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Freshwater mussel shells (Unionidae) chronicle changes in a North American river over the past 1000 years

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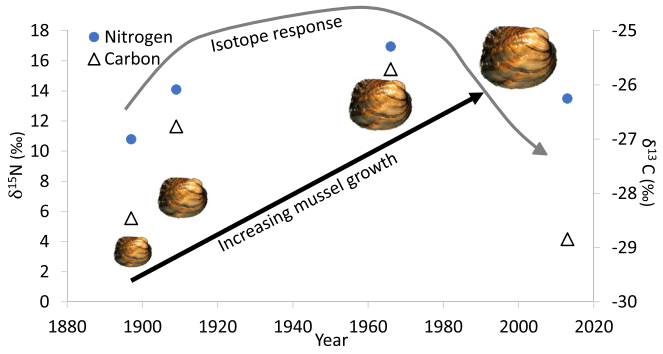
HIGHLIGHTS

- Examined changes in mussel growth and shell isotopes after long-term human impacts
- Mussel growth and size increased over the past 1000 years, mainly after 1900.
- $\delta^{13}C$ (periostracum) increased after 1900, but returned to historical levels after 1960s.
- $\delta^{15}N$ (periostracum) increased after 1900 and remains elevated relative to historical levels.
- Shell growth and isotopic signatures track eutrophication and other human impacts

GRAPHICAL ABSTRACT



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ABSTRACT

The Illinois River was substantially altered during the 20th century with the installation of navigational locks and dams, construction of extensive levee networks, and degradation of water quality. Freshwater mussels were affected by these changes. We used sclerochronology and stable isotopes to evaluate changes over time in age-and-growth and food sources for two mussel species: *Amblema plicata* and *Quadrula quadrula*. Specimens were collected in years 1894, 1897, 1909, 1912, 1966, and 2013, and archeological specimens were collected circa 850. The von Bertalanffy growth parameter (K) was similar between 850 and 1897, but it increased by 1912 and remained elevated through 2013. Predicted maximum size (L_{inf}) increased over the past millennium, and 2013 individuals were over 50% larger than in 850. Growth indices showed similar patterns of continual increases in growth. Shells were enriched in ^{13}C and ^{15}N during the 20th century, but exhibited a partial return to historical conditions by 2013. These patterns are likely attributable to impoundment, nutrient pollution and eutrophication beginning in the early 20th century followed by recent water quality improvement.

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1. Introduction

River ecosystems have been modified extensively by humans. Dams have radically shifted riverine hydraulic habitats to more lentic conditions, and dredging for navigation has further altered natural river channels (Gregory, 2006). Levee construction has disconnected rivers from their backwaters and floodplains, which historically were important sources of allochthonous nutrients (Junk et al., 1989; Bayley, 1995). Finally, water pollution from myriad sources has fundamentally altered riverine communities and food webs (del Giorgio et al., 1991; Gavrilescu et al., 2015). The effects of these impacts on species richness and community structure are well documented, and human activities may even have caused changes in aquatic communities in prehistory (Ekdahl et al., 2004; Peacock et al., 2005). However, more subtle impacts to aquatic organisms such as changes in growth or food sources are virtually unknown. River conservation and restoration depends on a better understanding of original habitat conditions and how human-induced changes have affected aquatic organisms (Willis and Birks, 2006).

The Illinois River was historically considered one of the most productive rivers in the U.S., but it has experienced the full range of human impacts, which badly degraded the ecosystem (Starrett, 1971). Portions of the river were impounded by dams prior to 1900, but the river was dammed completely for navigation by the 1930s, resulting in a minimum 2.7 m-deep channel; channel depth was further maintained by dredging. The river was formerly associated with extensive floodplain lakes and wetlands, but many of these habitats were drained or isolated from the river by levees in the first half of the 20th century. Industrial, domestic, and agricultural water pollution affected the river from an early date. The Illinois and Michigan Canal was completed in 1848 to facilitate ship traffic between the Great Lakes and the Mississippi River basin via the Illinois River. In 1892, flow from the Chicago River, which carried much of Chicago's sewage, was partially diverted via the canal to the Illinois River. This diversion was completed after opening of the much larger Chicago Ship and Sanitary Canal (CSSC) in 1900, which directed virtually all of the city's waste, most of which was untreated, into the Illinois River. This massive influx of sewage created abysmal conditions in the river, particularly in the upper reaches. The water was "continuously foul, with a distinct privy smell. Bubbles of gas continuously broke the surface […] and putrescent masses of soft grayish matter floated on the surface" (Forbes and Richardson, 1913). As late as the 1960s, dissolved oxygen often was <1.0 ppm and occasionally reached 0 (Starrett, 1971). In addition to sewage pollution, the Illinois River drains an intensively agricultural region and receives high inputs of nitrogen, phosphorous, and pesticides (Kelly et al., 2015).

Impoundment and water pollution resulted in radical changes to the aquatic biota of the Illinois River. Massive fish and mussel kills occurred in the early 20th century, and most aquatic life was eliminated from much of the upper river (Forbes and Richardson, 1913; Richardson, 1928). Of the 45 mussel species recorded throughout the river historically, only 23 were found in the 1960s, and the upper river remained devoid of mussels (Starrett, 1971). Subsequent to the 1960s, water quality improved in the Illinois River due to more effective sewage treatment and a reduction in the volume of water diverted from Chicago (Thompson, 2002; Novotny et al., 2007), and fish and mussel populations have rebounded in the upper river (Sietman et al., 2001; Pegg and McClelland, 2004). These changes are remarkably well documented by researchers affiliated mainly with the Illinois Natural History Survey (INHS). INHS maintains extensive collections of mussel shells collected from the Illinois River from the 1800s to the present. In addition, mussel shells harvested for food by pre-Columbian people and excavated at archeological sites provide information about mussel assemblages prior to European settlement.

Mussel shells provide a wealth of information about past and current conditions in aquatic ecosystems. Mussels form annual rings in their shells that reflect a reduction of growth that often occurs in fall or winter (Dettman et al., 1999; Schöne et al., 2004; Haag and Commens-Carson, 2008). These rings can provide precise information on growth rate and ontogenetic age, and they can be used as a shell calendar (Rypel et al., 2008; Haag and Rypel, 2011). Mussel size and growth can be influenced by a wide array of environmental factors (Dunca et al., 2005; Schöne et al., 2007; Haag, 2012). Mussels also incorporate into their shells isotopic signatures that reflect environmental conditions and food sources (Dettman et al., 1999; Delong and Thorp, 2009; Gillikin et al., 2016). Mussels are filter feeders that consume primary producers such as algae, diatoms, and bacteria (Makhutova et al., 2013), and isotopic signatures of mollusks reflect the dominant sources of primary production in aquatic systems (Post, 2002; Delong and Thorp, 2009). Primary productivity is influenced by human-induced environmental changes such as eutrophication and nutrient enrichment (Power et al., 1996). The isotopic signatures of mussel shells are expected to reflect these changes. For example, impoundment, nutrient enrichment, and loss of floodplain wetlands may have resulted in changes in primary productivity in the Illinois River, which would alter mussel food sources. However, long-term changes in freshwater mussel isotopic signatures have rarely been studied.

We used archeological, historical, and contemporary mussel shells to examine changes in growth and isotopic signatures in the Illinois River over the last 1000 years. We examine these patterns in the context of the chronology of human impacts to the river during this period. This approach provides insights into changes in stream conditions not obtainable by other methods.

2. Materials and methods

2.1. Study site and species

Our study site was located on the Illinois River at Havana, Illinois, USA (WSG84: 40.306060,-90.067066). The Illinois River at Havana was first impounded by La Grange Lock and Dam in 1889 (Cooley, 1914), which was subsequently replaced by a larger lock and dam constructed in 1939 (U.S. Army Corps of Engineers, 2015). An INHS field station has been in continuous operation at Havana since 1894 and provides a record of stream conditions and biological resources at the site, including a substantial amount of freshwater mussel shell material. Sewage from Chicago and other upstream locations resulted in increases in plankton in the Illinois River at Havana as early as 1897 (Kofoid, 1903), but major effects of water pollution were not reported until after 1915 (Richardson, 1921). From 1913 to 1920, dissolved oxygen at Havana dropped from 4 ppm to 1 ppm, and about 70 species of benthic organisms other than mussels were eliminated from this vicinity (Richardson, 1925). Of the 43 mussel species originally reported in the reach affected by La Grange Lock and Dam, only 18 were found by 1966, and dissolved oxygen generally remained <1.5 ppm in the vicinity of Havana (Starrett, 1971). Quantitative estimates of mussel abundance are not available for this period, but several mussel beds, representing dense mussel aggregations, were found in this reach in 1912 and none were found in 1966. Declines in mussel species richness and abundance probably are attributable to the combination of impoundment and water pollution. Subsequent to the 1960s, water quality in the Illinois River at Havana has improved steadily. Fish populations have rebounded and native fish species richness has increased since the 1970s (McClelland et al., 2012). In 1994–2002, dissolved oxygen consistently remained above 5.0 ppm during winter and fell below this level in only 25% of summer samples (Johnson and Hagerty, 2008).

We focused our research on two species: *Amblema plicata* and *Quadrula quadrula.* These two species survived impoundment and water pollution (although probably at reduced abundance), and they are numerically dominant both in historical collections and in contemporary mussel assemblages in the river. Historical shell material for these species was available from the INHS Mollusk Collection for the following years: 1894, 1897, 1909, 1912, 1966, and 1994. We pooled

specimens from 1894 and 1897 into one group (1897) and pooled specimens from 1909 and 1912 (1912). Contemporary shells were live collected during the summer of 2013. We also obtained specimens of *Amblema plicata* that were collected from archeological excavations along the Illinois River near Havana (dated c. 1000–1200 years bp) and currently housed at the Illinois State Museum. The age of these specimens was based upon the proximity of the shells to pottery and other excavated artifacts that are consistent with Native American cultural associations in this region c. 1000–1200 years bp (Warren, 2014). For archeological specimens, we assigned their date of collection as 850 [1950–1100 (radiocarbon dating convention minus the midpoint of the estimated age)] to allow placement of these individuals within our chronology; we emphasize that this date should be viewed as an approximation for illustrative purposes rather than an association with a specific calendar year. Together, these samples provided specimens of *Amblema plicata* from five time periods: 850, 1897, 1912, 1966, and 2013; and specimens of *Quadrula quadrula* from four time periods: 1897, 1912, 1994, and 2013. We obtained a total of 81 *A. plicata*, including 76 historical or recent specimens and 5 archeological specimens, and 49 historical and recent specimens of *Q. quadrula* (Table 1).

2.2. Sample preparation for age and growth

We processed mussel shells for age and growth analysis following established methods (Neves and Moyer, 1988; Haag and Commens-Carson, 2008). Briefly, the right valve of each specimen was cut radially from the umbo to the ventral margin along the height access with a diamond-embedded blade on a low-speed saw (Buehler, Lake Bluff, Illinois, USA). One half of the cut shell was mounted with epoxy to a microscope slide and cut again to produce a single ~300 μm-thick thin-section. Thin-sections were interpreted under transmitted light with a stereomicroscope by two experienced readers. Readers interpreted thin-sections independently and identified shell rings as annuli or non-annual features such as disturbance rings. If the two readers disagreed on the interpretation of a thin-section and could not reach consensus following joint examination, that specimen was omitted from the dataset. Three *A. plicata* specimens were omitted. After interpretation, thin-sections were scanned into digital images and we measured growth increment widths for each year as the linear distance along the radial shell axis between adjacent annuli at the boundary between the nacreous and prismatic shell layers (see Rypel et al., 2008) using ImageJ software (ImageJ, open source). For each increment observation, we determined the age of the individual at the time of increment deposition by counting the number of annuli present prior to increment deposition. All specimens except archeological specimens had a recorded date of collection allowing each growth increment to be associated with a specific calendar year. We also assigned a calendar year for growth increments of archeological specimens assuming collection in 850 (see previous), but these assignments should be viewed as approximate.

Table 1
von Bertalanffy growth parameters for *Amblema plicata* and *Quadrula quadrula* from the Illinois River in different time periods. N is the number of individuals examined for each time period.

Time period	N	Growth rate (K)	95% CI (±)	Max. size, mm (L_{inf})	95% CI (±)
Amblema plicata					
2013	16	0.133	0.019	83.9	4.9
1966	25	0.154	0.022	71.7	4.4
1912	11	0.130	0.018	68.7	3.5
1897	24	0.090	0.016	65.5	5.3
850	5	0.097	0.017	55.1	3.7
Quadrula quadrula					
2013	19	0.213	0.016	67.5	1.3
1994	3	0.226	0.033	64.7	3.0
1897	23	0.103	0.020	55.9	5.1

2.3. Sample preparation for stable isotope analysis

Samples were processed for stable isotope analysis following Delong and Thorp (2009). The right valve of each specimen was washed with distilled water and a soft-bristled brush to remove adhered sediments. We then removed a sample of periostracum (the proteinaceous outer layer of the shell) from the ventral margin of the shell by scraping with a scalpel. The ventral margin of the shell represents material deposited most recently, and we sampled from this region so that isotopic signatures would most closely reflect conditions at the time of specimen collection. These samples encompassed the final 2–3 years of specimens' lives. Periostracum samples were dried at 60 °C for 48 h then ground into a homogenous powder using a Wig-L-Bug grinding mill (International Crystal Laboratories, Garfield, New Jersey, USA). Periostracum powder was placed into glass scintillation vials and 100 μL of distilled water was added to each vial to moisten the sample. Vials were placed into a glass desiccator dome containing 300 mL of concentrated reagent-grade 12 M hydrochloric acid and sealed for 48 h to allow the acid vapor to remove inorganic carbon from the samples (Yamamuro and Kayanne, 1995). After acidification, samples were removed from the desiccator and dried again at 60 °C for 48 h. Samples were then shipped to the North Carolina State University Stable Isotope Laboratory, where a 0.2–0.3 mg subsample of each sample was analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios. The samples underwent flash combustion at 1050 °C in a Carlo Erba NC 2500 Elemental Analyzer prior to analysis on a Finnigan MAT Delta Plus XL mass spectrometer (Thermo Fisher Scientific, Carlsbad, California, USA).

By convention, C and N isotope ratios are expressed as δ, the deviation from standards in parts per thousand (‰), according to the following equation:

$$\delta X\ (‰) = \left[\left(R_{sample} - R_{standard}\right)/R_{standard}\right] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Values were normalized to the following international and North American isotope standards: IAEA-C-6 = sucrose, $\delta^{13}C(PDB) = -10.45‰$; IAEA-NO-3 = KNO_3, $\delta^{15}N(AIR) = 4.720‰$; Atropine, $\delta^{13}C = -29.349‰$ and $\delta^{15}N = -12.537‰$, Nicotinammide, $\delta^{13}C = -40.867‰$ and $\delta^{15}N = -1.979‰$, and L-glutamic acid, $\delta^{13}C = 37.63‰$ and $\delta^{15}N = 47.577‰$. Instrument precision was ±0.2‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$.

2.4. Statistical analysis

We examined changes in growth over time in two ways. First, we characterized freshwater mussel growth with the von Bertalanffy growth equation.

$$L_t = L_{inf}\left(1 - e^{-K(t-t0)}\right)$$

where L_t is height (mm) at time t (age in years), L_{inf} is height (mm) at time infinity (the predicted mean maximum height for the population), K is a growth constant that describes the rate at which L_{inf} is attained (mm year^{-1}), t is age (year), and t_0 is the time at which height = 0 (Ricker, 1975). The parameter K is often interpreted as a growth rate because it represents the rate at which individuals reach maximum size. We interpreted differences in K and L_{inf} among time periods as reflecting differences in growth rate and size, respectively. Second, we directly examined differences in growth increment width among time periods. We removed age-related variation (i.e., faster growth in young individuals and slower growth in older individuals) with a detrending function as follows. We fit a negative exponential function

to the relationship between increment width and age for all observations. We used this relationship to generate predicted increment width for each observation based on the age of the specimen at the time of observation. The observed increment width divided by the predicted increment width provided a unitless, relative growth index (GI) for each observation. The GI has a mean of 1.0. Observations with GI > 1.0 represented years with higher than average growth, and values <1.0 represent years of lower than average growth. We calculated the mean GI for all observations in a time period; this measurement was based on the mean GI for each individual (across all years in that individual's chronology) to avoid problems with non-independence of multiple measurements for a single individual. The mean chronology length across all specimens and time periods was 11.7 years (minimum = 2; maximum = 30); the mean number of observations in each calendar year was 8.4 (minimum = 1; maximum = 29). We tested the null hypothesis that mean GI did not differ among time periods with Analysis of Variance, followed by a Tukey post-hoc test (SAS, version 9.1; SAS Institute, Cary, North Carolina).

3. Results

3.1. Age and growth

The von Bertalanffy growth parameter (K) for *A. plicata* was similar between 850 and 1897, but it increased sharply by 1912 and remained at similarly higher levels through 2013. Predicted maximum size (L_{inf}) increased over the past millennium, with 2013 individuals reaching a predicted maximum size over 50% larger than in 850 (Table 1; Fig. 1). *Quadrula quadrula* showed a similar pattern of increases in K and L_{inf} since 1897, and K more than doubled between 1897 and 1994. Values of K and L_{inf} for 1912 were exceptionally small and large, respectively, and associated confidence intervals were large. This probably is due to the small sample size for this time period and the uniformly small size of individuals in the sample, and we consider these values uninterpretable.

Growth indices showed similar patterns of continual increases in growth over time for both species (Table 2, Fig. 2). Both species showed high annual variability within time periods, but mean GI differed significantly among time periods (*A. plicata*: $F_{4,76} = 15.55$, $p = 0.0001$; *Q. quadrula* $F_{3,45} = 24.78$, $p = 0.0001$). For *A. plicata*, GI increased significantly over the past millennium, with the highest GI recorded in 2013.

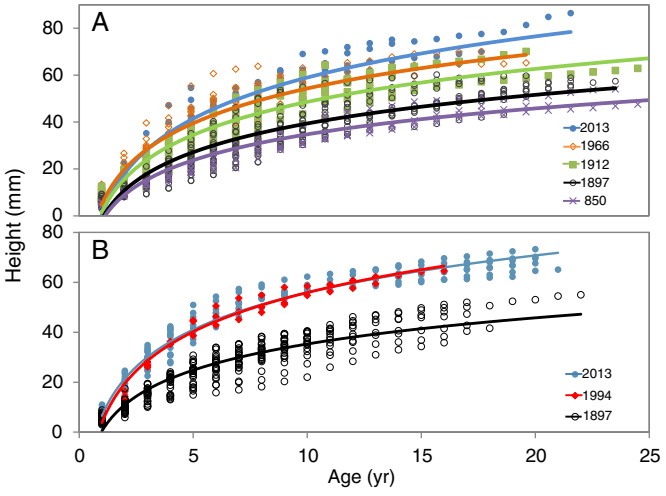

Fig. 1. Height-at-age curves for *Amblema plicata* (A) and *Quadrula quadrula* (B) from the Illinois River in different time periods.

Table 2
Growth indices (GI) for *Amblema plicata* and *Quadrula quadrula* from the Illinois River in different time periods. N is the number of individuals examined for each time period. GI for time periods with the same letter (significance) are not significantly different (Tukey post-hoc test, $p < 0.05$).

Time period	N	Mean GI	95% CI (±)	Significance
Amblema plicata				
2013	16	1.21	0.13	A
1966	25	1.09	0.08	A B
1912	11	1.05	0.08	B C
1897	24	0.87	0.06	C D
850	5	0.73	0.07	D
Quadrula quadrula				
2013	19	1.15	0.13	A
1994	3	1.08	0.07	A B
1912	4	0.99	0.13	B
1897	23	0.83	0.04	B

For *Q. quadrula*, GI was significantly higher in 2013 than 1897 and 1912, but GI in 1994 did not differ from any other time period.

3.2. Stable isotopes

Stable isotope values also showed marked shifts over time, and these results were similar for both species (Fig. 3). Values of both $\delta^{13}C$ and $\delta^{15}N$ increased dramatically between 1897 and 1912, and increased still further by 1966 for *A. plicata* (samples of *Q. quadrula* were not available for this period). By 2013, values of $\delta^{13}C$ had returned to levels similar to 1897, but $\delta^{15}N$ remained at elevated levels similar to 1912 (Table 3).

4. Discussion

The Illinois River has been altered massively by humans during the last 150 years, and our results provide additional detail about the nature of these changes. From an ecosystem perspective, the changes in carbon and nitrogen isotope ratios in mussel shells suggest fundamental alteration of energy sources and food webs beginning in the early 20th century. Unfortunately, we have no data on isotope ratios in pre-Columbian times because samples from those shells were below detection for ^{13}C and ^{15}N, using the analytical techniques prescribed by Delong and Thorp (2009). Nonetheless, enrichment of ^{13}C and ^{15}N after 1900 depicts immense changes in the structure and function of the Illinois River ecosystem. Previous studies have indicated increases of 2–12‰ in the $\delta^{15}N$ of algae, macroinvertebrates, and fishes collected below wastewater treatment plants and industrial outflows (Kendall, 1998; Wayland and Hobson, 2001; Morrissey et al., 2013; Loomer et al., 2015) and our data depict a similar trend in $\delta^{15}N$ following the opening of the Chicago Sanitary and Ship Canal and the release of Chicago-area wastes into the lower watershed.

To the best of the authors' knowledge, the reported $\delta^{15}N$ values for samples collected in 1966 (mean 16.95‰) represent some of the highest ever recorded in mussel tissues. However, these values are not unexpected considering the results of previous analyses from this region. Fry and Allen (2003) reported relatively high $\delta^{15}N$ ratios (15–16‰) in zebra mussel shells collected from the lower Illinois River near Alton, Illinois. Similarly, Newton et al. (2013) documented freshwater mussel $\delta^{15}N$ values ranging from 12–16‰ at four locations in North America: Oklahoma, Michigan, Wisconsin, and Ontario. While we assume that the observed changes in $\delta^{15}N$ between 1897–2013 can be attributed to pollution and other anthropogenically derived nutrient sources, background levels of $\delta^{15}N$ in the Illinois River (as interpreted from 1897 samples) are still high relative to observations from other similar studies where the effects of sewage and industrial waste on freshwater mussel $\delta^{15}N$ values was measured (Wayland and

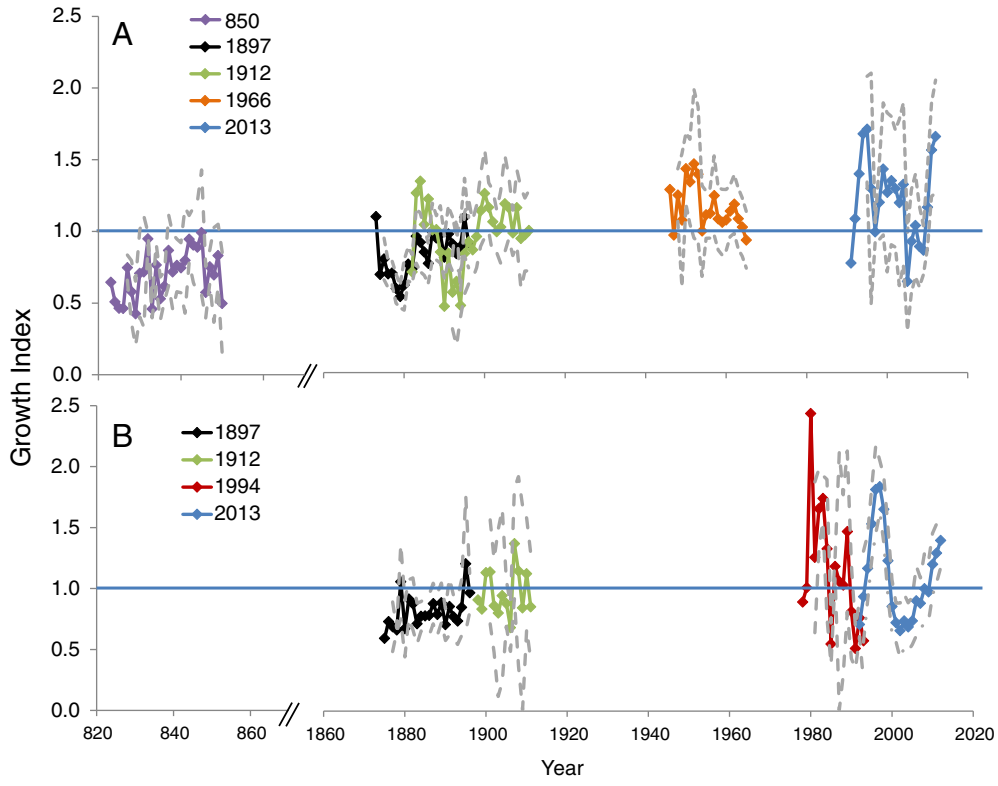

Fig. 2. Growth indices (GI, ±95% CI) for *Amblema plicata* (A) and *Quadrula quadrula* (B) from the Illinois River in different time periods. The mean value of GI across all observations is 1.0 (solid blue line); values <1.0 indicate years of lower than average growth, and values >1.0 indicate higher than average growth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Hobson, 2001; Morrissey et al., 2013; Loomer et al., 2015). Fry and Allen (2003) posit that regional geochemical mechanisms may contribute to these relatively high values via unique nitrification/denitrification processes occurring in the Illinois River watershed. While other explanations for our observations of high δ^{15}N could plausibly be attributed to the decomposition of predator tissues following fish kills during the middle of the 20th century (Gregory-Eaves et al., 2007), we feel that the nitrification/denitrification hypothesis detailed by Fry and Allen (2003) and explored further by Panno et al. (2006) provides the most direct explanation of these relatively high δ^{15}N values observed in mussels collected before the onset of the drastic environmental changes that began in 1900.

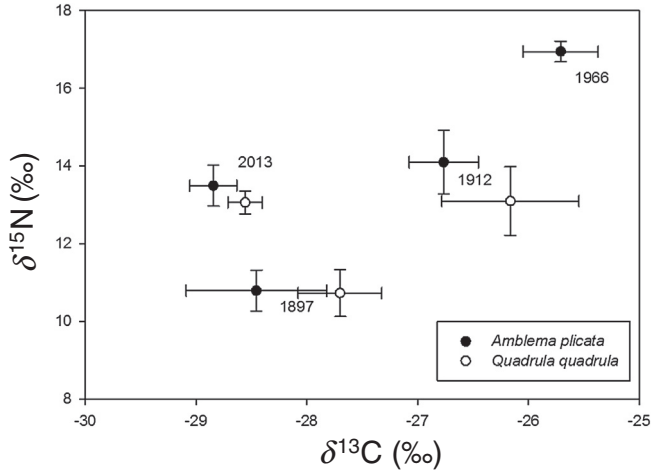

Fig. 3. δ^{13}C and δ^{15}N values (mean ± 95% CI) for *Amblema plicata* and *Quadrula quadrula* specimens from the Illinois River in different time periods.

Carbon isotope signatures of contemporary mussels provide evidence of reduced sewage inputs probably in response to improved sewage treatment and other measures since implementation of the Clean Water Act and related legislation. However, δ^{15}N remains elevated at levels similar to those seen in 1912, which is indicative of continued deposition of anthropogenically-derived nitrogenous compounds such as fertilizers, animal wastes, and urban wastewater (Kelly et al., 2015).

Changes in mussel growth provide important information about the effects of ecosystem alteration on aquatic organisms apart from documented declines in species richness and abundance. Mussels in 1897 appeared to grow similarly to those in 850. The only evidence of changes between these two time periods is a greater predicted maximum size for 1897 individuals compared with 850. However, this could be due to the propensity of aboriginal harvesters to avoid larger, less palatable mussels; large mussels occur infrequently in archeological contexts and are usually modified for use as implements (Haag, 2009). In contrast, scientific collectors did not harvest with palatability in mind. All other measures of growth suggest that environmental conditions were similar between 1897 and pre-Columbian times.

After 1897, all measures of mussel growth indicate dramatic and consistent increases in growth rate and size. Unlike the possible size bias present in archeological samples, all historical and recent samples were collected by scientists and there is no reason to suspect a systematic bias sufficient to create this pattern. Rather, these changes may indicate organism responses to ecosystem alteration, but the mechanism for these responses is unclear. Several authors have proposed that nutrient enrichment and subsequent increases in primary

Table 3
$\delta^{13}C$ and $\delta^{15}N$ isotope values, age, and length for *Amblema plicata* and *Quadrula quadrula* specimens from the Illinois River in different time periods.

$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	Collection year	Age (years)	Length (mm)
Amblema plicata				
10.02	−28.07	1897	24	57.4
9.45	−28.26	1897	16	60.2
10.97	−29.05	1897	18	57.5
11.17	−29.50	1897	12	47.8
11.92	−28.87	1897	8	35.4
11.71	−28.57	1897	20	50.9
11.90	−30.48	1897	10	36.6
10.70	−28.96	1897	19	43.2
10.18	−27.10	1897	9	53.7
11.27	−27.53	1897	4	24.3
9.40	−26.64	1897	6	23.9
14.69	−27.21	1912	13	59.8
14.75	−27.18	1912	16	64.9
13.92	−26.40	1912	9	54.7
14.81	−26.24	1912	11	64.3
14.67	−26.94	1912	14	59.8
14.40	−26.69	1912	12	57.1
13.75	−26.51	1912	14	63.3
14.55	−27.39	1912	30	66.3
13.75	−26.68	1912	14	50.4
15.63	−27.49	1912	20	70.1
10.11	−25.69	1912	3	19.6
17.44	−25.49	1966	20	65.2
17.58	−25.33	1966	18	70.1
17.61	−24.81	1966	15	59.5
17.04	−25.12	1966	8	63.8
16.93	−25.47	1966	12	58.8
16.48	−26.22	1966	8	49.0
16.47	−25.46	1966	5	38.9
16.72	−26.41	1966	6	36.2
16.76	−26.79	1966	5	30.3
17.10	−25.78	1966	8	38.7
16.27	−25.93	1966	10	56.5
13.53	−29.44	2013	5	41.5
14.41	−29.02	2013	22	86.4
14.34	−28.58	2013	6	39.8
12.62	−29.17	2013	5	42.7
14.58	−28.48	2013	5	29.8
14.39	−28.31	2013	5	45.7
13.63	−28.69	2013	3	26.2
12.59	−29.05	2013	5	54.6
11.70	−28.77	2013	18	70.0
13.21	−29.27	2013	14	75.1
13.43	−28.50	2013	17	64.8
Quadrula quadrula				
11.34	−28.25	1897	14	39.4
11.05	−27.56	1897	17	42.8
9.12	−27.43	1897	9	33.1
12.57	−28.70	1897	9	27.9
10.27	−28.02	1897	11	37.0
9.93	−27.01	1897	8	32.1
9.66	−28.15	1897	12	36.0
11.07	−27.38	1897	17	52.0
12.24	−27.98	1897	22	55.0
10.42	−26.32	1897	10	32.4
10.33	−27.92	1897	17	47.3
13.29	−26.22	1912	14	55.9
13.95	−26.78	1912	11	45.2
11.63	−25.15	1912	8	32.5
13.52	−26.51	1912	4	18.1
14.02	−28.43	2013	8	58.1
12.51	−28.41	2013	4	38.3
12.82	−28.96	2013	2	20.2
13.78	−28.72	2013	4	41.1
12.66	−28.84	2013	3	28.1
13.08	−28.32	2013	5	44.8
12.91	−28.20	2013	7	49.3
12.82	−28.60	2013	20	70.2
13.27	−28.31	2013	19	66.7
12.73	−28.79	2013	20	73.3

productivity should result in increased mussel growth, and field studies generally support this idea (Arter, 1989; Ostrovsky et al., 1993; Mutvei et al., 1996; Dunca et al., 2005; Strayer, 2014). Our growth results, coupled with the changes we show in isotopic ratios, also support this idea, but our data are the first to show this response in a historical context.

In the Illinois River, enrichment from sewage and fertilizers likely directly resulted in increases in primary productivity, which may have supported higher mussel growth. Plankton production in 1909–1910 was 69% higher than measured in 1897–1898 (Forbes and Richardson, 1919). However, the impact of sewage in our study reach is confounded by the impact of impoundment. By increasing retention time and water temperature, impoundment can result in increased primary productivity and eutrophication even in the absence of severe anthropogenic enrichment (Reynolds and Descy, 1996; Ochs et al., 2013). The influence of impoundment on mussel growth has not been studied directly, but mussels from lentic or depositional environments can grow faster and reach larger sizes than those in streams (Zieritz and Aldridge, 2011; Haag, 2012). It is likely that nutrient enrichment and impoundment acted in concert to increase primary productivity and facilitate higher mussel growth in the Illinois River.

Increased growth is often viewed by default as a positive attribute, but this assumption deserves scrutiny. As for many organisms, growth rate of mussels is strongly negatively correlated with lifespan (Haag and Rypel, 2011); this and other unknown tradeoffs may have important ramifications for population dynamics. More directly, increased mussel growth beginning in the early 1900s coincided with dramatic declines in mussel abundance and species richness in the Illinois River, suggesting that increased growth was a factor in these declines. More likely, increased growth may have been simply a collateral response associated with other factors such as low dissolved oxygen, which were directly responsible for mussel declines. This is supported by the observation that mussel growth rates remain high today despite increasing mussel populations in the Illinois River. The adaptive significance of increased growth rates also should be viewed in the context of differences in food requirements and other attributes among mussel species. *Amblema plicata* and *Q. quadrula* adapt readily to impoundment and other radical habitat alterations (Haag, 2012), suggesting that they are able to use a wide array of food resources. Specific food requirements are poorly known for most species (Nichols and Garling, 2000; Vaughn et al., 2008; Newton et al., 2013), but the loss of nearly half of the original mussel species richness in the Illinois River suggests that many species were unable to adapt to changes in food resources or other habitat conditions brought about by nutrient enrichment and impoundment. For these reasons, it is prudent to view increased mussel growth rates potentially as indicative of environmental changes that have broad, negative effects on overall ecosystem integrity.

Massive habitat alteration and nutrient enrichment by humans is a compelling explanation for the patterns we observed, but other mechanisms should be considered, particularly for growth. Bivalve growth can be influenced by long-term climatic cycles resulting in decade-long periods of slower or faster growth (e.g., Schöne et al., 2004; Butler et al., 2013), and such patterns could be in part responsible for our finding of growth differences among time periods due to the relatively short duration of our chronologies. However, other studies of temporal variation in mussel growth found less frequent oscillations with durations of only 2–4 years (Rypel et al., 2008; Black et al., 2010), a time period that would have been captured within our chronologies. Increasing water temperatures or other effects related to global climate change also could be factors in increased mussel growth in the last 150 years, but at this time, the effects of climate change on bivalve growth remain unclear (Zippay and Helmuth, 2012). Freshwater mussel shells represent a valuable opportunity for studying a wide variety of ecosystem changes, and the large number of historical specimens in museum collections facilitates examination of changes over long time scales. A nearly continuous growth chronology spanning 217 years has been constructed for

the European pearl mussel (*Margaritifera margaritifera*; Schöne et al., 2004), and similar studies in other parts of the world are needed.

5. Conclusions

Mussel growth showed little change in the Illinois River between pre-Columbian times and the late 1800s, despite human impacts in the 19th century and perhaps earlier. After 1900, shell growth and size increased dramatically and steadily coincident with an accumulation of severe human impacts to the river. Changes in shell stable isotopes also show marked changes during the 20th century. Changes in shell size and isotopic signatures probably are due to a combination of nutrient enrichment and other forms of water pollution, as well as impoundment. $\delta^{13}C$ has returned to historical levels since the 1960s, which may reflect improvement in water quality. However, $\delta^{15}N$ and mussel size and growth remain elevated, suggesting continued impairment of the Illinois River.

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