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**Long-term increases in shell thickness in *Elliptio complanata* (Bivalvia: Unionidae) in the  
freshwater tidal Hudson River**

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## Abstract

1. The shells of freshwater mollusks are highly plastic in response to environmental and ecological conditions, which can affect ecological interactions and ecosystem functioning.
2. We tested for changes in relative shell thickness in the unionid bivalve *Elliptio complanata* in the freshwater tidal Hudson River over 1991-2017, a period of changing water chemistry and predation pressure.
3. Shells of both juveniles (shells <20 mm long) and larger animals became substantially (~10-25%) and significantly heavier (for a given shell length) over the study period. This parallels previously published results for the non-native zebra mussel *Dreissena polymorpha* in the Hudson.
4. Increased shell thickness during the study period could be explained by rising pH, alkalinity, and temperature, which increased calcite saturation and favored the precipitation of calcium carbonate shells, as well as a response to greater predation by shell-crushing predators.
5. Because the factors that affect shell thickness (e.g., calcium carbonate saturation and presence and abundance of predators) are changing rapidly in many lakes and rivers, similar large changes in shell thickness may be occurring in fresh waters around the world, affecting ecological interactions and ecosystem functioning.

## Introduction

The shells of freshwater mollusks can be highly plastic, so that the dimensions and appearance of a single species can vary greatly across sites or times. Because this plasticity complicates traditional shell-based taxonomy, the nature and causes of shell plasticity have received considerable attention. Variation in shell morphology may be caused by differences in habitat type (i.e., creeks vs. large rivers – Ortmann, 1920), water chemistry (chiefly calcium, pH, and inorganic carbon concentrations – e.g., Agrell, 1949; Brodersen & Madsen, 2003; Green, 1972; Hunter & Lull, 1977), predation (e.g., Covich, 2010), ecosystem productivity (Agrell, 1949), exposure (i.e., the strength of physical forces from currents and waves – Bailey & Green, 1988; Brown et al., 1938), and growth rates (Haag & Rypel, 2011).

Although it has not received as much attention as other aspects of shell plasticity, shell thickness is an ecologically important, plastic trait. Previous authors have found substantial intraspecific variation in shell thickness or strength (e.g., Brodersen & Madsen, 2003; Hunter & Lull, 1977; Lewis & Magnuson, 1999), which has been attributed to all of the causes listed in the previous paragraph. Whatever its cause, intraspecific differences in shell thickness can be ecologically important. Thick shells are more resistant than thin shells to shell-crushing predators such as fish and decapods (e.g., Covich, 2010). Furthermore, thick shells persist longer than thin shells in the environment because they dissolve more slowly (Strayer & Malcom, 2007) and are more resistant to breakage, and so have more potential to transform habitats (Gutierrez et al., 2003; Strayer & Malcom, 2007).

Previously we found that shells of the non-native zebra mussel (*Dreissena polymorpha*) became ~20% heavier (for a given shell length) over the first 25 years of its invasion of the freshwater tidal Hudson River, New York (Natesan & Strayer, 2016). Here, we investigated whether the shells of a native unionid bivalve (the eastern elliptio, *Elliptio complanata*) likewise became thicker (i.e., heavier for given shell dimensions) over the same time period. We also assessed likely causes of observed changes in shell thickness in both bivalves.

## Methods

### *Study Area*

The study area was the freshwater tidal Hudson River in eastern New York, extending between RKM 99 and RKM 247 (RKM is river kilometers upriver of The Battery near the mouth of the river). This section of the Hudson is a large, fertile, hardwater (calcium ~25-30 mg/L) river with predominately sandy and muddy sediments (Caraco et al., 1997; Levinton & Waldman, 2006; Strayer, 2012). Although the water in the study area is fresh, rarely with even a trace of sea salt, the entire study area is strongly tidal, with tidal amplitudes of 0.8-1.6 m, and daily tidal flows usually are much greater than net downriver flows. Zebra mussels first appeared in the Hudson in 1991, and the population has been large but variable since autumn 1992 (Strayer et al., 2020).

### *Study design*

Methods for the collection and handling of the unionids used in this study were described by Strayer & Malcom (2018). Briefly, we collected unionids in midsummer from 1992 through 2017 using a standard PONAR grab at 44 sites arrayed in a stratified random design throughout

the study area. Sediments were sieved in the field through a 2.8-mm screen. Material retained on the sieve (including living unionids) was put on ice and frozen upon return to the laboratory. The sieve residue was later thawed and searched for small unionids. After removing attached dreissenids, the bodies of unionids were removed from their shells, and the shells were air-dried. Shell dimensions (length, width, and height) were measured to 0.1mm with calipers, and shell mass was measured to 0.01 g using a Mettler Model XS802S top-loading balance or (for small shells) to 0.01 mg using a Mettler Model XPE205 side-loading balance.

Although several unionid species lived in the Hudson in the early 1990s (Strayer et al., 1994), only *Elliptio complanata* (henceforth “*Elliptio*”) remained abundant after 1995 (Strayer & Malcom, 2018), so we restricted our analysis to this species. *Elliptio* is native to the Hudson, and often is the most abundant unionid in creeks, rivers, reservoirs, and lakes from Georgia to Nova Scotia.

Water chemistry samples were taken every other week during the ice-free season (usually April-December) near Kingston (RKM 148). Water temperature was measured 0.5 m below the surface with a YSI oxygen probe, and water samples were taken with a peristaltic pump at the same depth, then kept cool until analyzed. Water samples for laboratory analysis of dissolved inorganic carbon (DIC) and pH were transferred without aeration using the peristaltic pump into glass BOD bottles to avoid loss of dissolved CO<sub>2</sub>. Samples for analysis of DIC were analyzed after headspace equilibration using a Shimadzu gas chromatograph (prior to 2007) or directly using a Shimadzu high-temperature combustion carbon analyzer. For the latter method, DIC samples were vacuum-filtered through pre-combusted glass-fiber filters. In another sample, pH was measured using a combination electrode calibrated to pH 4 and 7 standards.

Water chemistry samples were also taken less frequently at three other stations that spanned nearly the length of the study area: Castleton (RKM 216), Hudson (RKM 184), and Poughkeepsie (RKM 117). Samples from these stations were typically taken every other month during the ice-free season, resulting in four samples/year in most years between 1987 and 2019. These samples were collected and handled like the samples from Kingston.

#### *Data analysis*

We used linear regression to test for changes in shell thickness over time. Because we expected a power-law relationship between linear shell dimensions and shell mass (Atkinson et al., 2020), we log<sub>10</sub>-transformed the shell-dimension and mass data before analysis. A plot of

shell length vs. mass identified 20 obvious outliers (points having an absolute residual  $>0.5$ ), which we removed from the data set before analysis. We then ran a multiple linear regression to predict  $\log_{10}$  shell mass from year (as a continuous variable) and  $\log_{10}$  shell length, height, and width. This model tests for a long-term directional change in relative shell thickness. Although shell length, height, and width are intercorrelated, best-subsets regressions showed that models using all three shell dimensions were as good to much better at predicting shell mass than any one- or two-variable model ( $\Delta AIC$  always  $>246$  for large *Elliptio* and always  $>0.5$  for small *Elliptio*).

We ran separate analyses for juvenile (shell length  $< 20\text{mm}$ ) and larger (shell length  $\geq 20\text{ mm}$ ) mussels, as we have done in previous analyses (e.g., Strayer & Malcom, 2018). The size distribution of the Hudson's *Elliptio* population is highly bimodal, with few animals 25-45 mm long (Strayer & Malcom, 2018). Further, juvenile and adult unionids can occupy different habitats and have different habits (Haag, 2012).

Our data also afforded the opportunity to test for changes in relative shell dimensions over time. We ran multiple linear regression of  $\log_{10}(\text{shell height})$  and  $\log_{10}(\text{shell width})$  on  $\log_{10}(\text{shell length})$  and year to test for long-term changes in relative shell dimensions.

We estimated the calcite saturation index as an indication of the thermodynamic tendency for biogenic calcification. An approximation of the saturation index based on Method 2330 B from APHA (2005) requires data on total alkalinity, pH, conductivity, temperature, and  $\text{Ca}^{2+}$  concentrations. Of these variables, we have data only for pH, conductivity, and temperature over the study period. We were able to estimate calcite saturation by making the following assumptions. First, at the slightly basic pH of the Hudson River (median, 7.82; range 6.92-9.00), total alkalinity is due almost entirely to bicarbonate ( $\text{HCO}_3^-$ ), and  $\text{HCO}_3^-$  is the predominant component of dissolved inorganic carbon (DIC) because free  $\text{CO}_2$  (overall mean,  $49\text{ }\mu\text{M}$ ) is  $<5\%$  of the DIC (range,  $\sim 900\text{-}1350\text{ }\mu\text{M}$ ) (Raymond et al., 1997). We therefore assumed that DIC was equivalent to  $\text{HCO}_3^-$  concentration, and that alkalinity was due solely to  $\text{HCO}_3^-$ . Second, we assumed that the  $\text{Ca}^{2+}$  concentration was balanced in charge equivalents by the  $\text{HCO}_3^-$  concentration. Full analyses of major ion chemistry in the Hudson River are not available for the entire period, but a representative set of major ion data summarized by Simpson (2006) supports this assumption: median concentrations for  $\text{HCO}_3^-$  and  $\text{Ca}^{2+}$  in the Hudson River at Poughkeepsie ( $n = 37$  samplings) were  $1,059$  and  $1,148\text{ }\mu\text{eq L}^{-1}$ , respectively.

Long-term change in pH and dissolved inorganic carbon in samples taken at Castleton, Hudson, and Poughkeepsie was assessed using ANCOVA; independent variables were year and season (as a class variable where 1 = day-of-the-year (DOY) 1-151, 2 = DOY 152-212, 3 = DOY 213-273, 4 = DOY 274-366). Season was included in the model because previous studies (Raymond et al., 1997) showed seasonal variation in inorganic carbon chemistry in the Hudson. Prior to running these ANCOVAs, we tested for homogeneity of slopes across seasons, and found no differences with  $p < 0.13$ .

## Results

Our final data set contained shell dimensions and masses of 445 juveniles and 1766 larger *Elliptio* collected from the Hudson River between 1991 and 2017. These data are freely available (Strayer et al., 2021). Shell mass (for given shell dimensions) of both large and small *Elliptio* in the freshwater tidal Hudson River increased significantly since the early 1990s (Table 1, Fig. 1). This increase was greater for large *Elliptio* than juveniles (Table 1), with increases in shell mass (for a given shell dimension) over the study period of ~25% for large animals and ~10% for juveniles. It appears that most of this increase occurred between 1991 and 2000, but the record is too noisy to be certain about the precise timing (Fig. 1). For adults, the widening confidence intervals in recent years reflect smaller sample sizes resulting from greatly reduced population densities (Strayer & Malcom, 2018).

We also observed changes in relative shell dimensions over the course of our study (Table 2). Shells of adults became markedly more inflated (greater width relative to length and weight) over time (Fig. 2). Juveniles became slightly but significantly more elongate (greater length relative to height and width) over time.

Water chemistry in the Hudson also changed over the study period, with significant increases in pH ( $r^2 = 0.13$ ,  $p < 0.0001$ ), alkalinity ( $r^2 = 0.12$ ,  $p < 0.0001$ ), and temperature (Seekell & Pace, 2011). These changes contributed to a significant rise in the calcite saturation index (Fig. 3). Both pH and dissolved inorganic carbon also increased over time at other less-intensively sampled stations that spanned most of the study area, and in most cases these increases were highly significant statistically (Table 3).

## Discussion

The shells of *Elliptio complanata* in the freshwater tidal Hudson River became substantially and significantly thicker between the early 1990s and the mid-2010s. It appears that

the degree of thickening was greater for large adults than for small juveniles. The shell-thickening parallels a similar finding for the non-native zebra mussel (*Dreissena polymorpha*) in the Hudson, whose shells became ~20% thicker over the same time period (Natesan & Strayer, 2016).

We also observed significant long-term changes in relative shell dimensions, particularly of adult *Elliptio*. We do not know the causes or consequences of these changes. Traditionally, inflated shells have been regarded as an adaptation to keep unionids from sinking into soft sediments, so increased inflation may be related to increased shell mass and thickness in the Hudson in recent years.

Among the ecological factors that have been reported to affect shell thickness, we probably can dismiss changes in productivity and exposure as likely causes of recent increases in shell thickness in Hudson River bivalves. Phytoplankton biomass changed little since the outbreak of zebra mussels in 1992 (Strayer et al., 2019), and there is no reason to think that tidal currents changed substantially since the early 1990s (sea level rose, but only slightly).

This leaves us with changes in water chemistry, predation, and bivalve growth rates as possible explanations for the observed changes in shell thickness in the Hudson. The calcite saturation index, which indicates the tendency for  $\text{CaCO}_3$  to dissolve or precipitate, increased over the period of interest in response to increases in  $\text{HCO}_3^-$  alkalinity, pH, and water temperature. Bicarbonate alkalinity has been increasing in a number of North American rivers, probably because of increased carbonate mineral dissolution in catchments (Raymond & Hamilton, 2018). Although it might seem obvious that freshwater mollusks would make thicker shells when calcium carbonate saturation is higher, evidence from previous studies is surprisingly mixed. Some broad-scale field surveys found no relationship between shell thickness and calcium/alkalinity/pH chemistry (Hunter, 1975; Hunter & Lull, 1977; Russell-Hunter et al., 1981), or positive correlations for some species, but no correlations (or even negative correlations) for others (Lewis & Magnuson, 1999). Nevertheless, several other field surveys (Green, 1972; Hinch et al., 1989; Hubendick, 1947; Russell-Hunter, 1957) and laboratory experiments (Brodersen & Madsen, 2003; Glass & Darby, 2009; Nduku & Harrison, 1976) reported the expected positive correlations between abundant  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  or high pH and thicker shells. Therefore, it seems reasonable to hypothesize that the observed increase in calcium carbonate saturation in the Hudson might have caused bivalve shells to thicken. Buried

juveniles may experience different water chemistry than exposed adults (cf. Strayer & Malcom, 2012), which could account for the different responses in adult and juvenile *Elliptio*.

Many mollusks thicken their shells in response to the presence or abundance of predators such as fishes or decapods, through either physiological or genetic mechanisms (e.g., Covich, 2010; Lewis & Magnuson, 1999). Although we do not have a continuous record of predation pressure on bivalves in the Hudson, we know that predation on both zebra mussels (Carlsson et al., 2011) and juvenile *Elliptio* (Strayer & Malcom, 2018) was substantially higher after 2000 than in the early 1990s. The predator responsible for this increase appears to be the blue crab in the case of zebra mussels, and a shell-crushing species (perhaps again the blue crab) in the case of *Elliptio*. Predation by blue crabs and other predators on *Elliptio* probably is highly size selective (Ebersole & Kennedy, 1994; Haag, 2012), but presumably could still induce shell thickening in adult *Elliptio*, even if they are not much eaten.

Finally, Haag & Rypel (2011) noted that unionids may continue to thicken their shells by depositing material on the shell interior even if length isn't increasing. This phenomenon has not been much investigated, but seems unlikely to fully explain events in the Hudson. We have not been able to estimate growth rates of adult unionids in the Hudson (their shells do not have well defined internal annuli – Strayer et al., 1994), but it is reasonable to think that their growth rates declined after the early 1990s. Body condition of adults and growth rates of small juveniles declined, at least temporarily, after the early 1990s (Strayer & Malcom, 2018). However, growth rates of zebra mussels did not decline over the study period (Strayer et al., 2020), so declining growth rates could not explain shell thickening in this species.

It is certainly possible that all three mechanisms – more favorable environmental conditions for deposition of calcium carbonate shells, induction of thicker shells by increased predation, and (in the case of *Elliptio*) slower growth rates – may have contributed to shell thickening in Hudson River bivalves. Studies of temporal changes in shell thickness in places other than the Hudson could help to resolve the importance of these and other mechanisms. Recent changes in calcium and dissolved inorganic carbon concentrations are very widespread in fresh waters, and differ in direction and magnitude across ecosystems (Weyhenmeyer et al., 2019), leading to different predictions about how shell thickness might have changed at different sites if water chemistry is a dominant factor. Likewise, large changes in the distribution or abundance of non-native predators (e.g., freshwater drum, large catfishes, rusty crayfish), or



drastic reductions in native molluskivores (such as sturgeons) are very common around the world, and lead to clear predictions about how shell thickness should have changed at different sites, if predation is an important driver. Extensive museum collections of freshwater mollusk shells (Sturm, 2006), which often extend back into the 19<sup>th</sup> century, could be very helpful in exploring long-term changes in shell thickness.

Regardless of the causes, increasing shell thickness can have important ecological consequences. Shell thickness affects vulnerability to shell-crushing predators (Covich, 2010; Haag, 2012), so shell thickening may affect freshwater mollusks, their predators, and their communities. Thicker shells should be less subject to fragmentation and dissolution than thin shells (Strayer & Malcom, 2007), resulting in more accumulation of spent shells and shell hash, and therefore greater effects on habitat structure (Gutierrez et al., 2003). Changes in water chemistry could thus have a double effect on shell accumulation – both producing shells that are more resistant to dissolution and slowing dissolution rates of calcium carbonate in shell deposits. Because of these potentially far-reaching consequences, the extent and magnitude of temporal changes in shell thickness of freshwater mollusks deserve closer attention.

## **Acknowledgments**

All three authors helped to design the study and write the manuscript. HMM and DLS supervised the field work, SKH and HMM supervised the laboratory measurements, SKH led the analyses of water chemistry, DLS and SKH led the statistical analyses, and DLS led the writing. This work was supported by grants from the National Science Foundation, including the Long-Term Research in Environmental Biology program (most recently DEB-1556246), and the Hudson River Foundation. We thank Lucas Pfeifer and Sarah Timperio for measuring and weighing shells, David Fischer for assistance in the laboratory and field, and many others who helped collect and process Hudson River samples over the years.

## **Data availability statement**

Data on shell dimensions and masses are freely available at <https://doi.org/10.25390/caryinstitute.13180007>.

## **Conflict of interest statement**

The authors declare no conflict of interest.

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Table 1. Results of multiple regressions using year and log<sub>10</sub>-transformed shell dimensions (length, width, and height) to predict changes in log<sub>10</sub>-transformed shell dry mass over time “Juveniles” have shells < 20 mm long, and “large animals” have shells ≥ 20 mm long.

Subject	Year	Slope (SE)
Large animals	$t = 16.31$ ( $p < 0.0001$ )	0.00422 (0.00026)
Juveniles	$t = 2.47$ ( $p = 0.014$ )	0.00165 (0.00067)

Table 2. Results of multiple regressions to test for changes in relative shell dimensions in *Elliptio complanata* in the Hudson River over time. Independent variables are year and log<sub>10</sub>(shell length). “Juveniles” have shells < 20 mm long, and “large animals” have shells ≥ 20 mm long.

Test	Year	Slope (SE)
Log <sub>10</sub> (shell width), large animals	$t = 11.88$ ( $p < 0.0001$ )	0.00255 (0.00021)
Log <sub>10</sub> (shell height), large animals	$t = -0.75$ ( $p = 0.45$ )	-0.00011 (0.00014)
Log <sub>10</sub> (shell width), large animals	$t = -2.39$ ( $p = 0.017$ )	-0.00084 (0.00035)
Log <sub>10</sub> (shell height), juveniles	$t = -2.56$ ( $p = 0.011$ )	-0.00074 (0.00029)

Table 3. Results of ANCOVAs testing for a rise over time in pH and dissolved inorganic carbon (DIC) concentrations at Poughkeepsie (RKM 117, n = 155 samples), Hudson (RKM 184, n = 140 samples), and Castleton (RKM 216, n = 139 samples). Independent variables were year and season (season of the year where 1 = DOY 1-151, 2 = DOY 152-212, 3 = DOY 213-273, 4 = DOY 274-366). Samples were taken at each station four times a year in most years between 1987 and 2019.

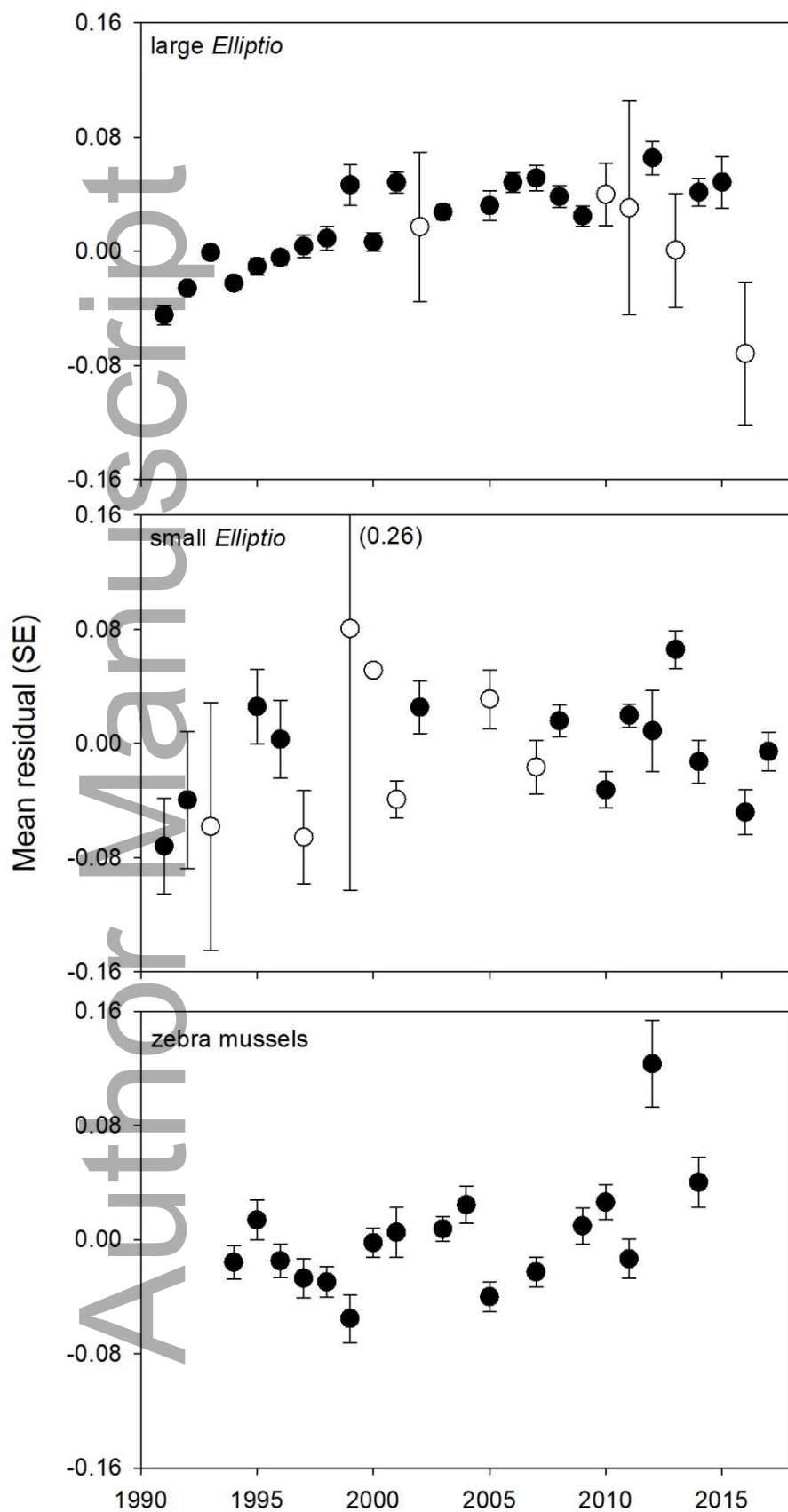
Site	pH (slope, <i>p</i> )	DIC (slope, <i>p</i> )
Poughkeepsie	0.0024 (0.11)	0.125 (<0.0001)
Hudson	0.0085 (0.0097)	0.134 (<0.0001)
Castleton	0.0089 (<0.0001)	0.105 (<0.0001)

#### Figure legends

Fig. 1. Residuals (mean  $\pm$  1SE) from regressions of shell dry mass on shell length, weight, and width (*Elliptio*) or shell length (zebra mussels) for bivalves in the freshwater tidal Hudson River, plotted against time. The upper end of the error bar for small *Elliptio* in 1999 (0.26) is truncated. Open symbols show years for which estimates are based on <10 specimens. Data on zebra mussels are from the study of Natesan & Strayer (2016). Residuals of -0.08 and 0.08 convert to a linear scale as 83% and 120% of what would be expected based on shell dimensions.

Fig. 2. Long-term changes in shell width:length ratios (mean  $\pm$  1SE) of adult *Elliptio complanata* from the freshwater tidal Hudson River. Open symbols show years for which estimates are based on <10 specimens.

Fig. 3. Estimated calcite saturation index for the Hudson River near Kingston, New York ( $r^2 = 0.19$ ,  $p < 0.0001$ ). A saturation index of zero represents thermodynamic equilibrium; positive values indicate a tendency for  $\text{CaCO}_3$  precipitation and negative values indicate a tendency for dissolution. See Methods for details of calculations.



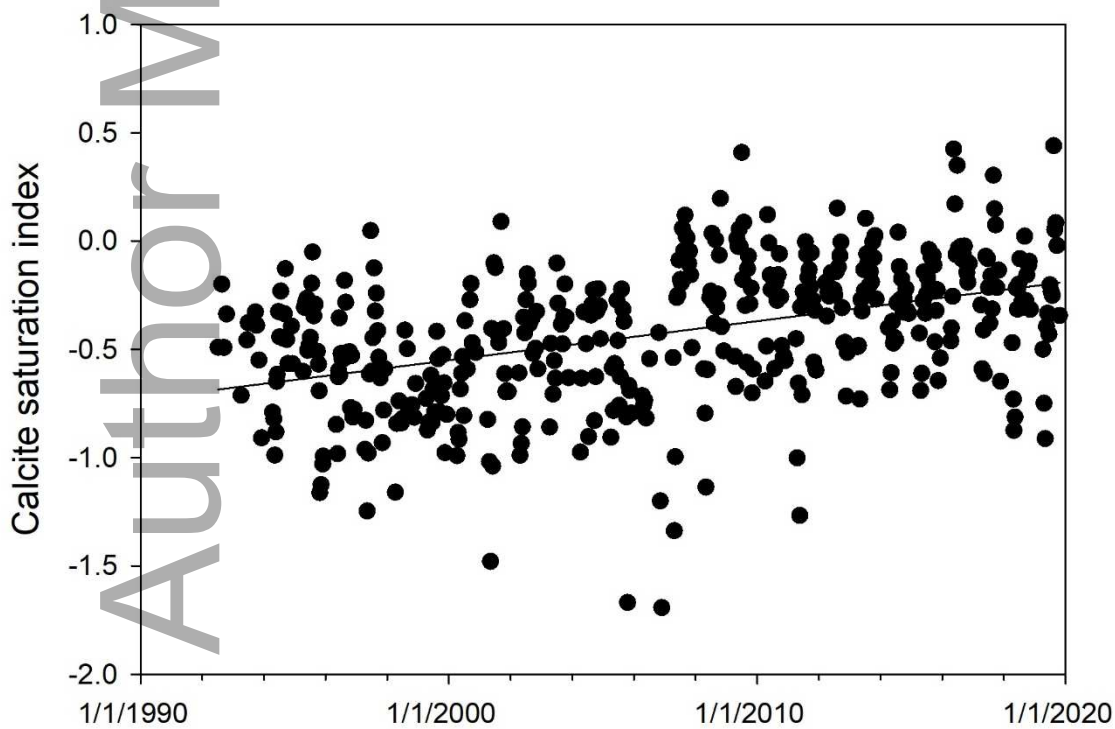
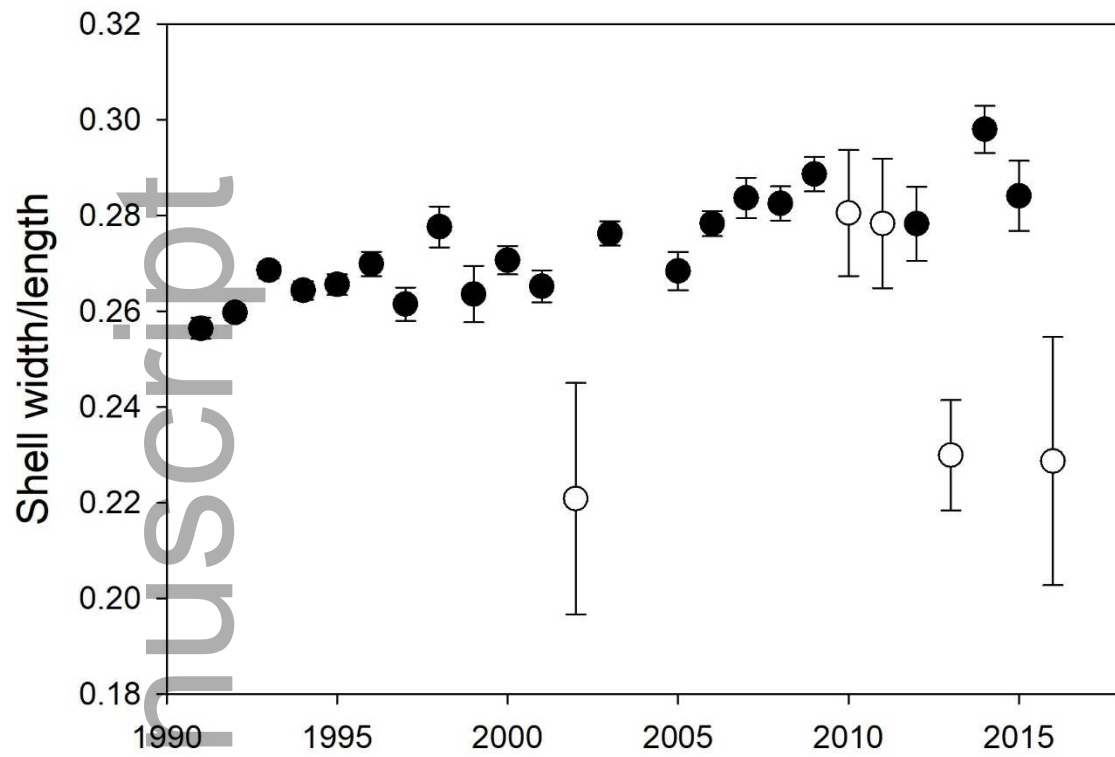




Table 1. Results of multiple regressions using year and  $\log_{10}$ -transformed shell dimensions (length, width, and height) to predict changes in  $\log_{10}$ -transformed shell dry mass over time “Juveniles” have shells  $< 20$  mm long, and “large animals” have shells  $\geq 20$  mm long.

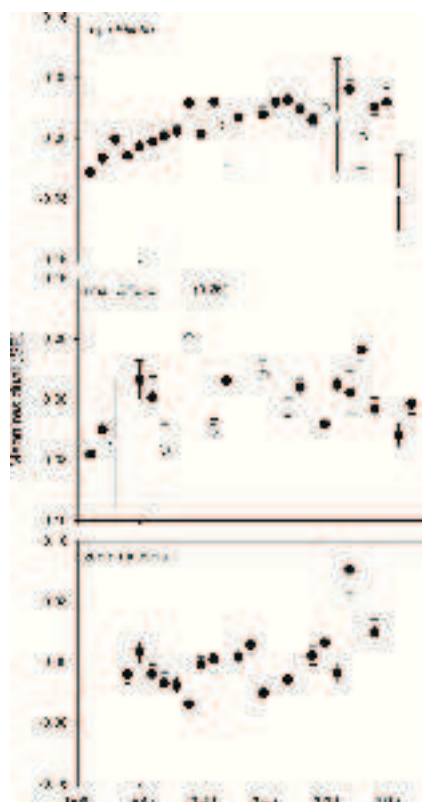
Subject	Year	Slope (SE)
Large animals	$t = 16.31$ ( $p < 0.0001$ )	0.00422 (0.00026)
Juveniles	$t = 2.47$ ( $p = 0.014$ )	0.00165 (0.00067)

Table 2. Results of multiple regressions to test for changes in relative shell dimensions in *Elliptio complanata* in the Hudson River over time. Independent variables are year and  $\log_{10}$ (shell length). “Juveniles” have shells < 20 mm long, and “large animals” have shells  $\geq$  20 mm long.

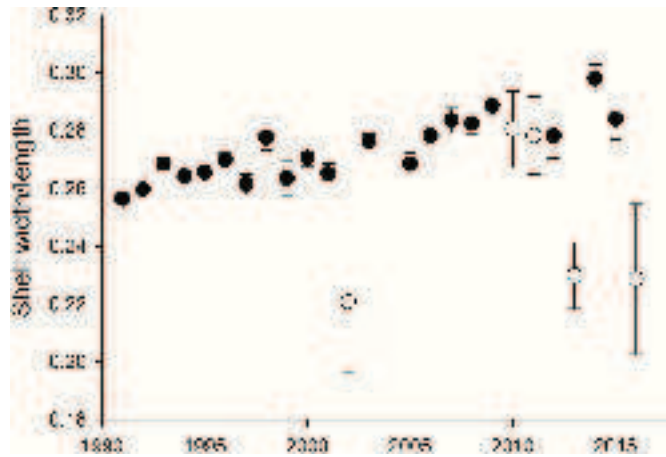
Test	Year	Slope (SE)
$\log_{10}$ (shell width), large animals	$t = 11.88$ ( $p < 0.0001$ )	0.00255 (0.00021)
$\log_{10}$ (shell height), large animals	$t = -0.75$ ( $p = 0.45$ )	-0.00011 (0.00014)
$\log_{10}$ (shell width), large animals	$t = -2.39$ ( $p = 0.017$ )	-0.00084 (0.00035)
$\log_{10}$ (shell height), juveniles	$t = -2.56$ ( $p = 0.011$ )	-0.00074 (0.00029)

Table 3. Results of ANCOVAs testing for a rise over time in pH and dissolved inorganic carbon (DIC) concentrations at Poughkeepsie (RKM 117, n = 155 samples), Hudson (RKM 184, n = 140 samples), and Castleton (RKM 216, n = 139 samples). Independent variables were year and season (season of the year where 1 = DOY 1-151, 2 = DOY 152-212, 3 = DOY 213-273, 4 = DOY 274-366). Samples were taken at each station four times a year in most years between 1987 and 2019.

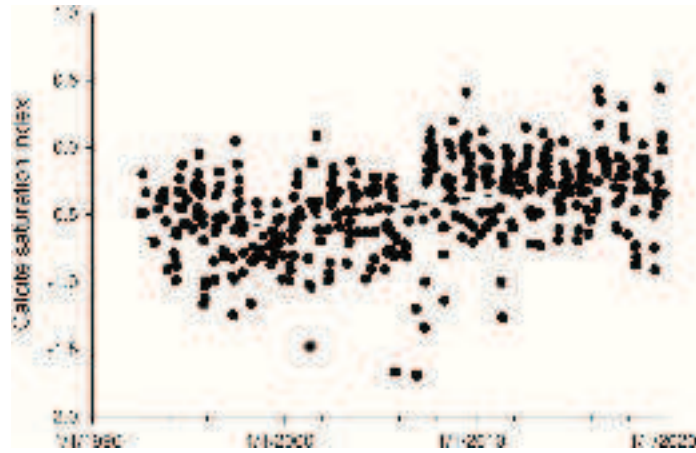
Site	pH (slope, p)	DIC (slope, p)
Poughkeepsie	0.0024 (0.11)	0.125 (<0.0001)
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