adhesives, Hilton Head South Carolina) to dry the glue quickly and avoid desiccation. The Hallprint® tags were used to identify *L. recta* individuals visually, as well as indicate the left and right valves; the left valve was labeled “A” and the right labeled “B”. Each PIT tag read a unique HEX code when scanned by the Biomark® reader, allowing for identification without needing to remove the individual from the substrate. Once the individuals were tagged, they were placed back at their corresponding flag and scanned using the Biomark™ reader. When scanned with the Biomark™ reader the Biomark™ software stores the geographic coordinates and the time that each tag was scanned. Up to seven *L. recta* found at each site were PIT tagged for Biomark™ scanning to track movement throughout one summer season.

To determine unionid community close to *L. recta* (i.e., in the immediate vicinity; hereafter referred to as the *L. recta* community; this also could be considered quadrat survey data) one 0.25 m × 0.25 m quadrat was excavated per *L. recta* individual, centered on the initial location where each *L. recta* was found. The quadrat was then excavated by hand to approximately 15 cm deep until no further unionids were found within the quadrat. Any live species found in the quadrats were removed, measured, recorded, and then replaced. Abiotic parameters were recorded for each quadrat to identify *L. recta* habitat use. Substrate composition within each quadrat was based on the Wentworth scale for sediment type (Wentworth, 1922). The relative proportion (%) of each sediment type was visually estimated by the same individual researcher at all sites. At each site basic water quality tests were collected with standard Hach™ strips (phosphate (ppm), ammonia (mg/l), and pH).

To measure water depth variation and temperature Onset HOBO® Data Loggers were installed just outside of the sampling location at each of the four survey sites. Locations of installation within the river were chosen so that loggers were off the bank, within the high flow channel of the river, and were outside the sampling area to avoid disturbance. These loggers were installed in PVC housings with venting, which were zip tied to crossed rebar that was hammered into the substrate. The loggers recorded depth and temperature in one hour intervals, and data were uploaded from the loggers twice over the duration of the study. Loggers provided information on depth and temperature events that may have impacted *L. recta* throughout the duration of the study.

Recapture visits

After the initial surveys, five recapture visits occurred throughout the summer, with scanning and abiotic data collected at the four sites during each visit. These visits occurred every 2 weeks, alternating between Great Lakes watersheds (Huron and Michigan; see Table 1) each week, and totaling to 6 visits during the sampling season (initial tagging visit and five recapture visits). At recapture visits tagged *L. recta* were not handled and no further community or quadrat data were collected. During some of the recapture visits additional *L. recta* were found haphazardly and added to the study, these *L. recta* were tagged and underwent the same protocol as stated above for newly found *L. recta*. Additionally added *L. recta* were only tagged up to the second revisit; anything found after the second revisit was not included in the study. Recapture scans for *L. recta* were done at all future recapture visits following their initial tagging to track geographic coordinates (accuracy ~ 30 cm). From the Biomark™ PIT tag recapturing, coordinates were uploaded using Biomark™ BioTerm software to provide information on exact locations of the individuals. Coordinates were compared against previous chronological data in this study to track patterns of movement using GIS ArcMap 10.7. Minimum convex polygons (MCP; see *Data analysis*) were used to assess overall minimum movement during the duration of the study (i.e., summer period). Based on relative accuracy some scans were removed due to obvious error or low confidence scans (e.g., lack of triangulation of satellites or single scan; see Sullivan & Woolnough, 2021 for challenges). To assess vertical movement burrowing data were collected at each recapture visit. Burrowing was quantified via a ranking scale that went from “not borrowed” (e.g., laying on top of the substrate) to being “fully burrowed” (e.g., only siphons visible at substrate level). For individuals that were “not burrowed at all” the valve in which the individual was laying on above the substrate was recorded.

Data analysis

All field data, including abiotic and biotic, was recorded and analyzed using Microsoft Excel, Biomark™ BioTerm, and R (version × 64 3.6.1) software. All geographic coordinates (accuracy ~ 30 cm) that were logged from the Biomark™ scanners were brought into ArcMap 10.7 for analysis. The minimum convex polygon (MCP) function in ArcMap (version 10.9) was used on each individual unionid, drawing polygons around all valid coordinates and calculating minimum individual MCP (m^2). Using MCP to track horizontal movement is a method that has been previously used in other species distribution and movement studies, including tracking the movement of a population of *Villosa iris* (I. Lea, 1829) (Rainbow) (Asher & Christian, 2012). MCP was also standardized by day (avg. MCP/number days tracked), as the number of days each individual was tracked varied by individual and river. An ANOVA was run for movement data to determine any significant differences among sexes, sites, and watersheds.

For all community data and quadrat data, the relative abundance and species composition was calculated at each site and compared across each; species were standardized by pph. A community analysis was done between the river community (timed search data) and *L. recta* community (quadrat data) and was standardized by pph and percent (%). Both river community and *L. recta* community were assessed by the number of dominant taxa and evenness at each site.

Dominant taxa and evenness values were calculated by finding the number of species that contribute up to 75% of the individuals (Mackie, 2001; percent contribution dominant taxa with a 75% threshold). An ANOVA was run for size class and burrow rating frequency to determine if there were any significant differences among sexes, sites, and watersheds.

Results

Ligumia recta movement and size

A total of 24 *L. recta* were found across all sites during this study, and all sites varied in total ph searched (Table 1). Mean sizes for all *L. recta* found across all four sites was 131.9 mm, 35.2 mm, 56.1 mm (length, width, height, respectively) (Fig. 2 and Online Resource 1). The largest individual found had a length of 168 mm (female; MA), and the smallest had a length of 76 mm (female; GR). Differences in length of *L. recta* among MA ($\bar{x} = 155.71$ mm), GR ($\bar{x} = 119.50$ mm), CH ($\bar{x} = 129.80$), and PI ($\bar{x} = 118.33$ mm) were statistically significant (Fig. 2; $P = < 0.05$). Width and height showed similar trends and statistical results (see Online Resource 1). Sizes among males and females across all sites did not significantly differ ($p = 0.865$), but average differences can be seen for length, width, and height, with most MA individuals being larger than the other three sites (Fig. 2 and Online Resource 1). The ratio of male ($n = 12$) and female ($n = 12$) *L. recta* individuals used in this study were equal but were not a design of the study; this even male:female ratio was not consistent across sites (Table 1). Gravidity in females was observed in four different individuals over the course of the study, with two occurrences at MA (June 26 and August 24, 2020; two separate individuals at 163 and 156 mm, respectively), one occurrence at GR (July 13, 2020; 108 mm), and one occurrence at CH (July 29, 2020; 109 mm).

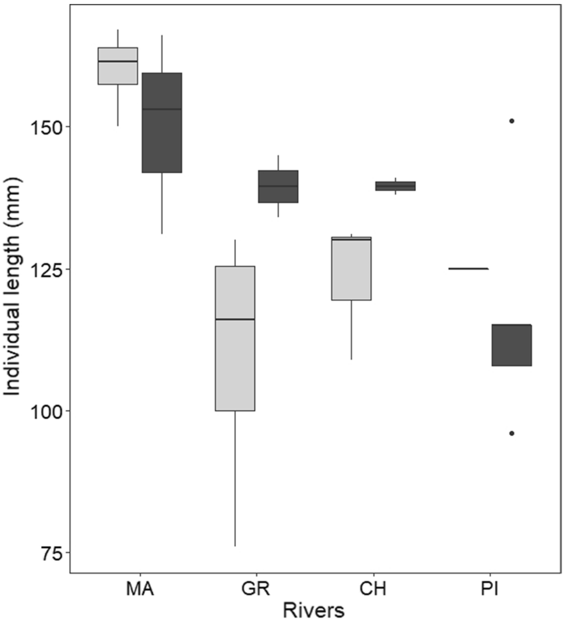

Fig. 2 Boxplots of measurements taken of *Ligumia recta* across four different rivers at the end of a two-month study during summer 2020 in Michigan, USA. A total of 24 individuals were measured for their length (above), width (Online Resource 1), and height (Online Resource 1) in millimeters (mm). Maple (MA), Grand (GR), Chippewa (CH), and Pine (PI) rivers. Female = Light Gray, Male = Dark Gray. Line of each boxplot indicates the median with the box outlining the interquartile range (IQR), the whiskers are 1.5 × IQR, and the dots indicate values beyond 1.5 × IQR

All geographic coordinates were mapped and visualized in GIS. Scans for *L. recta* movement tracking and recapture were reviewed and checked for discrepancies that could have occurred due to GPS error (e.g., "high noise" during scanning which inhibited proper triangulation of satellites). Scans were removed if there were obvious errors when data were visualized in GIS. The movements of all *L. recta* individuals were greater than the accuracy of the geographic coordinate error (accuracy ~ 30 cm), thus all other movements, other than those stated above, were considered accurate.

Movement, as calculated via MCP for all *L. recta* individuals in this study, had an average area of 81.86 m^2 ($n = 24$) over the 59—69 days (depending on the site due to scheduling logistics) of recapture surveys (Fig. 3a). It should be noted that these observed movements were either active (i.e., individuals moving with muscular foot) or passive (i.e., with flow of river) and distinguishing between these movements were beyond the scope of this study. Also, these movements are minimal movements over the time period as there were likely unobserved movements between recapture events. PI had the least variation in movement area, with a difference of 55.46 m^2. Both GR and CH had similar movement area variation (range = 82.21 m^2; 85.19 m^2,

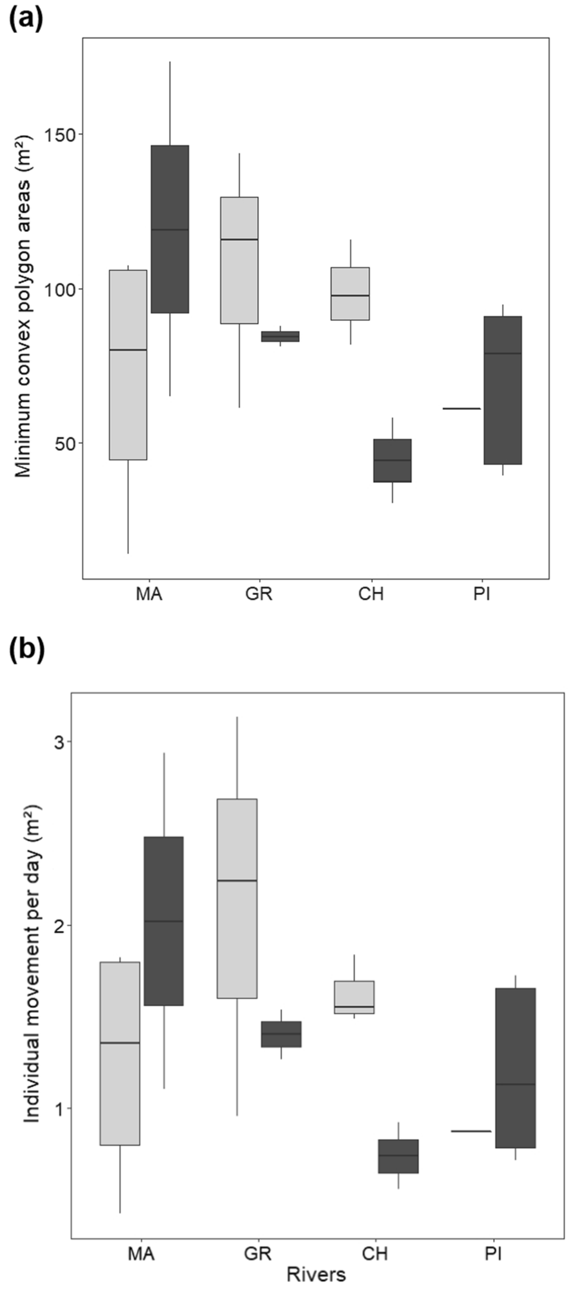

Fig. 3 Average minimum individual area moved per day (m^2), calculated via **a** Minimum Convex Polygon areas (MCP) and **b** standardized by day, of tagged *Ligumia recta* tracked via Biomark™ recapturing at four different sites over summer 2020 in Michigan, USA. Movement was tracked in the Maple (MA), Grand (GR), Chippewa (CH), and Pine (PI) rivers. Geographic coordinates were analyzed and computed into minimum convex polygons (m^2) to find the minimum movement during a two-month period. Female = light gray, male = dark gray

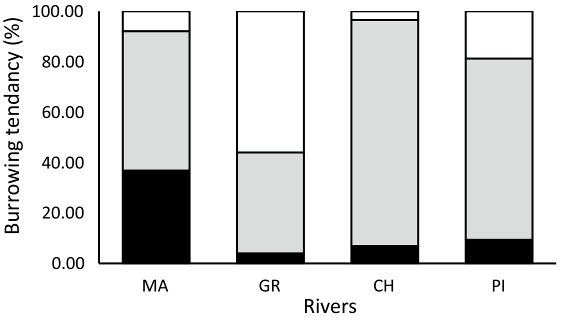

Fig. 4 Burrowing tendency of 24 monitored *Ligumia recta* individuals over two months during summer 2020 in Michigan, USA. Burrowing was quantified by ranking position of the individual in the substrate as the following: "not burrowed" (black), "partially burrowed" (gray), or "fully burrowed" (white). Burrowing was tracked in the Maple (MA), Grand (GR), Chippewa (CH), and Pine (PI) rivers

respectively). MA had the most variation in movement area (range = 159.33 m^2) as well as the overall smallest (13.96 m^2) and largest (173.28 m^2) MCP areas for all four sites (Fig. 3a). MCP for all individuals were not significantly different among the four sites visited ($P = 0.618$) and the same result was seen between sexes ($P = 0.524$). Movement (as calculated by MCP) was then standardized by day (Fig. 3b). In standardizing by day, it was seen again that MA had a large variation of average movement per day among individuals (range = 2.51 m^2) (Fig. 3b).

In analyzing vertical movement (i.e., burrowing), 55–90% of the time *L. recta* were burrowed partially below the substrate except at GR. Individuals at GR were most commonly fully burrowed (56%) compared to being not burrowed 4% of the time. This differs from MA, in which individuals were not burrowed 37% of the time (Fig. 4). When *L. recta* were observed not burrowed, 72.7% of the time they were laying on their right valve, with their left valve (which had the PIT tag attached) facing upwards. Burrowing in gravid females was observed throughout the study. Two of the gravid females were at MA, with both partially burrowed at the time they were discovered. The gravid female at GR was located in a high depth variability area (Fig. 5) and was observed to be fully burrowed at the time. This individual was found fully burrowed following a day (July 2nd) when there was a large increase in depth at GR (see Fig. 5) indicating an

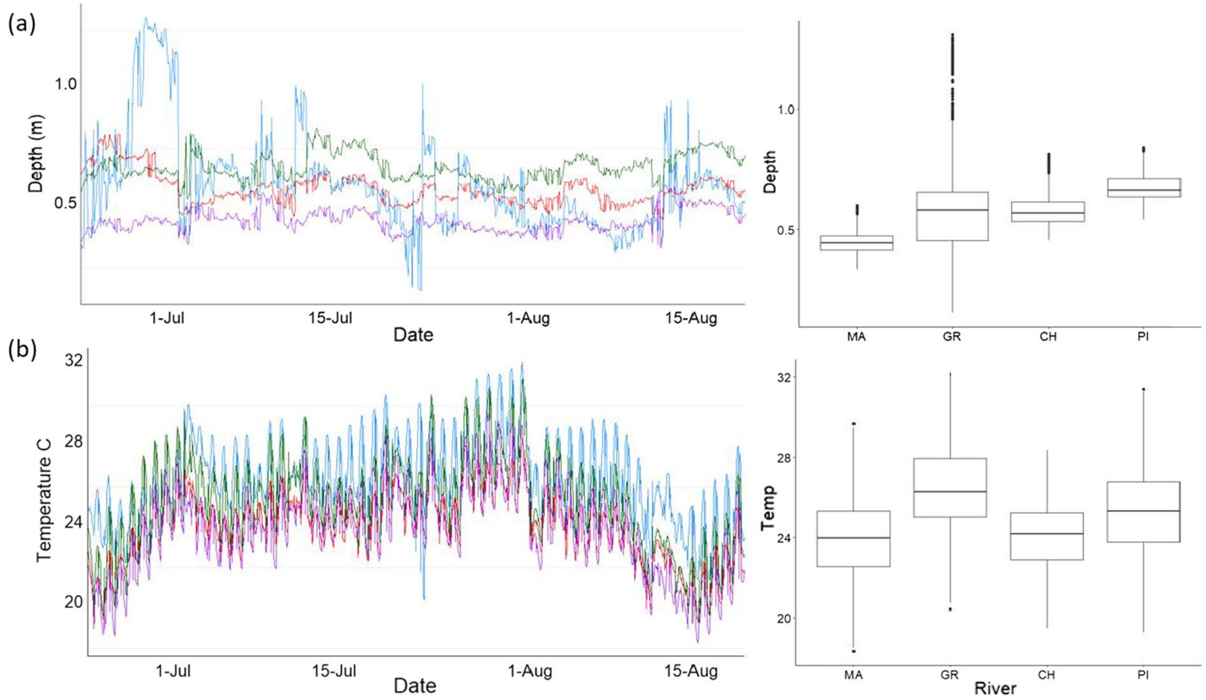

Fig. 5 Changes in depth in meters **a** and temperature in °C **b** logged every hour from June 23 – August 19 using Onset HOBO® Data Loggers at four sites in Michigan, USA. Summary boxplots are to the right of each detailed plot. Loggers were installed in the Maple (purple), Grand (blue), Chippewa (red), and Pine (green) rivers. Line of each boxplot indicates the median with the box outlining the interquartile range (IQR), the whiskers are 1.5 × IQR, and the dots indicate values beyond 1.5 × IQR

increase in flow (e.g., either dam release of water or rain event). The final gravid female *L. recta* was found at CH and was observed to also be partially burrowed at the time it was discovered.

Community

Although species richness of the river community was similar among sites, total individuals pph and species composition was highly variable (Tables 1 and 2). GR yielded the lowest total individuals and PI had the most individual unionids. For PI surveys changed after ~ 6 ph due to a high number of *Actinonaias ligamentina* (Lamarck, 1819) (Mucket) found during the first half of sampling. Following 6 person hours *A. ligamentina* was excluded from collection at PI, with all other species continually sampled for the entire time search. This change in collection of *A. ligamentina* was considered for all calculations, standardizing by ph before doing further analyses. Juvenile unionids (i.e., small < 2 distinct external annuli) were found during river community surveys, with the smallest being a *Lampsilis cardium* Rafinesque, 1820 (Plain Pocketbook) at 22 mm in length at MA. The largest individual found during surveys that was not *L. recta* was an *Amblema plicata* (Say, 1817) (Threeridge) at 157 mm in length, which was also found at MA. The most common species in the river community by percent composition (%) differed among the different rivers (Table 2). The most abundant species across all sites was *A. ligamentina*, with the highest percent composition at CH and PI (Table 2). The number of dominant taxa (i.e., representing the top 75% individuals in survey) highlighted the large number of *A. ligamentina* found at both CH and PI, therefore only one dominant taxa was observed at these sites (Table 1).

In order to compare river community to *L. recta* community (i.e., in immediate vicinity of *L. recta*; see Methods), community analysis was standardized by percent (%). For the Lake Michigan watershed sites (MA and GR) it was found that *A. plicata*

Table 2 Community across the Maple, Grand, Chippewa, and Pine rivers during summer 2020 surveys in Michigan, USA. River community represents the frequency of species found during timed tactile searches, standardized by % composition and per person hour (pph)

Tribe	Genus	species	Common Name	River (pph)				*Ligumia recta* (m^{-2})				River (%)				*Ligumia recta* (%)			
				MA (TS)	GR (TS)	CH (TS)	PI (TS)	MA (Q)	GR (Q)	CH (Q)	PI (Q)	MA (TS)	GR (TS)	CH (TS)	PI (TS)	MA (Q)	GR (Q)	CH (Q)	PI (Q)
Anodontini	*Alasmidonta*	*marginata*	Elktoe	–	0.24	–	S	–	–	–	–	–	2.08	–	–	–	–	–	–
	Alasmidonta	*virdis*	Slippershell	–	S	S	–	–	–	–	–	–	–	–	–	–	–	–	–
	Anodontoides	*ferussacianus*	Cylindrical Papershell	–	–	–	S	–	–	–	–	–	–	–	–	–	–	–	–
	Lasmigona	*complanata*	White Heelsplitter	–	S	–	0.08	–	–	–	–	–	–	–	0.08	–	–	–	–
	Lasmigona	*costata*	Fluted-shell	1.95	0.24	0.07	0.08	0.14	–	–	–	6.70	2.08	0.31	0.08	4.55	–	–	–
	Pyganodon	*grandis*	Giant Floater		S	–	S	–	–	–	–	–	–	–	–	–	–	–	–
	Strophitus	*undulatus*	Creeper	0.07	0.08	–	–	–	–	–	–	0.25	0.69	–	–	–	–	–	–
	Utterbackia	*imbecilis*	Paper Pondshell	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amblemini	*Amblema*	*plicata*	Threeridge	4.19	4.24	0.14	1.63	0.14	0.17	–	0.17	14.39	37.51	0.61	1.54	4.55	11.11	–	4.00
Lampsilini	*Actinonaias*	*ligamentina*	Mucket	2.24	0.08	20.11	101.37	–	0.17	0.20	2.83	7.69	0.69	85.63	95.69	–	11.11	14.29	68.00
	Cambrunio	*iris*	Rainbow	1.81	–	0.07	0.08	–	–	–	–	6.20	–	0.31	0.08	–	–	–	–
	Epioblasma	*triquetra*	Snuffbox	0.36	0.79	–	S	–	–	–	–	1.24	6.95	–	–	–	–	–	–
	Lampsilis	*cardium*	Plain Pocketbook	6.51	2.83	1.58	0.33	0.71	–	–	–	22.33	25.00	6.73	0.31	22.75	–	–	–
	Lampsilis	*siliquoidea*	Fat Mucket	0.80	–	0.14	–	–	–	–	–	2.73	–	0.61	–	–	–	–	–
	Ligumia	*recta*	Black Sandshell	0.51	0.47	0.36	0.49	1.00	1.00	1.00	1.00	1.74	4.17	1.53	0.46	31.85	66.67	71.43	24.00
	Ptychobranchus	*fasciolaris*	Kidneyshell	0.51	–	0.29	0.08	0.29	–	0.20	–	1.74	–	1.22	0.08	9.10		14.29	–
	Toxolasma	*parvum*	Lilliput	–	0.31	–	–	–	–	–	–	–	2.78	–	–	–	–	–	–
	Truncilla	*truncata*	Deertoe	–	–	–	S	–	–	–	–	–	–	–	–	–	–	–	–

Table 2 (continued)

Tribe	Genus	species	Common Name	River (pph)				*Ligumia recta* (m^{-2})				River (%)				*Ligumia recta* (%)			
				MA (TS)	GR (TS)	CH (TS)	PI (TS)	MA (Q)	GR (Q)	CH (Q)	PI (Q)	MA (TS)	GR (TS)	CH (TS)	PI (TS)	MA (Q)	GR (Q)	CH (Q)	PI (Q)
	Venustaconcha	*ellipsiformis*	Ellipse	0.36	0.16	0.07	–	–	–	–	–	1.24	1.39	0.31	–	–	–	–	–
Pleurobemini	*Eurynia*	*dilatata*	Spike	1.52	S	0.07	0.24	0.14	–	–	–	5.21		0.31	0.23	4.55	–	–	–
	Fusconaia	*flava*	Wabash Pigtoe	4.41	0.39	0.57	1.30	0.29	–	–	–	15.14	3.47	2.45	1.23	9.10	–	–	–
	Pleurobema	*sintoxia*	Round Pigtoe	0.51	S	–	0.16	0.14	–	–	0.17	1.74	–	–	0.15	4.55	–	–	4.00
Quadrulini	*Cyclonaias*	*pustulosa*	Pimpleback	3.40	1.02	–	–	0.29	–	–	–	11.66	9.03	–	–	9.10	–	–	–
	Cyclonaias	*tuberculata*	Purple Wartyback	–	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Quadrula	*quadrula*	Mapleleaf	–	0.47	–	0.08	–	0.17	–	–	–	4.17	–	0.08	–	11.11	–	–

An "S" indicates that only shells were found for that species. *Ligumia recta* community represents the frequency of species found within 0.25 m^2 quadrats done on top of *L. recta* individuals

was more likely to occur in the river than next to *L. recta* themselves (Table 2). Conversely, at PI (a Lake Huron watershed site), *A. plicata* was somewhat more likely to be near *L. recta* (Table 2). Therefore, the two Lake Michigan watershed sites had a lower probability of *A. plicata* occurring near *L. recta* than the Lake Huron watershed site did. An opposite relationship was seen for *A. ligamentina*; GR (a Lake Michigan site) had a higher probability of *A. ligamentina* occurring near *L. recta* than the Lake Huron sites (CH and PI) (Table 2). In comparing species, it was also seen that *Ptychobranchus fasciolaris* (Rafinesque, 1820) (Kidneyshell) is more likely to be found next to *L. recta* than in the rest of the river for both MA and CH (Table 2). When comparing across tribes for all sites for river community, more live species were found in the Lampsilini tribe than any other tribe during surveys ($n = 10$ species) (Table 2). In comparison, the next most largely represented tribe was Anodontini, which only had four live species represented for river community (Fig. 6).

Abiotic habitat characteristics

Data gathered from the HOBO® Data Loggers showed fluctuations of depth and temperature that were proportionally similar across all sites except at GR (Fig. 5). Although the loggers were installed at different times, only the dates June 23—August 19 were analyzed, as this was the time frame that all four loggers were logging at the same time. GR experienced major depth fluctuations due to its location downstream of a hydroelectric dam (Fig. 5a). Two major fluctuations were observed at GR with a major increase in depth around June 28, 2020 and a major lowering of depth around July 21, 2020 (Fig. 5a). The large increase in depth on June 28 was not the result of a rain event, but rather the hydroelectric dam upstream. Additionally, this major lowering of depth correlates with a drop in benthic water temperature on that same day (Fig. 5b). Overall, while GR had the most variation in depth, it was PI that had the highest average depth, and MA that had the lowest average depth (Fig. 5a); all sites had a statistically different depth from one another (ANOVA and Tukey test; $P << 0.05$ and $P << 0.05$ for each comparison, respectively). For all sites the range and fluctuations of temperatures was similar for all (Fig. 5b); all sites had significantly different average temperatures

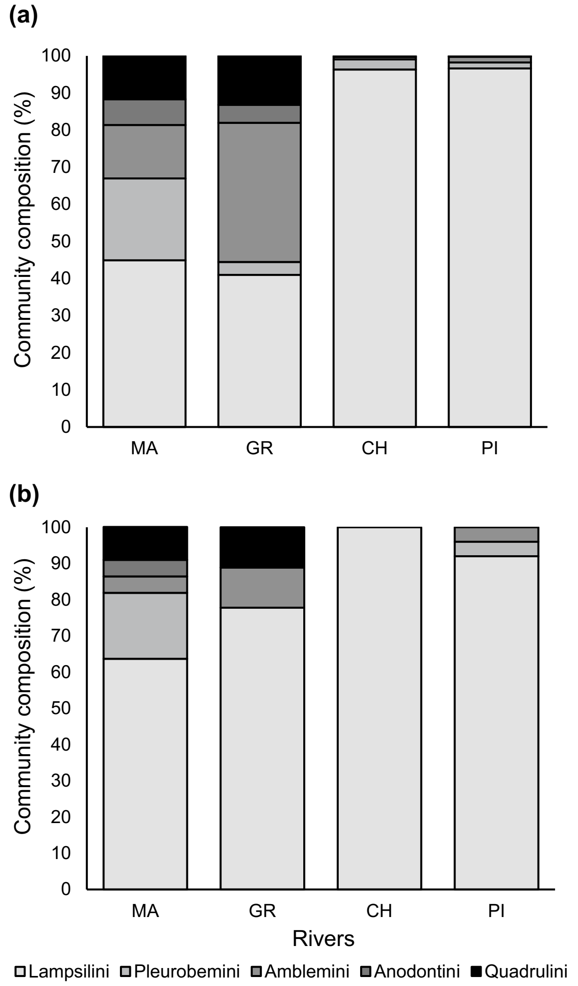

Fig. 6 Unionid community composition broken down by tribes for both **a** timed searches to assess river wide community and **b** quadrat surveys to assess community occurring directly next to *Ligumia recta*. Community assessment based on tribes was done for the Maple (MA), Grand (GR), Chippewa (CH), and Pine (PI) rivers based on the compiled community data for timed searches and quadrats, respectively

over the study except MA and CH, which are both upstream sites but in different Great Lakes watersheds (ANOVA $P < < 0.05$; Tukey test $P << 0.05$ all comparisons except MA-CH $P = 0.302$).

Substrate assessment based on the Wentworth scale revealed differences among all four *L. recta* sites. Both MA and GR had high rubble and sand in their quadrats, while both CH and PI lacked sufficient rubble for substrate makeup (Online Resource 2). MA was the only site that had clay and muck, however these substrates made up a very low percentage of the overall substrate composition for their respective quadrats (Online Resource 2). Basic water quality taken every visit revealed no major extremes or deviations from expected values. Abiotic data collected with HACH strips at initial visits did not show any large differences among the sites, and all values were deemed normal for good water quality, with phosphate at 40 ppm at CH, and 30 ppm at the other sites. Total ammonia was less than 0.25 mg/L and pH ranged between 7.8 and 8.0 for all sites.

Discussion

The most notable results observed in this study included the unique adult movement patterns of the globally rare *L. recta*. This study documented, for the first time, the extent to which these individuals can move over the course of a few months during the summer season. The success of the bi-weekly mark-recapture methods used shows that this technique can be used to reliably recover unionid individuals repeatedly, even with depth variations over a season. With the average movement (MCP) reaching 1.43 m^2 per day for one individual, these observations showed large and influential movements (e.g., could influence reproduction, avoidance of high flow). Further, the characteristically large differences seen in MCP and burrowing behavior at MA compared to other sites brings to light the range *L. recta* can have in movement behaviors. The community analysis shows the major trends of what species co-occur with *L. recta*, providing information on species co-existence. This is highlighted by 14 species co-occurring with *L. recta* in a singular river reach. Species occurring directly next to *L. recta*, although lower in species number (maximum species excluding *L. recta* of $n = 8$), showcases a distinct trend of species of similar tribes occurring most often together. The collection of community information can be useful for future studies and surveys of *L. recta*. It can suggest that studying community composition may be helpful for sampling rare species. The quantified numbers of *L. recta* in each river can be used for community recovery in the future and provide baseline data for long-term monitoring sites, any further studies on this species, as well as comparisons for other *L. recta* populations in North America.

Previous studies have shown correlations between hydrology and unionid mussel movement (Maio & Corkum, 1997; Schwalb & Pusch, 2007; Steuer et al., 2008; Sullivan & Woolnough, 2021)—the results found in this study also support these findings. Unionids will burrow in high flow, which may result during flooding and high depths, as a way to stay in place and avoid being swept downstream due to the shear stress and unstable substratum that results from high flow (Strayer, 1999; Steuer et al., 2008). When burrowed to take refuge during flooding conditions, movement of unionids would be presumably minimal, as large movements could expose them to extreme depth changes (and high flows), causing potential dislodgement (Poznańska-Kakareko et al., 2021). This behavior in relation to high depth and flow was seen in our study, at GR specifically, where more than half of the time *L. recta* individuals were fully or partially burrowed, and not burrowed only 4% of the time. GR was also the site with the most complete burrowing overall. This agrees with the conclusions of Strayer (1999) since GR is the site with the most variability in depth (and thus resulting changes to flow). GR also displayed flood-like conditions, such as rapid increases in water depth due to a water release from the hydroelectric dam. When compared to MA, in the same Lake Michigan watershed, the depth was consistently low and 37% of the time individuals were completely above the substrate. Low depth and flow conditions as well as small substrate sizes at MA may have allowed for larger and more variable *L. recta* burrowing movement, which supports the results of a positive correlation between discharge and depth of burrowing as seen by Schwalb & Pusch (2007). Both sites yielded similar numbers of *L. recta,* indicating that at least older adult *L. recta* can survive in conditions of variable habitat. *Ligumia recta* at both sites (GR and MA) had similar densities, providing evidence that *L. recta* can persist, to some degree, in both low and moderately high depth habitats.

Ligumia recta are large individuals, considered to be of the largest and most oblong in the Great Lakes region (Mulcrone & Rathbun, 2020). The large size of *L. recta* could possibly make burrowing, an already energetically costly behavior, more costly (Goodchild et al., 2016). While burrowing differences among species are still debated, it has been shown that shell length has an impact on burrowing behavior (Sullivan & Woolnough, 2021). *Ligumia recta* are also known to lay on their sides above the surface for luring and display for reproduction (Corey et al., 2006); however, prior to this study this behavior has not been quantified across populations. For this reason, it was expected that most *L. recta* individuals would be found above the surface of the substrate, especially females during their spawning season from mid-July until August (Mulcrone, 2006). As expected, *L. recta* were often observed exposed and lying on their sides during revisits, and they were completely above the substrate frequently at low depth sites. However, this study showed that some *L. recta* individuals, including gravid females, could be partially or fully burrowed. In our study, one gravid female was fully burrowed; this female was found in a high depth area, potentially explaining why it was the only gravid female fully burrowed. The behavior of this one gravid female, as well as the occurrence of gravid *L. recta* females into August, contradicts observations of Corey et al. (2006) regarding typical behavior of *L. recta* and gravid females.

Despite the fact that the sites differed quantitatively (e.g., by landscape factors), certain species from specific tribes were common across all sites, suggesting that these species are commonly co-occurring with *L. recta*. Species from the tribe Lampsilini (the tribe from which *L. recta* belongs) were found most often at *L. recta* sites, including *A. ligamentina* and *L. cardium*, which were found at every site visited. Although these other Lampsilini species are common, these are still species that have the same tolerance and general habitat preference as *L. recta*. Although not a part of the Lampsilini tribe, *Lasmigona costata* Rafinesque, 1820 (Flutedshell), *A. plicata* and *Fusconaia flava* Rafinesque, 1820 (Wabash Pigtoe) were also found at every site visited, suggesting that these are also species that commonly co-occur with *L. recta*, sharing generally the same tolerances and habitat. Generally, the tribe Anodontini was not found with *L. recta*, despite species of this family being fairly common across Michigan. This trend may be because Lampsilini have higher tolerances to contaminants and stressors that may be observed in these agricultural watersheds. Lampsilini trends seen may also be explained by substrate similarities and differences across sites. The tribe Anodontini does not have the same tolerance (Pandolfo et al., 2010; Wang et al., 2017), and generally are thinner shelled species, which contrasts the thick shelled *L. recta* (Cope et al., 2008; Mulcrone & Rathbun, 2020). The trend seen that species of the same tribe are occurring together is not surprising, as tribes represent the evolutionarily distinct lineages of Unionidae, thus differences seen in characteristics and life history are expected (Haag, 2012).

Analysis of the presence of certain species co-occurring with *L. recta* (*L. recta* community) or not showed that the different sites across Michigan had differences in species occurrence. Abiotic and biotic factors such as hydraulic effects and substrate type can have an impact on species composition (Steuer et al., 2008), which was seen at PI in comparison with the other sites. With a sampling rate of 101.4 *A. ligamentina* pph, PI would have also been expected to yield quadrats that had a higher rate of *A. ligamentina* per quadrat than what was observed. Instead, in both the Huron River watershed sites (CH and PI) *A. ligamentina* were not occurring as frequently (or at all in the case of MA) in quadrats with *L. recta*. This result may be due to differences in substrate or hydrology characteristics within each quadrat; however, this type of analysis was beyond the scope of this study. Patchy community structure has been observed elsewhere (Newton et al., 2008) but the data from our current study indicate that the patchiness may be variable, and perhaps predictable. For example, we have shown evidence that certain species (e.g., *A. ligamentina* at GR) are more likely to co-occur with *L. recta* than be found throughout the river reach. The understanding of the community structure and distribution could be very important in conservation actions (e.g., relocation and restoration) of rare unionids like *L. recta*.

When comparing across all sites the number of dominant taxa as compared to evenness showed evidence of large differences. Dominant taxa and abundance can reveal a lot about the community structure of an ecosystem (Vaughn et al., 2004). A high species richness is important in unionid faunal communities, as they have such a prominent role in the structure of nutrient availability (Nichols et al., 2005). At PI, there was only one dominant taxa, suggesting the absence of evenness. This may be concerning, as evenness is highly important for the success of multiple aquatic ecosystem processes (Soininen et al., 2012). Sites such as MA displayed higher species richness, with more species representing the top 75%, which suggests higher evenness. This creates a better balance of species and possibly healthier community structure. This study shows how dominant taxa and evenness could be used to compare populations in need of conservation and could suggest that conservation of one species (e.g., *L. recta*) could concurrently help many of the surrounding species.

Size class for *L. recta* across all sites within this study ranged from 76 to 168 mm. The maximum size of *L. recta* is typically 175 mm to 250 mm in length (Benson, 2020; Mulcrone & Rathbun, 2020). Although aging was not done, it can be assumed that these large individuals were older, and no juvenile *L. recta* were found. This lack of juveniles brings to question the reproduction and recruitment success of this species, as most individuals found were usually older and long lived (Corey et al., 2006; Haag & Rypel, 2011; Mulcrone & Rathbun, 2020). For unionids, when recruitment ceases, larger and older unionids typically dominate populations (Randklev et al., 2013). It was considered that the larger individuals sampled could also be due to size class sampling bias because smaller individuals and smaller species can be overlooked and under-sampled due to their size during time search (i.e., visual) surveys (Dunn, 2000). This sampling bias could mean younger *L. recta* may have been overlooked, and perhaps in the future excavation techniques could be used to target smaller individuals (Strayer & Smith, 2003). However, non- *L. recta* juveniles were found during this study, including juveniles from species that are generally larger in size. The smallest individual found was a juvenile *L. cardium* (during a time search), which is generally a larger species reaching up to 180 mm in length (Mulcrone & Rathbun, 2020). If our surveys had a strong size class sampling bias these individuals would have also been overlooked, suggesting that something other than size class sampling bias (e.g., reproduction or recruitment success) is contributing to the low numbers of young *L. recta* found.

Site location impacted both the habitat and general community where *L. recta* was found, indicating that rivers may provide variable, yet useable habitat. Differences across and within watersheds due to land use, flow regimes, channeling, and stream size can have a large impact on the unionid assemblages (Goodding et al., 2019). Due to surrounding agricultural landscape and its location below a low head dam MA was expected to have variations in general community and substrate, which was seen in our study in the variation and high species count for river community. GR experienced the highest and most variable depth (Fig. 5a), which could have influenced the observed low unionid density at GR compared to other sites. This observation supports what other research has found that high depth and flow is negatively correlated with unionid density, causing stress and impacting substrate stability (Goodding et al., 2019). GR is located below a hydroelectric dam in the Grand River, causing high variations in depth (and resulting flow), which may have been why GR had the lowest unionid individuals found pph (11.31 pph). GR is most likely experiencing the highest stress compared to the other sites due to these depth and flow fluctuations, which may create less suitable unionid habitat. With two *L. recta* being captured prior to this study, GR had both the lowest unionid river community and lowest occurrence of *L. recta* relative to effort. Habitat and hydrology can have a large impact on the detection of unionids during surveys and can impact the effectiveness of a survey overall (Sanchez & Schwalb, 2021). These findings may explain why a site like GR yielded less *L. recta* found. CH and PI did not experience any extreme depth fluctuations like those observed at GR. Despite hydrological habitat differences among sites, the average *L. recta* found per person hour for MA, CH, and PI showed fairly similar results, with GR being the only exception.

The substrate found in the quadrats described the habitat use of *L. recta* in representative sites of Lake Michigan and Huron watersheds. Despite there being an overall low number of quadrats relative to the size of both watersheds, these data suggest what substrate types may be suitable for *L. recta*. These conclusions can be further confirmed by the high effort put in at each site, with all sites having greater than 12 ph of tactile searches. A high sampling effort suggests that a high proportion of *L. recta* that were present at each site were likely sampled, and their substrate assessed. Overall, the suitable habitat for *L. recta* was mostly pebbles, rubble, and sand. This habitat use aligns with those of other species in the Lampsilini tribe, in which species occur in stable and more gravel and sand dominated substrates, much like what is traditionally suggested for *L. recta* habitat (MNFI, 2020). For sites with lower depths and flows, in this case MA, it was observed that there was at least one quadrat that had clay and/or muck (Online Resource 2). Clay and muck are formed as a result of high organic matter and are often associated with lentic systems (Hoyer et al., 2017). Although MA was the site that most mimicked a lentic system, *L. recta* were still found in high numbers at this site, suggesting *L. recta* can persist in areas with lower flow and finer, softer substrates.

Future applications

The concerns raised that only older and larger *L. recta* individuals were found prompts questions on the reproductive success and population stability of this species. While a sampling bias could be influencing this finding, it is likely that the *L. recta* population in Michigan is comprised mostly of older individuals, which is enough to prompt additional research and conservation efforts for this state endangered species. Further species-specific surveys and research on the reproduction of *L. recta* may be beneficial to address these concerns. Many of the population dynamics for this species remains unknown, even at the National scale, therefore it is difficult to make concrete conservation plans. There is also a lack of knowledge about the known and reported host fish of *L. recta. Ligumia recta* have been observed both on naturally infested fish as well as in laboratory infestations; however, host suitability for juvenile metamorphosis is still not well understood (Khym & Layzer, 2000). The presence of suitable host fishes can have a large impact on reproductive success; therefore, it should be considered in future species-specific studies.

This study focused on the assessment of movement and burrowing during the summer season. Other seasons and latitudinal variation should be considered as well as studies at differing spatial scales. This is especially true when looking at females during their gravid season or males when they are reproductively active. Additionally, these methods could be used to explore the basic movement and burrowing patterns of other species. Our data show that movements occurred at > 1 m per day and therefore using a small quadrat may be limiting the co-occurring community data; scale of co-occurring community could be considered, in the future, at a larger scale. A limitation of this study was also that no control sites were used, which limits the inference that can be drawn about habitat variables but is challenging in riverine studies. This is an important caveat that should be considered in future analysis of *L. recta* habitat.

The potential impact of tagging on burrowing behavior, should be further addressed in future burrowing studies. In this study, *L. recta* laying on their sides were most often observed to have their PIT tag facing upwards. A study on the impacts of PIT tagging on unionid burrowing has shown that these tags can decrease burrowing rate (Wilson et al., 2011). This should be considered in the interpretation of this study's observations. The valve in which the PIT tag is on specifically should also be considered and further explored, as it may have an impact on typical behavior.

Conclusion

The goal of this study was to quantify movement and burrowing of *L. recta* in Michigan, specifically during the summer season. The collection of data focused on movement, co-occurring unionids, and occurrence of *L. recta* in this study contributes to recognized knowledge gaps of the National Strategy. Until this study, the value of movement had not been quantified for *L. recta*. In addition, the specific, *L. recta* community data was also documented for the first time. Movement patterns for *L. recta* showed an average MCP area of 1.43 m^2 per day over a two-month period during the summer season in Michigan, USA. It was unique to find that *L. recta* did not always occur above the substrate, which is important to consider when looking at energy use in unionids. When looking at community data there were many species in same river reach as *L. recta*; however, most often species of the Lampsilini tribe were found with *L. recta*—the tribe to which *L. recta* belongs. Assessments of substrate in which *L. recta* were found showed that they most often occurred in a combination of pebble, rubble, and sand (based on Wentworth, 1922), occurring often in finer substrates however not in silt. While more data are necessary to properly assess the conservation needs of the Michigan endangered *L. recta*, our data shows that *L. recta* found in multiple Great Lakes watersheds are larger (i.e., long-lived individuals). This raises concerns about *L. recta* reproductive success and should prompt further conservation efforts. Through understanding the movement, community preference, and ideal habitat of *L. recta*, which was quantified during this study, more species-specific plans for conservation can exist.

Acknowledgements We would like to thank the Central Michigan University (CMU) Biology Department, the CMU Summer Scholars Program, The Institute for Great Lakes Research, the CMU Honors Program, and the Ionia Conservation District for helping to fund this study. Thanks to the Michigan Department of Natural Resources for supporting and granting permits for this research. Additionally, thank you to the following student researchers (CMU) for aiding in data collection during the COVID pandemic: Scott LaValley, Nathan Ring, Alex Frankila, Kiara Cushway, Hanna Muntz, Julia Wilsey, and Michael Chatterton. Thank you to editors and two anonymous reviewers for comments that improved this manuscript. This paper is #177 of the Institute for Great Lakes Research.

Author contributions MEM: conceptualization, methodology, formal analysis, investigation, writing—original draft, writing—review & editing, visualization. DAW: resources, writing—review & editing, supervision, project administration.

Funding Ionia Conservation District, Central Michigan University (CMU) Biology Department, CMU Institute for Great Lakes Research and CMU Summer Scholars Program.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

Ethical approval All data were collected with USFWS Scientific Collection Permit, Michigan Endangered and Threatened Species Permit, and Michigan Scientific Collection Permit to DAW.

Consent to participate Not applicable.

Consent for publication These data have not been published or submitted for publication elsewhere.

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