Environmental drivers of shell shape in a freshwater gastropod from small and large lakes

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Abstract: *Elimia livescens* (Menke 1830) is a freshwater gastropod common in the Laurentian Great Lakes region. Geometric morphometric analysis was conducted to determine the variation in shell shape among sites along the shoreline of Lake Michigan (4 sites) and 3 inland lakes on Beaver and Manitou Islands (8 sites) in Michigan, USA. Canonical Variates Analysis (CVA) showed significant variation in shell shape among the sites at inland lakes and those on the Lake Michigan shoreline. Based on shell shape, 82.5% of individual snails could be correctly assigned to their lake of origin, and 62.8% could be correctly assigned to their site of origin. CVA axes were tested for correlations with the environmental variables. Shell shape in *E. livescens* was correlated most strongly with fetch length and specific conductance. Higher fetch lengths produce higher-energy wave action and may select for individuals with a larger aperture, more globose shape, and lower spire (better for anchorage). Lower fetch lengths produce lower-energy wave action and may select for snails with a smaller aperture, more elongate shape, and higher spire (better for navigating above soft sediment). Environmental processes like those documented in classic studies on marine snails appear to affect shell shape in freshwater snails in similar ways. Furthermore, our study highlights that fetch plays a key role in structuring benthic communities and may play a parallel role in structuring populations. Our study suggests that shell shape variability is a critical factor in regional adaptation and success in this widely distributed gastropod.
Key words: *Elimia livescens*, phenotypic variation, geometric morphometrics, Pleuroceridae, fetch length, Laurentian Great Lakes

Evolutionary history (genotype), environmental variables (e.g., water chemistry, water movement, and habitat), and predation pressure are known drivers of morphological variation (Agrawal 2001). Among aquatic organisms, gastropods are among the groups most often studied for understanding of drivers of morphological variation (e.g., Hollander et al. 2006, Hoverman and Relyea 2009, Dunithan et al. 2012). Environmental pressure can influence selection of favorable genotypes, which affect the expression of phenotypic traits (e.g., Preston and Roberts 2007) and thereby drive the structure of populations (e.g., Minton et al. 2008, 2011, Dunithan et al. 2012) and community composition (Scheifhacken et al. 2007, Harris et al. 2011, Cooper et al. 2014).

Freshwater gastropods in the family Pleuroceridae display morphological plasticity in their shells, which makes them ideal organisms for studying morphological variation. Morphological variation in pleurocerid snails is strongly correlated with environmental variables. In headwater streams, shells of pleurocerid snails tend to be smooth, elongate, and delicate compared to more ornamented, globose, and robust shells downstream (Adams 1915, Minton et al. 2008, Dunithan et al. 2012). This variation in shell shape is hypothesized to be related to variation in predation pressure and damage caused by dislodgment from substrate (Minton et al. 2008). Shell shape variation in pleurocerid snails along environmental gradients has led to considerable uncertainty surrounding the systematics and taxonomy of the group and highlights the potential problems associated with use of only shell characters to establish species boundaries (Hayes et al. 2007, Minton et al. 2007, 2011, Whelan et al. 2012, Dillon et al. 2013, Whelan and Strong 2015). Other morphological characters, such as radular morphology and other internal characters (i.e., reproductive organs), are poorly studied in pleurocerids and freshwater gastropods, in general, but may prove useful for resolving systematic and taxonomic issues (Whelan and Strong 2015).

Elimia livescens (Menke 1830) is a widely distributed member of the family Pleuroceridae found throughout the northern sections of the Mississippi and Ohio River and Great Lakes drainages of eastern North America (Strong 2005, Johnson et al. 2013). Dunithan et al. (2012) sampled *E. livescens* from streams and small lakes in these drainages and found that that shell obesity was significantly correlated with water flow, drainage area, water

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temperature, conductivity, substrate type, and presence of woody debris. Furthermore, they suggested that shell shape variation in *E. livescens* probably was an essential contributor to the wide distribution of this species in eastern North America.

Geometric morphometric analysis is based on the use of landmark points and spatial coordinates to compare associations among the shapes of individual specimens (Webster and Sheets 2010). The objective of our study was to quantify morphologic variation in *E. livescens* by comparing shell shape in a variety of small inland lakes to shell shapes in large exposed habitats in coastal Lake Michigan (Laurentian Great Lakes). We predicted that shell shape would vary greatly within and among the lakes sampled based on findings of previous studies (e.g., Wiebe 1926, Goodrich 1934, Dunithan et al. 2012).

We predicted that fetch length would be the key environmental metric correlated with variation in shell shape. Fetch length, the distance over water that wind has blown without being impeded by land, is used to estimate potential hydrologic (wave) energy in lakes and oceans (Mackie 2004). Wiebe (1926) hypothesized that wave action was a contributor to shell shape differences in *E. livescens* among exposed and protected shoreline sites in western Lake Erie. Goodrich (1934) reiterated the Wiebe (1926) hypothesis and discussed that globose shell shapes occurred in more turbulent and fast-flowing environments. We tested Wiebe's (1926) hypothesis with modern geometric morphometric methods. As in previous studies in riverine (Dunithan et al. 2012) and marine (Hollander et al. 2006) systems, we predicted that the key drivers would be related to water movement and hydrologic energetics.

METHODS

Collection of *E. livescens* specimens took place during summer (June–July 2014) on inland lakes of Beaver and North Manitou Islands in Lake Michigan: 10 collection sites on Beaver Island (3 on Lake Geneserath, 3 on Barney's Lake, and 4 along the island's Lake Michigan shoreline) and 2 on North Manitou Island (Lake Manitou) (Fig. 1A–C). Lake Geneserath is mesotrophic with a surface area of 197.9 ha and maximum depth of 17.4 m. Barney's Lake is eutrophic with a surface area of 18.2 ha and maximum depth of 4.0 m. Lake Manitou is mesotrophic with a surface area of 103.6 ha and maximum depth of 13.7 m. Specimens were hand-collected haphazardly from the littoral zone of each lake with wading and snorkeling collection techniques. Collection duration ranged from 10 to 20 min, depending upon the time needed to collect 50 individuals with undamaged shells. Maximum shell lengths were measured to the nearest mm along the columellar axis (apex to base of aperture). Samples were
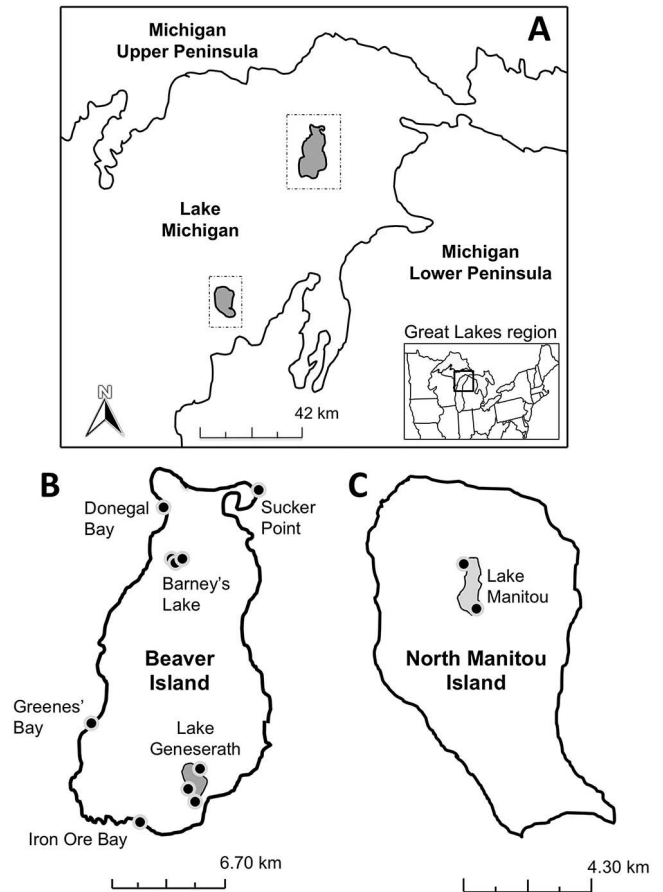

Figure 1. A.—Map showing islands where samples were collected in Lake Michigan, USA, with inset of the Laurentian Great Lakes region. B.—Beaver Island sampling sites. C.—North Manitou Island sampling sites.

preserved in 95% ethanol for sorting and later photography in the laboratory.

Multiple environmental variables were measured at each site. Site coordinates were recorded using a handheld global positioning system (GPS; Garmin, St Olathe, Kansas). Water temperature, pH, turbidity, and specific conductance were measured with a Hydrolab multiprobe (Hach/Hydrolab, Loveland, Colorado). Collection depth, depth of soft sediment, and % substrate composition also were measured at each collection site. Depth of soft sediment was estimated by pushing a polyvinyl chloride (PVC) meter stick into the substrate until resistance was met. Percent substrate composition at each site was estimated along a Wentworth scale (boulder: >25 cm, cobble: 6–25 cm, gravel: 0.2–5.9 cm, sand: 0.01–0.19 cm, silt: <0.01 cm, clay: smaller than silt but with conglomerating particles, muck: similar to silt and clay but more loosely aggregated). Maximum fetch length at each site was measured based on Google Earth™ images and tools. Prevailing fetch was measured as the maximum length over water that the prevailing (westerly) wind can blow. Mean fetch was cal-

culated as the average distance between the maximum and prevailing fetch. Shoreline slope was estimated for each site based on available bathymetric maps of Lake Michigan (National Oceanographic and Atmospheric Administration) and inland lakes of Beaver Island (Central Michigan University Biological Station, unpublished data) and North Manitou Island (C. Otto, Sleeping Bear Dunes National Lakeshore, personal communication).

Subsequent to specimen collection and water-quality testing, snail specimens were returned to the laboratory and photographed using a Stylus 850 SW digital camera (Olympus, Center Valley, Pennsylvania) taken through a Leica (model EZ4; Wetzlar, Germany) dissecting microscope. Snail specimens were mounted for imaging in positions identical to those used by Dunithan et al. (2012). These images were then uploaded into a computer for morphometric analysis. Shell length (apex to base of aperture opening) was measured and analysis of variance (ANOVA) was used to test for differences ($\alpha = 0.05$) in length among sites and lakes sampled. The proportion of individuals with a decollated apex (≥ 1 eroded apical whorl) was calculated.

Landmarks were placed in locations similar to those described by Dunithan et al. (2012), columella (1), maximum width of shell aperture (2, 6), suture of outer aperture lip and body whorl (7), median of 1st suture (8), 2nd suture of spire (9, 10), shell apex (11), and widest margin of body whorl (12) (Fig. 2). To measure changes in shape along the curved outer lip of the aperture, 3 pseudo-landmarks (3, 4, and 5; Fig. 2) were placed with the comb function in MakeFanMac in the Integrated Morphometrics package (IMP; version 7; Sheets 2010). A line segment was drawn between landmarks 2 and 6, and MakeFanMac generated a comb of 5 orthogonal and equidistant line segments that allowed landmarks 3, 4, and 5 to be placed along the outer margin of the shell aperture. Using a comb to estimate the shape of a curve is a standard method for placing pseudolandmarks (Webster and Sheets 2010). TPSDig2 morphometric analysis software (Rohlf 2009) was used to digitize the 12 landmarks onto each shell image.

Landmark point coordinate data were uploaded into CoordGenMac of IMP7 (Sheets 2010) to be translated into size-variation-controlled groups by the process of superimposition. Superimposition forced the 12 landmark-point groups from each individual shell to overlap as closely as possible in a graphic representation of shell morphometry, while removing variation associated with specimen location, orientation, and size, which are irrelevant in comparisons of shell shape (Webster and Sheets 2010; Fig. 3).

Canonical Variates Analysis (CVA) was implemented in CVAGenMac of IMP7. CVA analyzes landmark data to test and visualize how shape varies among lakes and sites. IMP7 software uses a CVA algorithm to organize the 12 landmarks from each individual shell into a single (x,y) coordinate. A priori groups (organized by site) were assigned and forced to be as different from other sites as
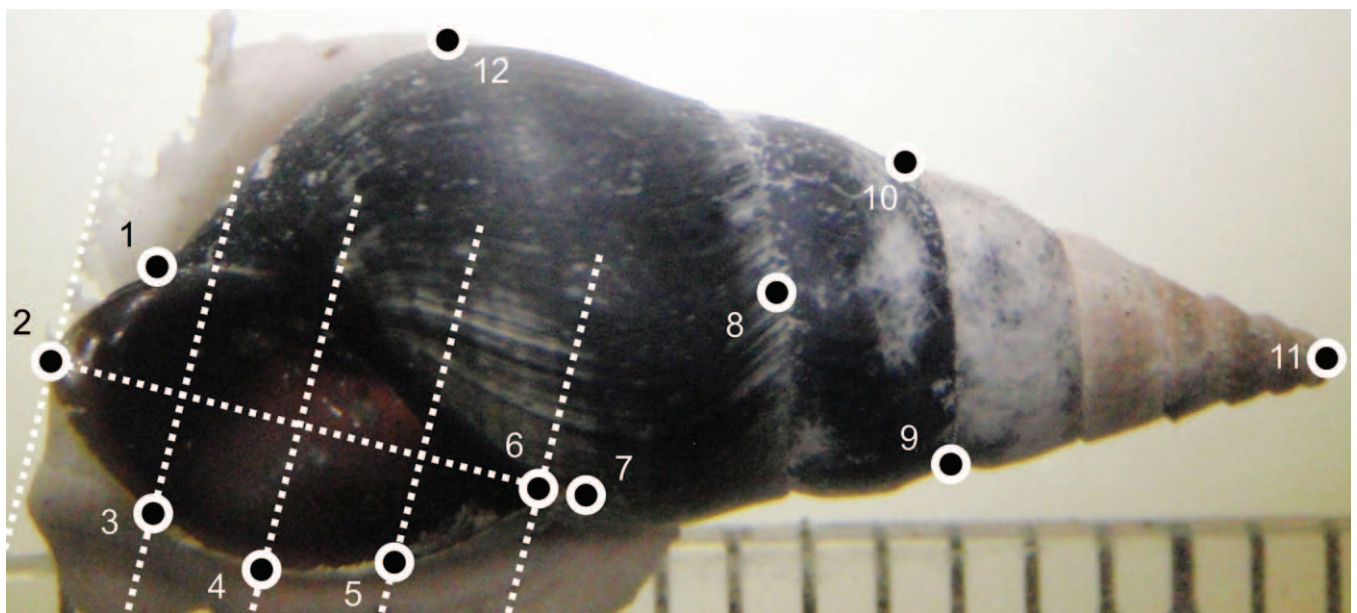

Figure 2. Placement of landmark points on a shell of *Elimia livescens*. Points denote columella (1), maximum width of shell aperture (2, 6), suture of outer aperture lip and body whorl (7), median of 1st suture (8), 2nd suture of spire (9, 10), shell apex (11), and widest margin of body whorl (12). Semilandmarks 3, 4, 5 denoting the outer margin of the aperture were placed using a comb drawn between landmarks 2 and 6 in MakeFanMac of IMP7 (Sheets 2010).
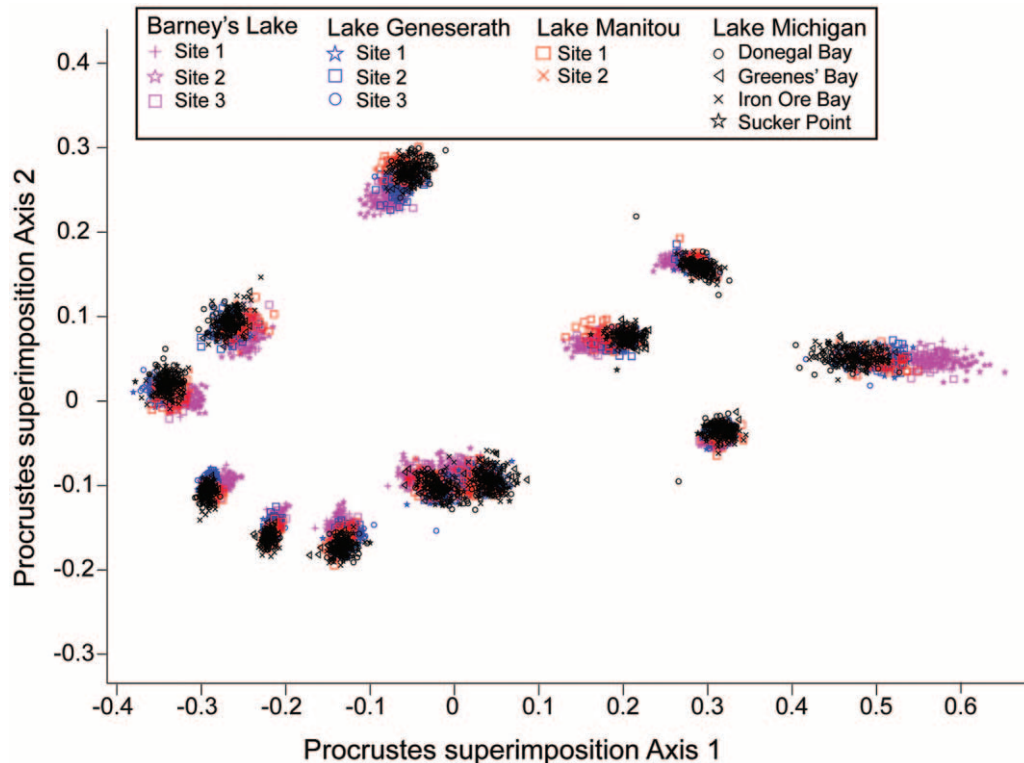
Figure 3. Procrustes superimposition of shell landmarks from *Elimia livescens*. Barney's Lake: $n = 150$, Lake Geneserath: $n = 150$, Lake Manitou: $n = 100$, Lake Michigan: $n = 200$.

possible. Differences in shell shapes along the first 2 significant canonical axes were visualized based on deformation grids and vectors on each landmark. The CVA data were used to assign specimens back to a priori groups (collection lakes and sites) with a jackknife assignment test implemented in CVAGenMac. Environmental variables were tested for correlations ($\alpha = 0.05$) with canonical axes using Pearson correlations (where data were normal) and Kendall rank correlations (non-normal data). z-tests were used to assess normality of the environmental data sets ($\alpha = 0.05$).

RESULTS

A total of 600 *E. livescens* specimens were collected from the 12 sites in 4 lakes (50/site). Mean shell length (apex to columella) was 16.83 mm (± 1.19 SE) and varied significantly among the lakes sampled (ANOVA, $p < 0.001$). The longest snails were found in Barney's Lake and the shortest in Lake Geneserath (Table 1). Of the 600 snails collected, 79.5% had a decollated apex with the highest mean percentages being 94.0% in Lake Manitou and 72.7% in Lake Geneserath (Table 1). *Elimia livescens* specimens collected for this study have been deposited in the University of Michigan Museum of Zoology (catalog number 304996–305007). Photographs of each specimen

used for morphometric analyses have been submitted to MorphoBank (Project P2283, MorphoBank accession numbers M401580–M401679; www.morphobank.org).

Environmental, water-chemistry, and substrate-composition data varied across the sites and lakes sampled (Table 2). Water depths at which specimens were collected varied between 0.35 and 0.90 m, temperature varied between 16.44 and 21.38°C, pH varied between 8.13 and 8.49, turbidity varied between 0.0 and 6.2 NTU, specific conductance varied between 0.156 and 0.288 µS/cm, and depth of soft sediment varied between 0.00 and 0.25 m. Fine sand substrates were the dominant substrate categories in the inland lakes, whereas cobble dominated in the Lake Michigan shoreline sites. Silt, cobble, boulder, and gravel substrates occurred at 70, 60, 30, and 20% of sites, respectively. Maximum fetch was highly variable among the sites sampled ranging from 0.386 to 277.2 km. Only fetch, bottom slope, pH, and specific conductance data were available for the Lake Manitou sites because these *E. livescens* specimens were collected as part of another study in 2009 (Harris et al. 2011).

CVA showed significant variation among groupings along 17 different axes ($p < 0.001$) with the greatest separation among groups (lakes and sites) occurring along axes 1 and 2 (Fig. 4). Specimens from Barney's Lake and Lake Michigan plotted along the extreme ends of CVA

Table 1. Mean (SE) lengths and percentage of individuals (n = 50/site) showing evidence of spire decollation (erosion of ≥1 apical whorls) of specimens collected at each site. Overall mean length = 16.83 ± 1.19 mm.

Lake	Site code	Mean length (mm)	SE	Percentage decollated (%)
Barney's Lake	BA1	17.80	1.02	64
	BA2	20.26	1.04	90
	BA3	17.50	1.46	66
Lake Geneserath	GE1	15.30	1.02	96
	GE2	16.04	0.88	28
	GE3	16.07	1.37	94
Lake Manitou	LMT1	15.96	0.91	94
	LMT3	16.91	1.17	94
Lake Michigan	LMSP	15.86	1.32	90
	LMIOB	17.13	1.25	88
	LMGB	17.01	1.36	98
	LMDB	16.19	1.50	72

axis 1, with specimens from Lake Geneserath and Lake Manitou being intermediate along axis 1. CVA axis 2 generally differentiated among specimens in Lake Geneserath and Lake Manitou.

Elimia livescens specimens could be assigned correctly to their lake and site of origin based on CVA data (Table 3). Overall, snails were assigned correctly to their lake of origin at a rate of 82.5%. The highest percentage of correct assignment was for snails originating from Barney's Lake (94.7%) and the lowest was for snails originating from Lake Manitou (69.0%). Overall, rate of correct assignment to site of origin was somewhat lower (62.8%). Rates of correct assignment of snails back to site of origin were 76.0% (Barney's Lake), 64.7% (Lake Geneserath), 57.0% (Lake Manitou), and 54.5% (Lake Michigan). Only 2.0% of specimens from Lake Geneserath (also on Beaver Island) and none from Lake Manitou or Lake Michigan were incorrectly assigned to Barney's Lake.

At Barney's Lake, *E. livescens* had high spires and narrow apertures (low values on CVA axis 1; Figs 4, 5A), and at Lake Michigan, snails had a more globose shape and larger apertures (high values along CVA axis 1, Figs 4, 5A). *Elimia livescens* collected from Lake Geneserath and Lake Manitou were generally intermediate in shape (intermediate values along CVA axis 1, Fig. 4), but could be differentiated along CVA axis 2. Snails at Lake Geneserath had a longer aperture and slightly narrower body whorl and shorter spire heights (Fig. 5B) in comparison with the extremes of Barney's Lake and Lake Michigan.

Several environmental variables were significantly correlated ($p < 0.05$) with CVA axes 1 or 2. CVA axis 1 was negatively correlated with % silt substrate (Kendall's τ = −0.580, p = 0.040) and temperature (Pearson's r = −0.739, p = 0.015). Maximum fetch (Kendall's τ = 0.818, p < 0.001), prevailing fetch (Kendall's τ = 0.493, p = 0.032),

mean fetch (Kendall's τ = 0.788, p < 0.001), and % cobble substrate (Kendall's τ = 0.532, p = 0.050) were positively correlated with variation in shell shape along CVA axis 1 (Fig. 4). Specific conductance was positively correlated (Kendall's τ = 0.534, p = 0.019) with CVA axis 2 (Fig. 4). Proportion of individuals showing evidence of spire decollation was not correlated with either CVA axis or any environmental variable (p > 0.05).

DISCUSSION

Elimia livescens is highly variable in shell morphology, a characteristic that allows it to inhabit freshwaters that vary greatly in energetics and water chemistry. This morphological variation may be key to *E. livescens* being among the more widely distributed of pleurocerid snails (Dunithan et al. 2012). The results of our study confirm that *E. livescens* is highly variable in shell shape even in geographically proximate microhabitats. Shell shape was predictive for lake of origin among the 4 lakes sampled and somewhat predictive for site of origin in each lake. Shell shape in *E. livescens* appears to be correlated primarily with local hydrologic energetics (wave action) and secondarily with water chemistry (specific conductance). Consistent with findings in open coastal areas in ocean systems, lakes with higher fetch lengths produce higher-energy wave action and have snails with larger aperture, more globose shape, and lower spire, which may be better for anchorage to rocky substrate during wave action (Parsons 1997, Hollander and Butlin 2010). Similar to protected embayments in ocean systems, sites on lakes with lower fetch lengths produce lower-energy wave action and have snails with a smaller aperture, more elongate shape, and higher spire, which may be better for

Table 2. Summary of environmental, water chemistry, and substrate variables from sites on Barney's Lake, Lake Geneserath, Lake Manitou, and Lake Michigan. Max = maximum, temp = temperature, cond = conductance.

| Lake name	Site code	Max fetch (km)	Prevailing fetch (km)	Mean fetch (km)	Bottom slope (depth/distance to local max depth)	Collection depth (m)	Temp (°C)	pH	Turbidity (NTU)	Specific cond (µS/cm)	Depth of soft sediment (m)	% sand	% silt	% cobble	% gravel	% boulder
Barney's Lake	BA1	0.602	0.100	0.351	0.071	0.50	21.04	8.46	0.0	0.211	0.09	80	20	0	0	0
	BA2	0.386	0.000	0.193	0.040	0.50	21.05	8.43	1.1	0.216	0.09	80	20	0	0	0
	BA3	0.435	0.420	0.428	0.010	0.50	21.38	8.49	1.3	0.212	0.09	80	20	0	0	0
Lake Geneserath	GE1	1.914	0.690	1.302	0.036	0.35	20.51	8.11	0.4	0.158	0.25	70	20	10	0	0
	GE2	1.334	0.000	0.667	0.007	0.48	20.14	8.25	0.0	0.156	0.06	20	50	30	0	0
	GE3	1.883	0.000	0.942	0.150	0.50	20.36	8.14	0.0	0.157	0.10	80	20	0	0	0
Lake Manitou	LMT1	1.550	0.530	1.040	0.120	–	–	8.13[a]	–	0.281[a]	–	–	–	–	–	–
	LMT3	1.530	0.000	0.785	0.081	–	–	8.13[a]	–	0.281[a]	–	–	–	–	–	–
Lake Michigan																
Sucker Point	LMSP	70.55	0.000	35.28	0.027	0.50	16.78	8.25	0.0	0.277	0.00	5	0	80	5	10
Iron Ore Bay	LMIOB	262.4	82.9	172.7	0.047	0.75	18.82	8.45	4.2	0.257	0.08	60	0	40	0	0
Greene's Bay	LMGB	216.6	78.4	147.5	0.034	0.60	19.20	8.43	6.2	0.280	0.00	5	5	60	10	20
Donegal Bay	LMDB	277.2	6.50	141.8	0.018	0.90	16.44	8.33	0.0	0.288	0.00	60	0	30	0	10

[a] from Harris et al. (2011)
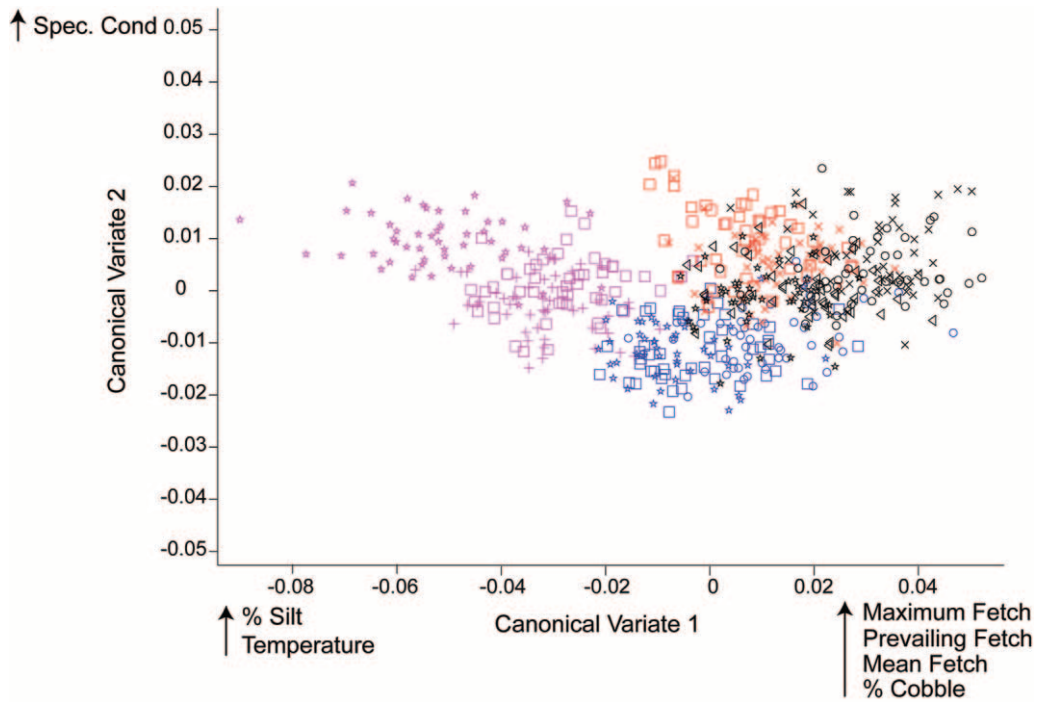
Figure 4. Results of Canonical Variates Analysis (CVA) of Procrustes-superimposed shell shape data from *Elimia livescens*. Colors and symbols represent lakes and sampling locations as in Fig. 3. Seventeen distinct canonical variates (CVs) were recovered (all with $p < 0.0001$). CVA 1 was significantly correlated with % silt substrate, temperature, maximum fetch, prevailing fetch, mean fetch, and % cobble substrate. CVA 2 was significantly correlated with specific conductance (spec. cond).

buoyancy and navigation above soft sediment usually present in low-energy environments (Parsons 1997, Hollander and Butlin 2010).

Past literature supports fetch, wave action, and hydrologic energy as determinants of shell shape in freshwater gastropods. Wiebe (1926) was the first to compare shell shape (using traditional morphometric data) of freshwater pleurocerid shells. In his study on *E. livescens* in Lake Erie, Wiebe (1926) determined the 'average obesity' (width divided by length) of mature snails collected from various sites on the lake selected by their degree of exposure to wave action. Wiebe (1926) and later Goodrich (1934)

Table 3. Jackknife test of sampling site assignments for total sample of 600 *Elimia livescens* specimens based on Canonical Variates Analysis (CVA) scores. Bold indicates correct assignments by lake of origin. Site codes as in Table 2.

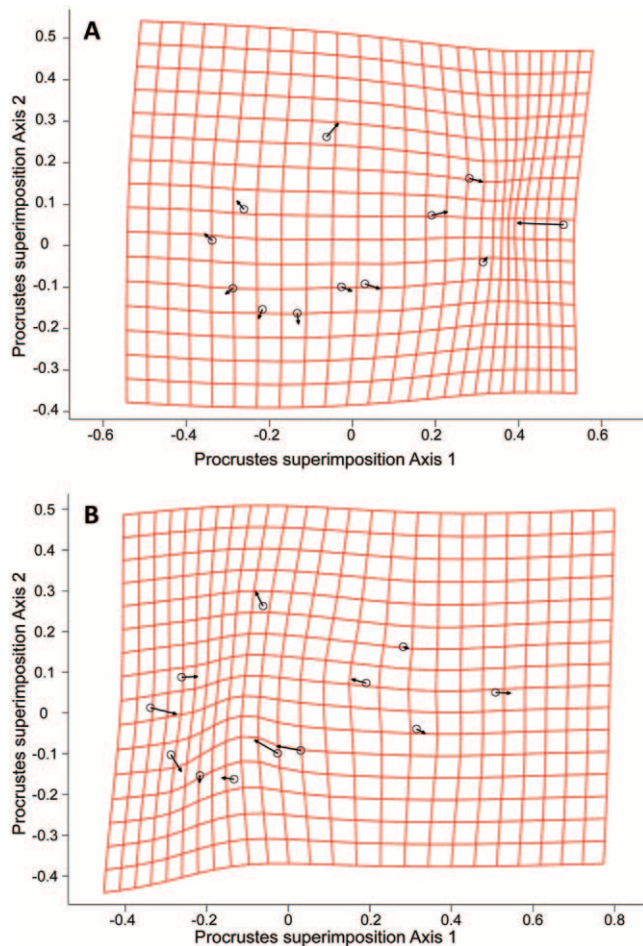| Collection site	CVA assigned site											
	BA1	BA2	BA3	GE1	GE2	GE3	LMT1	LMT3	LMDB	LMGB	LMIOB	LMSP
BA1	**36**	**0**	**10**	0	3	0	0	0	0	0	0	1
BA2	**1**	**43**	**5**	0	0	1	0	0	0	0	0	0
BA3	**10**	**2**	**35**	0	1	1	1	0	0	0	0	0
GE1	0	0	0	**34**	**3**	**4**	2	0	3	2	0	2
GE2	1	0	2	**4**	**30**	**7**	0	2	0	1	0	3
GE3	0	0	0	**8**	**7**	**33**	0	0	0	0	1	1
LMT1	0	0	0	2	0	1	**36**	**6**	1	1	0	3
LMT3	0	0	0	3	1	1	**6**	**21**	1	7	3	7
LMDB	0	0	0	0	0	1	0	4	**23**	7	9	6
LMGB	0	0	0	4	1	2	0	6	5	**22**	4	6
LMIOB	0	0	0	3	0	0	2	5	5	3	**32**	**0**
LMSP	0	0	0	0	1	2	1	9	2	3	**0**	**32**

Figure 5. Deformation grids and vectors showing relative strength of differences in Procrustes-superimposed shell shape along CVA axis 1 (A) and CVA axis 2 (B).

demonstrated that extreme variation in shell obesity occurred in response to wave action. The results of our study based on modern geometric morphometrics largely confirm this hypothesis. Dunithan et al. (2012) showed that shape of *E. livescens* was correlated with flow rate and habitat in freshwater rivers and streams of Indiana. Snails had a smaller aperture and a more streamlined shape at sites with small watersheds and slower water flow. Protected sites (small fetch) in lakes and smaller (lower order) streams appear to have snails with similar elongated shapes and small apertures, and exposed sites (large fetch) in lakes and larger (higher order) rivers have snails with similar globose shapes and large apertures (Minton et al. 2008, 2011, Dunithan et al. 2012).

A secondary environmental correlate to shell shape was specific conductance. Specific conductance is related to the concentration of ions in water and can be highly correlated with Ca^{2+} and CO_3^- ions (Mackie 2004). The underlying bedrock of Lake Michigan is primarily limestone (Larson and Schaetzl 2001), so these ions can be assumed to be major components of the ions dissolved in the waters of the lakes studied. Calcium carbonate ($CaCO_3$) is the primary material from which mollusk shells are constructed. We speculate that incorporation of higher concentrations of Ca (as measured by higher specific conductance) into the snail shells may be responsible for the thicker and more robust shell shapes that we observed along CVA axis 2 (Figs 4, 5B).

Coastal areas of the Great Lakes appear to have processes similar to those along oceanic coastlines in terms of factors affecting snail shell morphology. Marine gastropods (e.g., littorinids) can display extreme variation in shape in response to a variety of factors. A key driver in the shape of marine gastropods is exposure to wave action (Lowell 1984, Parsons 1997, Hollander and Butlin 2010). Inland lakes of the islands of Lake Michigan have similar energetic processes to protected embayments in marine systems. Results of our study could be applied to bay areas with similar environmental variables.

Fetch and wave energetics are well known for playing key roles in structuring coastal communities and habitats. Longer fetch resulting in increased wave action and shear stress in the littoral zone of lakes can influence the abundance and biomass of the benthic community (Scheifhacken et al. 2007). In the Laurentian Great Lakes, coastal wetlands with higher fetch had high abundances of insects and low abundances of crustaceans and gastropods relative to other regions (Cooper et al. 2014). Cyr (2009) suggested that fetch has strong influences on the distribution and functional roles of unionid mussels in littoral benthic communities. Our results suggest that fetch plays a key role in structuring benthic communities and may play a parallel role in structuring populations.

Predator presence also can affect shell shape in snails (e.g., aperture and shell width, thickness, mass, and crushing resistance; Hollander et al. 2006, Lakowitz et al. 2008, Hoverman and Relyea 2009). We suggest future research to determine the extent to which predation affects shell shape in *E. livescens* in the lake systems in our study. During collections of *E. livescens*, we observed crayfish and molluscivorous fish (e.g., carp, sunfish, Round Goby) at many of our sampling sites, but did not quantify these. Differences in predator abundance and type may also influence shell shape in *E. livescens*.

Whether genetic differences are correlated with differences in shell shape in *E. livescens* is not known. A heritable genetic link to shell shape variation may exist in pleurocerids given the findings in marine periwinkles (Parsons 1997) and other freshwater gastropods (Dillon and Jacquemin 2015). Highly variable genetic markers (e.g., microsatellites, single nucleotide polymorphisms [SNPs]) for fine-scale analysis will have to be developed for *E. livescens* and pleurocerid snails in general before this question can be addressed. This type of analysis has been used in *Placostylus* land snails, with little admixture

shown between morphotypes in different environments (Dowle et al. 2015). Analyzing population-level variation of biomineralization genes (e.g., Sun et al. 2015) may be an exciting avenue of future research in pleurocerids and would be better than using proxy genes to characterize genetic diversity and correlating it with shell morphological variation. Genetic analysis in combination with a solid understanding of the drivers of variation in shell shape will help to clarify whether the extreme variation in shell shape in pleurocerids is truly adaptive and will help clarify the systematics and evolutionary history (e.g., Whelan and Strong 2015) of this diverse, ecologically important, and increasingly imperiled clade of freshwater gastropods (Johnson et al. 2013).

ACKNOWLEDGEMENTS

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