

# Environmental controls on long-term growth of freshwater mussels in an oligotrophic lake

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**Abstract:** Freshwater mussels are one of the most endangered groups of animals and live in some of the fastest changing ecosystems in the world. Unfortunately, very little is known about how their life history and ecology are influenced by their environment, especially for lake-dwelling populations. In this study, we paired ~30 y of extensive environmental data to lifetime and annual growth rates of a population of Fatmucket mussels (*Lampsilis siliquoidea*) living in a cool-water oligotrophic lake in northern Wisconsin, USA. This population displayed one of the slowest growth rates and longest lifespans within its phylogenetic tribe (Lampsilini). Growth rates were highly variable between individuals and, in contrast to studies in other systems, not related to temperature, growing season, or any indicators of primary production. However, growth rates were positively correlated with changes in lake level. We hypothesize that mussel growth in this system is linked to landscape-level environmental conditions and allochthonous resource limitation.

**Key words:** freshwater mussels, Unionida, lakes, sclerochronology, growth chronology

Freshwater mussels (Unionida) are one of the most imperiled groups of organisms on Earth (Ricciardi and Rasmussen 1999, Lopes-Lima et al. 2017) and inhabit some of the fastest changing ecosystems worldwide (Vörösmarty et al. 2010, Carpenter et al. 2011). It is important to better understand the ecology and life history of freshwater mussels because these aspects of mussel biology affect how mussels will respond to future global environmental changes. Growth rate is a fundamental life-history attribute that dictates a mussel's survival and reproductive success; however, the environmental conditions that control growth are understudied (Haag 2012). Understanding how mussel growth is controlled by divergent environmental conditions may be of significance to mussel conservation in our changing world.

Mussels maintain long-term records of lifetime growth archived in their shells, in some cases providing 30 to 300 y of annualized growth information (Schöne et al. 2005, Helama and Valovirta 2008, Rypel et al. 2008). In the shells of most species, a conspicuous and often narrow dark band appears in the shell record during periods of low to no growth. In temperate climates, these dark bands coincide with growth cessation during winters, which can allow for exact dating

of historical mussel growth (Helama et al. 2006, Haag and Commens-Carson 2008, Rypel et al. 2008, Schöne 2013). Interpretation of growth rings (annuli) can be used to estimate ages of individual mussels as well as describe long-term variations in annual growth rates. When mussels are collected from closely monitored ecosystems, past growth records can be compared to environmental records to explore how mussel growth is related to their environment (i.e., sclerochronology; Schöne et al. 2004, 2005, Black et al. 2010).

Linking mussel growth to environmental conditions using sclerochronology has been reasonably well documented in both marine and freshwater systems. In marine systems, bivalve growth has been shown to correlate strongly with diverse environmental controls, such as temperature (Archambault et al. 1999, Schöne et al. 2005), primary productivity (Smaal and van Stralen 1990), chlorophyll *a* (Chl *a*) (Page and Hubbard 1987, Archambault et al. 1999), particulate organic C (Page and Hubbard 1987), and zooplankton biomass (Wanamaker et al. 2009). In freshwaters, most research on mussels has been conducted in fluvial systems (but see Kendall et al. 2010) where growth is strongly associated with physical variables, such as discharge or temperature (Schöne et al.

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2003, 2004, Rypel et al. 2009, Black et al. 2010, Dycus et al. 2015,) and in which biological or chemical environmental variables have not been detected as controls on growth.

Freshwater mussels are understudied in lake ecosystems, with the notable exception of a large number of studies on the ecological effects and autecology of invasive species, such as Zebra (*Dreissena polymorpha* Pallas, 1771) and Quagga (*Dreissena rostriformis bugensis* Andrusov, 1897) mussels (reviews by Higgins and Vander Zanden 2010, Karatayev et al. 2015). Native lake mussels may have received less research attention because of reduced species diversity and abundances compared to those found in fluvial ecosystems. However, lake-dwelling mussels pose an interesting opportunity for studying growth dynamics.

Flow is often the primary determinant of annual growth of mussels in fluvial ecosystems (Rypel et al. 2008, Rypel 2009, Black et al. 2010, Dycus et al. 2015), which leads us to ask: How do drivers of freshwater mussel growth change when there is little to no flow, such as in a lake? One might expect that lakes are particularly challenging environments for mussels (these challenges may be the reason for lower abundances and lack of species diversity found in lakes). Unique lake ecosystem characteristics like the lack of flowing water and seasonal stratification, which controls important environmental conditions such as temperature, dissolved oxygen, and plankton assemblages, may greatly hinder the food-capturing abilities of filter-feeding mussels. The environmental characteristics of lake environments lead us to ask a 2<sup>nd</sup> question: Is the growth of lake-dwelling mussels controlled by food availability or an environmental condition that is unique to or more pronounced in lake ecosystems? Griffiths and Cyr (2006) found that lake-dwelling Eastern Elliptio (*Elliptio complanata* Lightfoot, 1786) had higher growth rates in upwind sites compared to downwind sites despite lower chlorophyll concentrations and colder water temperatures at upwind sites. The unique environmental conditions mussels experience in lakes and unexpected growth responses in systems in which they have been studied, like the findings of Griffiths and Cyr (2006), should inspire greater attention to lake-dwelling mussels in our attempts to better understand how these animals are influenced by their environment.

Here, we describe lifetime growth dynamics of a lake-dwelling population of Fatmucket mussels (*Lampsilis siliquoidea* Barnes, 1823). Our specific goals were to: 1) develop a von Bertalanffy growth curve to describe lifetime growth trajectories for this population and place the growth of *L. siliquoidea* in context to that of related species; 2) construct a chronology describing long-term growth variations of mussels within the lake; and 3) describe any relationships found between annual mussel growth and long-term environmental conditions (abiotic or biotic) in the lake. We hypothesized that lake ecosystems (especially cool, soft-water, oligotrophic environments like the one in this study) pose unique environmental challenges that strongly limit mussel somatic growth. We predicted that there would be variability in growth

rates among years that is synchronous among individuals in the population and that this variability would correlate with at least 1 environmental driver consistent with the potential difficulties of living in a lake ecosystem.

## METHODS

### Site description

Trout Lake is located in a temperate climate in the Northern Highland Lake District of Wisconsin, USA. It is a cool-water, dimictic, oligotrophic lake that freezes annually and has an area of 1608 ha, a mean depth of 14.9 m, and a maximum depth of 35.7 m. It has an average summer Chl *a* concentration of 2.4 µg/L and a long-term average calcium concentration of 12.6 mg/L (Magnuson et al. 2019a, b). Sediment characteristics within the lake and at the sample site are primarily sand with some cobble; the sample site was characterized as having very shallow sloping bathymetry, and there were no macrophytes present. As one of the pioneering sites of the Long-term Ecological Research program, Trout Lake has been continuously studied for physical, chemical, and biological variables since 1981. *Lampsilis siliquoidea* is the most abundant unionid species found in the lake. Plain Pocketbook (*Lampsilis cardium* Rafinesque, 1820) and Giant Floater (*Pyganodon grandis* Say, 1829) are also present but fewer in number (VLB, personal observation).

### Sample collection and processing

From Trout Lake, we collected individual mussels from depths of 2 to 3 m within the same mussel bed (~46°01'00''N, 89°40'35''W) during the summers of 2014 and 2017. We chose this site based on qualitative pilot surveys indicating that this site had noticeably higher mussel density than any other known locations. We collected only live mussels of 1 species (*L. siliquoidea*), and we sacrificed them immediately after collection in both years. We collected a total of ~75 mussels but used only a subset of these in our analyses (see below for additional explanation). Of the mussels that we used in the analyses, 7 were collected in 2014 (4 female, 3 male) and 19 in 2017 (11 female, 8 male). Sex was determined by shell morphology because sexual dimorphism is readily apparent in *L. siliquoidea*. We generally focused on collecting larger (and presumably older) individuals to develop the longest chronologies possible. However, large size might also result from faster growth rates and lead to a potential over-estimate of average growth rates of individuals in the population.

In the lab, we measured the length and width of each shell. We used a rock-cutting saw to cut 1 valve of each shell ~halfway between the major and minor axes of growth from the umbo to the shell margin (the valve used varied by which valve could be best gripped by the saw's vice in a proper orientation for the cut). We smoothed the mussel half-shells with 14-µm grit suspended in water until polished, then adhered each of them to a transparent glass slide with epoxy.

After the epoxy set, we cut the shells to ~1-mm thin sections and again polished them.

Two independent observers interpreted shell thin sections for annuli counts (Fig. 1). Annuli were identified and measured at the boundary of the nacre and prismatic layer for consistency in identification of annuli between observers and between shells—annuli at this location are commonly referred to as internal annuli in contrast to lines observed on the external shell. Discrepancies between observers were compared until both observers agreed on the presence of each annulus. There was a low threshold for excluding thin sections from analysis based upon readability; we included in the final analysis only shells for which both observers self-reported having a high level of certainty in accurate dating of the internal annuli to their associated years. Of the ~75 individuals initially collected from the lake, 61 were cut into shell thin sections, and 35 of these were omitted because 1 or both observers reported less than a high level of confidence in annuli detection. Consequently, we used 26 shell sections in this study's analyses. To estimate annual growth, we measured the distance between annuli to the nearest 0.01 mm by using a Leica S8AP0 microscope (Leica, Wetzlar, Germany) with the Leica Application Suite software (version 3.7.0; Leica Microsystems, Buffalo Grove, Illinois).

### Chronology validation

We quality checked each chronology of annual growth increments with COFECHA (Fritts 1976, Holmes 1983), a

software program that uses crossdating to check appropriate dating of chronologies. Each chronology was crossdated in COFECHA following the methods of Rypel et al. (2008). Briefly, each annual growth increment chronology was 1<sup>st</sup> detrended by using an exponential curve and then smoothed with a cubic spline that retained 50% of variability over 32-y periods to remove ontogenetic and low frequency patterns in the chronology prior to crossdating (Fritts 1976). In the crossdating process, all the chronologies were averaged together to create a master chronology against which each individual chronology was compared in a leave-1-out design as a first assessment for an appropriately dated chronology (Fritts 1976). Each chronology was also cut to sequential series of 8 y in length and lagged -3 to +3 y, and its correlation to the master chronology was assessed. We considered chronologies to have been validated if their unlagged position had the highest correlation with the master chronology. If a chronology exhibited a substantially higher correlation when lagged, both reviewers re-examined the shell, and it was only adjusted to the lagged position if both reviewers agreed. Otherwise, it was included in its original position. We assessed variation by sex in interannual growth rates with a *t*-test assessing whether the standard deviation differed between male and female chronologies. We checked assumptions for normality (graphically with histograms and QQplots) and equal variance (using Levene's test) for all *t*-tests and analysis of variance (ANOVA) models (below). We conducted all statistical analyses in the programming language R (version 3.6.3; R Project for Statistical Computing, Vienna, Austria).

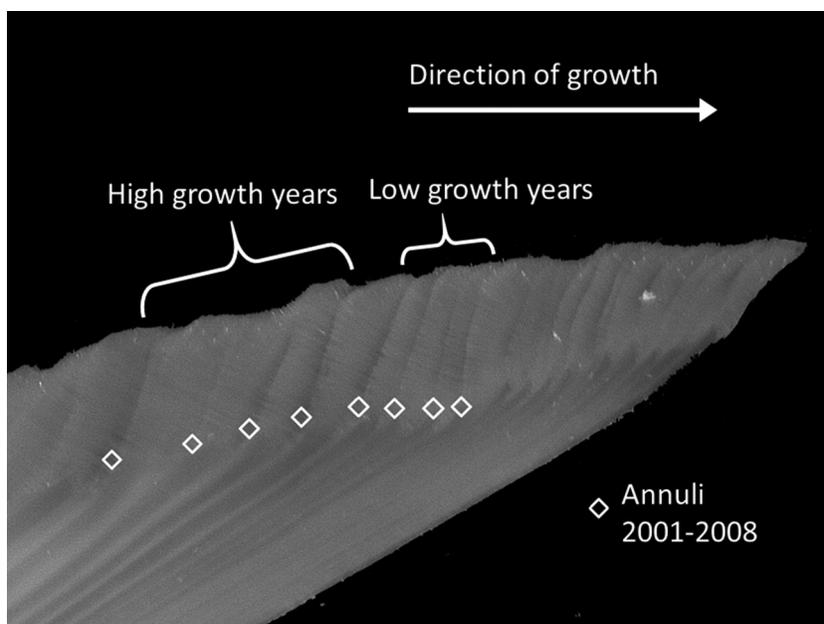


Figure 1. Close-up of shell thin-section from *Lampsilis siliquoides*. Note conspicuous dark bands indicative of winter growth cessation. Diamonds indicate reference points of annuli at the prismatic layer/nacre margin from where measurements of annual growth were recorded.

### Master chronology construction

We imported validated chronologies into ARSTAN (version 44h3; Cook and Holmes 1984), a software program designed for detrending individual chronologies and constructing a master chronology for time series analysis. Each chronology was fit with a negative exponential model to create a model of predicted growth for a mussel for any year, and deviations from this model represent above- or below-expected growth for that year. We chose the “stiffer” fit of a negative exponential model compared to the spline used in the chronology validation process to retain as much low-frequency and climate signal as possible (Fritts 1976, Rypel et al. 2009). Each model fit was confirmed by eye, and none contained any obvious bias in the residuals of the model fit.

We calculated standardized growth indices (SGIs) by dividing the residuals by the model predictions. This approach is a standard process in sclerochronology to remove age-related growth dynamics from chronologies (Fritts 1976). SGIs >1 represent above-expected growth for that year, whereas SGIs <1 represent below-expected growth. A master chronology was created from the ‘RESID’ (residual) output from ARSTAN using methods described by Cook and Holmes (1984). This is a common process that first whitens out (i.e., diminishes) any autocorrelation in individual chronologies by making the time series behave more like white noise, then calculates a robust biweight mean that is designed to enhance common signals among individual chronologies (Kadafar 1983, Cook and Holmes 1984).

We characterized lifetime growth trajectories by sex as well as for the general population with the von Bertalanffy equation:

$$L_t = L_\infty \left( 1 - e^{K(t - t_0)} \right) \quad (\text{Eq. 1}),$$

where  $L_t$  is the length (in mm) at time  $t$  (age in years),  $L_\infty$  is the mean maximum length for the population,  $K$  is a growth constant that describes how quickly an individual approaches  $L_\infty$ , and  $t_0$  is the time at which length = 0. We used the R packages *FSA* (version 0.8.32; Ogle et al. 2020) and *nlstools* (version 1.0.2; Baty et al. 2015) for the von Bertalanffy analyses using the default approach (2<sup>nd</sup>-degree polynomial) to create starting values for  $t_0$ . For the model, we calculated  $L_t$  from a ratio of the length of the thin section to the length of the major axis of the valve. The von Bertalanffy model was fit to males and females separately. If  $t_0$ ,  $L_\infty$ , or  $K$  in the von Bertalanffy model did not differ between sexes (by testing for a difference in means with a 2-tailed  $t$ -test), the model was then fit to all individuals combined. We assessed differences in von Bertalanffy estimates by sex via a 1-way ANOVA testing whether parameter estimates differed between a model where all estimates were allowed to vary by sex and a model where the parameter of interest did not vary by sex. We assessed how the von Bertalanffy parameter estimates for *L. siliquoidea* related to those previously reported for the Lam-

psilini tribe by Haag and Rypel (2011) by using a simple rank order.

### Environmental data filtering and analysis

To assess the relationship between mussel growth and environmental characteristics, we examined a number of environmental variables, including lake-scale variables as well as broader macroclimate variables. Environmental variables used in our analysis include those that have been shown to influence mussel growth in other systems, such as indicators of primary and secondary production, water temperature, and growing season length (Rypel et al. 2009, Wanamaker et al. 2009, Black et al. 2010), as well as other variables we expected may influence mussel growth directly or indirectly (Table 1). We also evaluated variables for filtering environmental data based on time periods (e.g., ice-off, spring mixing), which we did as an informal way of conducting a sensitivity test (e.g., if data from spring mixing were included, would that drastically change our findings?). Filtering environmental data to different time windows did not change our findings (likely because the numerous measurements collected during the summer stratified period outweighed the effects of the inclusion of a few spring samples), so these time period variables were not included in the final analysis. The Trout Lake environmental data used in our analysis have been collected and curated by the North Temperate Lakes site of the Long-term Ecological Research network for ~40 y (Magnuson et al. 2019b, c, 2020a, b, c, d). All limnological measurements were collected at a centrally located buoy ~500 m from our mussel collection location. Data on macroclimate indices, specifically the North-Atlantic Oscillation (NAO) and Pacific Decadal Oscillation (PDO), were provided by the National Centers for Environmental Information managed by the National Oceanic and Atmospheric Administration ([www.ncdc.noaa.gov/teleconnections](http://www.ncdc.noaa.gov/teleconnections)).  $NAO_{\text{winter}}$  and  $PDO_{\text{winter}}$  are the mean indices for the North Atlantic and the Pacific Decadal Oscillations, respectively, during the immediately preceding winter months (these macroclimate indices primarily reflect winter precipitation in the study region). Precipitation data were downloaded from a nearby weather station in Minocqua, Wisconsin (GHCND:USC00475516).

We filtered environmental data to best reflect the conditions most likely experienced by the mussels during their growing season. Unless otherwise specified, we summarized all environmental data from the lake by the mean value from data filtered to include only data from the epilimnion during the summer stratified period to highlight the environmental conditions most likely to influence mussel growth (Amyot and Downing 1997, Hallmann et al. 2009). We calculated only a few variables differently: lake level $_{\Delta}$  is the difference (in m) from the previous mean summer lake level, total precipitation is the cumulative water equivalent amount of precipitation that was recorded in the water year (beginning 1 October of previous calendar year),  $SRP_{\text{spring}}$  is the mean

Table 1. Environmental variables explored for potential relationships to growth of the freshwater mussel *Lampsilis siliquoidea*. Pearson  $r$  reports the linear correlation between the master growth chronology and the environmental variable. Data for all limnological variables were collected and curated by the North Temperate Lakes Long-term Ecological Research site, NAO<sub>winter</sub> PDO<sub>winter</sub> data were downloaded from the National Centers for Environmental Information, and precipitation data were downloaded from a local weather station in Minocqua, Wisconsin, USA. Lake level<sub>Δ</sub> is the difference (in m) from the previous mean summer lake level. Color refers to water color.

Variable	Mean	Range	Units	Pearson $r$
Lake level <sub>Δ</sub>	0.004	-0.25, 0.21	m	0.58
Soluble reactive phosphorus (SRP <sub>spring</sub> ) <sup>a</sup>	0.58	0.19, 0.87	μg/L	-0.36
Chlorophyll <i>a</i>	2.4	0.29, 5.9	μg/L	-0.02
Total cladoceran <sup>b</sup>	10.6	4.4, 18.5	no./L	0.13
Total phosphorus	0.74	0.19, 0.95	μg/L	0.03
O <sub>2</sub>	9	8.4, 9.6	mg/L	-0.23
pH	8.3	8.0, 8.5	-	-0.08
Ca <sup>2+</sup>	12.6	11.2, 14.2	mg/L	-0.13
NO <sub>3</sub> + NO <sub>2</sub>	3.1	0.1, 10.5	μg/L	-0.01
Total organic carbon	3	2.5, 3.4	mg/L	-0.05
Dissolved organic carbon (DOC)	3.1	2.4, 3.4	mg/L	-0.09
Specific ultraviolet absorbance (SUVA) at 254 nm	1.84	0.92, 5.15	L mg <sup>-1</sup> C m <sup>-1</sup>	0.2
Slope ratio	1.38	0.84, 2.1	(ratio of S <sub>275-295</sub> to S <sub>350-400</sub> )	0.06
Linear slope 275-295	-0.024	-0.03, -0.014	log(slope of the abs scan over 275-295 nm)/nm	0.17
Color	17.7	2.5, 108.5	abs at 254 nm (1 m path length)	0.11
Total precip water year	107.7	3.5, 331.2	cm	0.44
North Atlantic Oscillation index (NAO <sub>winter</sub> )	0.1	-1.6, 1.4	-	0.26
Pacific Decadal Oscillation index (PDO <sub>winter</sub> )	0.27	-1.6, 2.5	-	0.34
Mean wind speed	1.25	0.3, 1.8	m/s	0.38
Duration stratification	141.3	123, 183	d	-0.03
Degree days	3336	2922, 3751	°C × d	0.001
Date last ice	113.3	79, 137	Day of year	-0.11
Date first ice	346.8	332, 369	Day of Year	-0.11
Water temperature (minimum)	13.3	9.9, 16.6	°C	0.02
Water temperature (10 <sup>th</sup> percentile)	14.8	11.5, 17.3	°C	0.12
Water temperature (25 <sup>th</sup> percentile)	17.3	14.5, 20.8	°C	0.1
Water temperature (mean)	19.3	17.6, 21.2	°C	0.15
Water temperature (85 <sup>th</sup> percentile)	21.5	18.3, 23.6	°C	0.17
Water temperature (90 <sup>th</sup> percentile)	22.6	20.1, 24.7	°C	0.26
Water temperature (maximum)	23.5	20.2, 26.3	°C	0.19

<sup>a</sup> Calculated from spring mixing period only.

<sup>b</sup> only including individuals of the taxa *Daphnia*, *Holopedium*, *Bosminidae*, and *Diaphanosoma*.

dissolved reactive phosphorus during the immediately preceding spring mixing period (a common approach to estimating summertime productivity in P-limited lakes), and degree days were calculated as the area under the curve of mean epilimnetic temperature beginning immediately after ice-out and ending at the end of summer stratification to capture as much of the potential growing season as possible (Amyot and Downing 1997). All data have a minimum temporal resolution of 2 wk except NAO<sub>winter</sub> and PDO<sub>winter</sub>,

which have a monthly temporal resolution, calcium, water color, specific UV absorbance at 254 nm (SUVA<sub>254</sub>), slope ratio, and linear slope 275-295, which are sampled once during summer months. We chose to include multiple variables associated with dissolved organic carbon (DOC) quality (SUVA<sub>254</sub>, slope ratio, linear slope 275-295) in our best attempts to characterize potentially meaningful DOC estimates (Jane et al. 2017). We summarized all continuous variables to a mean value. We calculated the Pearson correlation

coefficient of each environmental variable to the standardized mussel growth indices. These correlation coefficients are included in Table 1 strictly for thoroughness in reporting. We also calculated Pearson  $r$  for correlations of DOC and water color with lake level $_{\Delta}$  because we were interested in describing how changes in lake level may have been associated with allochthonous inputs.

We chose an exhaustive model selection approach to identify environmental variables likely to influence mussel growth (R package *MuMIn*, version 1.43.17; Bartoń 2020). Prior to model selection, we standardized all independent variables ( $\bar{x} = 0$ , standard deviation [SD] = 0.5) to more easily compare their relative importance. Exhaustive model selection is similar to a stepwise model selection except, instead of comparing model fitness by eliminating or adding 1 variable at a time, all possible combinations of variables are examined and compared. This approach means that exhaustive model selection is robust to collinearity between predictor variables because it independently assesses all variable combinations and does not drop potentially important variables as would be possible in a stepwise model selection approach. We used Bayesian Information Criterion (BIC) to assess the relative model fit and to discourage the selection of complex models (BIC more heavily penalizes complex models than does Akaike Information Criterion). Because the top model did not substantially outperform the next best fitting models ( $\Delta\text{BIC} < 2$ ), we chose a model averaging approach that allowed us to estimate average effect size for each variable across the highest performing models. This approach also allowed us to report how often a variable was included in the set of highest performing models. If a variable is included in more of the highest performing models, it is more likely to have a causal relationship. Only models with a BIC score within 2 units of the highest performing model's BIC score were considered top performing models and included in the model averaging step. We averaged model estimates, or mean effect sizes, by using a conditional average approach that calculates the average effect size for each parameter across all of the top performing models (within 2 units of the lowest BIC score) in which that parameter is present. Variables that were identified as potentially being important, based on having been included in the top 2 performing models, showed no indication of collinearity (assessed via variance inflation factors). Each potentially important variable was used in independent simple linear regression models to test whether the parameterized model outperformed the null model according to a least squares assessment. The use of linear regression also allowed us to report the relationships of the environmental variables and mussel growth in an easier to interpret fashion. We ultimately identified 2 variables of potential importance (lake level $_{\Delta}$  and SRP $_{\text{spring}}$ ), and we created 2 independent linear regression models, 1 containing lake level $_{\Delta}$  and the other containing SRP $_{\text{spring}}$ , to assess the independent effects of these variables on standardized mussel growth indices. We used a generalized

least squares approach to assess the linear model of SRP $_{\text{spring}}$  on growth to account for heteroskedasticity in the model.

## RESULTS

Individual growth chronologies ranged from 14 to 32 y ( $n = 26$ ), spanning 1985 to 2016, and had a mean length of 20 y. Within the Lampsilini tribe of unionid mussels, this population of *L. siliquoidea* displayed one of the lowest recorded growth rates as described by  $K$  in the von Bertalanffy model (population  $K = 0.119$ , 95% confidence interval: 0.11, 0.13) (Table S1, Fig. 2A, B). Our population-wide  $t_0$  estimate was  $-0.494$  y (95% confidence interval:  $-0.81$ ,  $-0.18$  y). Based on 2-tailed  $t$ -tests, there was no difference in  $K$  or  $t_0$  between males and females ( $K$ :  $p = 0.57$ ,  $t_0$ :  $p = 0.92$ ). Males did reach a larger  $L_{\infty}$  (73.4 mm, 95% confidence interval: 70.6, 76.2 mm) than females (66.4 mm, 95% confidence interval: 63.7, 69.3 mm) ( $p = 0.02$ ), which is not surprising given the sexual dimorphism of *L. siliquoidea* (Fig. 2C). There was a moderate level of synchrony in growth within the population (series intercorrelation: 0.390) (Fig. 3). However, there was substantial variability in the SGI between the different chronologies of individual mussels across all years (mean of the SD: 0.39). There was no difference in interannual variability by sex ( $p = 0.65$ ).

Exhaustive model selection identified only 1 additional model within 2 BIC units of the lowest BIC score (highest performing model) (Table 2). Lake level $_{\Delta}$  was included in both models, whereas springtime dissolved reactive phosphorus (SRP $_{\text{spring}}$ ) was included in 1. Lake level $_{\Delta}$  was suggested to be positively correlated with growth, whereas SRP $_{\text{spring}}$  was suggested to be negatively related to growth (Table 2). No other environmental variables were identified through this method as likely controls of growth.

Based on a linear regression approach, lake level $_{\Delta}$  explained a moderate amount of the total variance in growth ( $R = 0.57$ ) and was likely positively related to growth ( $p < 0.01$ ) (Table S2, Fig. 4A). SRP $_{\text{spring}}$  explained relatively little of the total variance in growth ( $R = -0.36$ ,  $p = 0.10$ ) (Table S3, Fig. 4B), and an ANOVA test indicated that a model containing both lake level $_{\Delta}$  and SRP $_{\text{spring}}$  was only marginally different from a model containing only lake level $_{\Delta}$  ( $p = 0.04$ ; Table S4). This finding suggests that, if SRP $_{\text{spring}}$  is related to mussel growth, it is likely less important than lake level. We assessed whether we could detect a relationship between lake level $_{\Delta}$  and indicators of allochthonous C inputs but found no correlation between lake level $_{\Delta}$  and water color (Pearson  $r = 0.08$ ) or lake level $_{\Delta}$  and DOC (Pearson  $r = 0.16$ ).

We attempted to describe the relationship of each individual mussel chronology with lake level $_{\Delta}$  and SRP $_{\text{spring}}$  to see whether the relationship of the population growth dynamics with these environmental conditions was characteristic of a general population relationship or just the result of a strong relationship for only a few individuals. Standardized effect

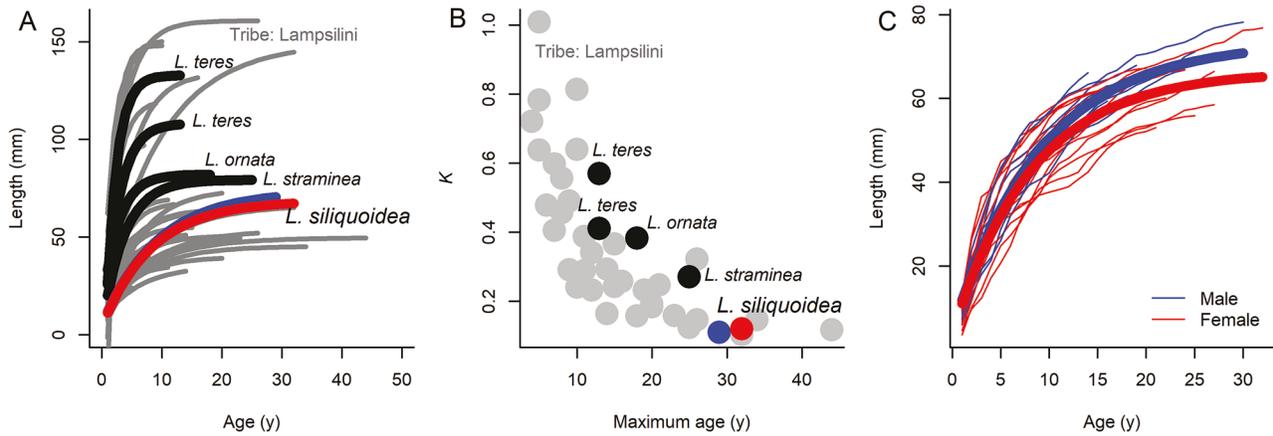


Figure 2. Growth characteristics of *Lampsilis siliquoidea* and its context within the Lampsilini tribe. A.—Growth trajectories of individual mussels color-coordinated by sex. Thick lines are growth trajectories for the population calculated using the von Bertalanffy equation:  $L_t = L_\infty(1 - e^{K(t-t_0)})$ , where  $L_t$  is the length (mm) at time  $t$  (age in years),  $L_\infty$  is the mean maximum length for the population,  $K$  is a growth constant that describes how quickly an individual approaches  $L_\infty$ , and  $t_0$  is the time at which length = 0. Males:  $K = 0.11$ ,  $L_\infty = 73.4$ ,  $t_0 = -0.59$ ,  $n = 11$ ; females:  $K = 0.12$ ,  $L_\infty = 66.4$ ,  $t_0 = -0.51$ ,  $n = 14$ ; only  $L_\infty$  was substantially different between sexes. Males are color-coded in red, females in blue, genus *Lampsilis* in black, and Lampsilini tribe in gray. B.—The von Bertalanffy growth coefficient  $K$  plotted against maximum observed age for populations within the Lampsilini tribe (gray dots) and genus *Lampsilis* (black dots) to highlight the unique growth characteristics of *L. siliquoidea* (data for panels A and B include all members of the Lampsilini tribe reported in Haag and Rypel 2011; Table S1). C.—The same colored growth curves from panel A with each individual chronology plotted underneath to display variation among individuals.

sizes (standardized estimates of the strength of the relationship between the environmental variable and mussel growth) were all positive for lake level $_{\Delta}$  and generally, but not all, negative for SRP $_{spring}$  (Fig. 5).

**DISCUSSION**

In this study, we were interested in describing lifetime growth dynamics of a lake-dwelling population of *L. siliquoidea*. We also wanted to construct a chronology describing

long-term growth variations of mussels within the lake and describe any relationships found between annual mussel growth and long-term environmental conditions in the lake. In this system, we were able to detect a relationship between growth and lake level, but other environmental variables (e.g., temperature, growing season) did not appear to be important controls on growth. However, this study used a limited sample size to describe growth characteristics of *L. siliquoidea* and their relationship to environmental conditions in 1 lake. *Lampsilis siliquoidea* has a wide geographic distribution and

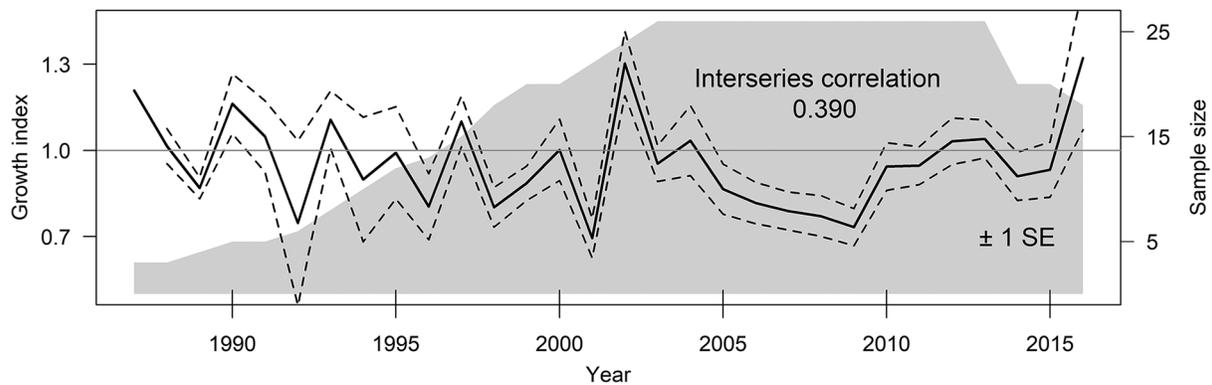


Figure 3. Master growth chronology of Trout Lake's *Lampsilis siliquoidea* population (black line)  $\pm 1$  standard error (SE) (dashed lines) developed from the standardized growth indices (see Methods for description of detrending and standardization procedure). Values  $>1$  indicate growth exceeded model expectations for that year, whereas values  $<1$  indicate growth was less than expected. Gray shading indicates the number of chronologies contributing to that year's estimate.

Table 2. Conditional averages of the top performing models (within 2 Bayesian information criterion units of best performing model) from an exhaustive model selection. Independent variables were standardized ( $\bar{x} = 0$ , standard deviation = 0.5) to easily compare effect size between variables. Lake level $_{\Delta}$  is the difference (in m) from the previous summer's mean lake level. SRP $_{\text{spring}}$  is the mean dissolved reactive phosphorus ( $\mu\text{g/L}$ ) from the immediately preceding spring mixing period.

Parameter	Estimate	Standard error	z-value	Pr(> z )	No. of models included
Intercept	0.93	0.03	26.16	<0.001	2
Lake level $_{\Delta}$	0.1	0.03	2.82	0.005	2
SRP $_{\text{spring}}$	-0.05	0.03	1.39	0.16	1

inhabits a range of habitats, and the extent to which the observed growth characteristics are common in other populations, or even in similar lake systems, is currently unknown. Lake size, depth, temperature, and trophic status are classically understood to be important in mediating the ecology of other freshwater taxa (Magnuson et al. 1979, Eadie and Keast 1984, Jeppesen et al. 2000), and future studies exploring their influence on lake mussels could be instructive.

### Growth characteristics

Growth rates of *L. siliquoides* mussels in Trout Lake, Wisconsin, were among the lowest recorded for the Lampsilini tribe, especially for a medium-sized species. Our focus on collecting larger individuals during sampling may have resulted in a bias toward faster growing individuals, so the true growth rate for this population may be even lower than what we found here. As is common with slower growing mussels, the maximum observed age was high compared to other Lampsilines. This slower growing, longer-lived life history, characteristic of an equilibrium strategist (Haag 2012), may be common in lake populations (Haag and Rypel 2011). This slow growth rate supports our hypothesis that oligotro-

phic soft-water lakes, such as Trout Lake, present unique environmental challenges to mussels, and these challenges are likely to impose a strong limitation on somatic growth.

### Relationship of growth and environment

Despite large variation among individuals, growth was strongly positively correlated with changes in lake level. There were no relationships with temperature or measures of productivity as have been found in marine (Page and Hubbard 1987, Smaal and van Stralen 1990, Archambault et al. 1999, Schöne et al. 2005) and fluvial systems (Schöne et al. 2004, Black et al. 2010). The relationship between growth and lake level suggests that mussels are responding to broad-scale ecosystem characteristics. Lake level is an aggregating environmental variable indicative of regional dynamics in precipitation and hydrology that link lake dynamics with the surrounding terrestrial landscape. It is unlikely that lake level had a direct influence on mussel growth, but rather it may act as a proxy for changes in other environmental characteristics. In fluvial systems, it has been hypothesized that a simple model for mussel growth has a parabolic relationship to discharge (Strayer 2008). During low to moderate flow,

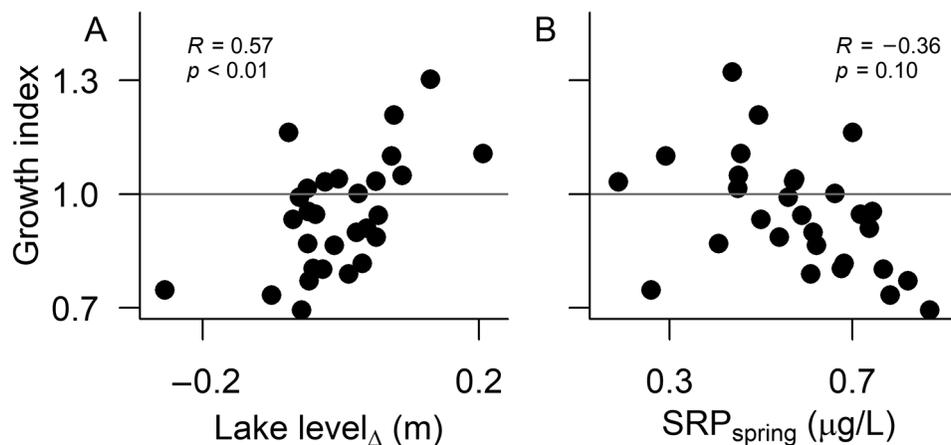


Figure 4. A.—Regressions of standardized growth indices (SGIs) on lake level $_{\Delta}$ . B.—Soluble reactive phosphorus (SRP $_{\text{spring}}$ ). Lake level $_{\Delta}$  is the difference (in m) from the previous mean summer lake level; SRP $_{\text{spring}}$  is the mean dissolved reactive phosphorus during the immediately preceding spring mixing period. Each linear regression was run independent of other environmental variables. Each dot represents average standardized growth of the population in 1 y. Growth indices >1 reflect a higher than growth for that year, whereas growth indices <1 reflect growth lower than expected for that year.

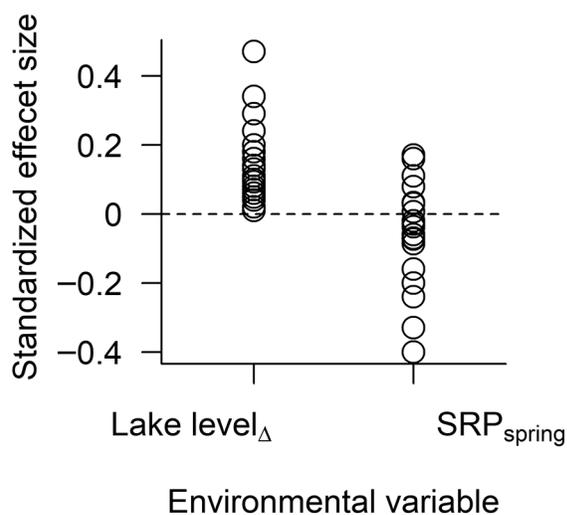


Figure 5. Estimates of effect size of lake level $_{\Delta}$  and soluble reactive phosphorus (SRP $_{\text{spring}}$ ) on individual mussel (*Lampsilis siliquoidea*) chronologies. Positive values indicate that the variable likely had a positive effect on that individual's growth; negative values indicate a likely negative effect on growth. Estimates farther from 0 suggest that the environmental variable had a stronger effect on mussel growth. Estimates were calculated independently of one another using linear models containing only the environmental variable (standardized;  $\bar{x} = 0$ , standard deviation = 0.5) being estimated and each individual chronology. Lake level $_{\Delta}$  is the difference (in m) from the previous mean summer lake level; SRP $_{\text{spring}}$  is the mean dissolved reactive phosphorus during the immediately preceding spring mixing period.

growth may be positively related to discharge as allochthonous resources and food capture rates increase. During high flow, the energetic costs of maintaining body position and expelling ingested suspended solids can outweigh the benefits of increased flow and result in a negative relationship between discharge and growth. The inverse relationship of growth to discharge has been well documented in systems of moderate to high levels of discharge (Black et al. 2010, 2015, Dycus et al. 2015), but studies supporting the hypothesized positive effects of increased allochthonous resources are rare (but see Schöne et al. 2007). We propose that lakes represent an extreme case of a low-flow system and that the positive response of mussel growth to increased lake level reflects changes in allochthonous subsidies during wetter years.

Terrestrial subsidies likely play an important role in the littoral habitats of Trout Lake, given that they are often responsible for the bulk of C in the lakes of this region (Wilkinson et al. 2013) and can provide a surprisingly large proportion of C for higher trophic levels (Weidel et al. 2008, Cole et al. 2011). We were, however, unable to detect changes in water color or DOC quantity or quality (proxies for allochthonous inputs) associated with changes in lake level or mussel growth. This lack of connection may be explained by differences between the sampling location and the location where water quality metrics were measured. The mussel bed

was just meters from shore and relatively close to a small inlet (~300 m), where individuals are likely to be exposed to allochthonous inputs immediately after runoff events. In contrast, lake water-quality variables were measured at a centrally located buoy in deep water ~500 m from our sampling site.

Mussel growth was not related to any other metrics indicative of food availability that we were able to include in our analysis. Neither Chl *a*, as a measure of phytoplankton biomass, nor cladoceran density had any relationship to growth. This lack of a relationship may result from multiple reasons: 1) there could be a mismatch in concentrations between littoral and pelagic habitats, as mentioned above for DOC; 2) pelagic resources may not be important or are not the limiting food sources for mussels in littoral habitats; 3) mussels may be integrating across or shifting between food sources, obscuring any clear relationship with any one potential source; or 4) food availability does not limit mussel growth in this system. Mussel diets vary by system and species, with feeding occurring across benthic and suspended sources that can include diatoms, phytoplankton, zooplankton, bacteria, cyanobacteria, fungi, and possibly dissolved organic matter (Newton et al. 2013, Fujibayashi et al. 2016, Weber et al. 2017). Mussel growth still may be limited by sources other than terrestrially derived food availability in this system, but the ability to detect these potential controls would be difficult because of potential shifting between food sources and the lack of data on certain sources (e.g., bacteria, fungi).

In addition to food, temperature is a fundamental determinant of metabolism and growth for all living things and is commonly associated with mussel growth rates in other systems (Hanson et al. 1988, Schöne et al. 2004, 2005, but see Cyr 2020). In this population, however, we failed to detect a relationship between water temperature and growth. Closely related variables often used as proxies for growing season, such as degree days and the duration of the summer stratified period, also surprisingly showed no relationship to growth. The most likely explanation for growth being unrelated to temperature could be that the range of summer epilimnetic temperatures in Trout Lake is small ( $\mu = 19.3 \pm 1^{\circ}\text{C}$ ) and may not be ecologically relevant for this population. Another possible explanation is that mussels may be regulating their temperature by moving within their habitat. Mussels are not entirely sedentary animals, and they move both vertically in the substrate and horizontally in response to environmental cues, such as temperature (Amyot and Downing 1997, Schwalb and Pusch 2007, Hernandez 2016).

#### Potential drivers of variation

Numerous factors likely contribute to the variability in growth among individuals. Despite the population level synchrony in growth, an interseries correlation of 0.39 is relatively low compared to fluvial mussel populations (Rypel et al. 2009, Black et al. 2010, Sansom et al. 2013). Within a lake, the distribution of mussels can be highly patchy, suggesting

that there may be spatial heterogeneity in habitat quality or the environmental controls within a lake. The moderately high variance in growth among individuals in this system is interesting, especially considering that these mussels were all comparable in age, residing in a similar substrate, and located within meters of each other. Although the open water is often fairly well mixed, benthic littoral habitats are more spatially heterogeneous (Downing and Rath 1988, Stoffels et al. 2005, Cyr 2019), and even mussels in the same bed may be experiencing different conditions.

Environmental conditions are but 1 set of factors that influence mussel growth, and unmeasured biotic drivers may play a stronger role in controlling growth. Physiological constraints on growth and the causes of physiological differences are often obscured and difficult to assess. We have a limited understanding of how characteristics such as sex and age affect growth dynamics of an individual. These effects are further complicated through differential investment in gonad development or glochidia brooding (instead of somatic in growth), which may vary substantially among individuals and over their lifetimes (Haag and Staton 2003, Moles and Layzer 2008). These factors are all overlaid upon the genetic variation between individuals, which can also be substantial (Larson et al. 2014). Other factors, such as the effects of competition, predation risk, parasites, and pathogens, may affect the physiology and growth of individuals within an assemblage non-uniformly and may be important drivers of variation in growth among individuals as well (Gangloff et al. 2008, Vaughn et al. 2008) but unfortunately have received relatively little attention. Our study of the growth of a small sample of 1 species of mussels from a single bed in 1 lake provides only a limited view into the dynamics of how mussel growth is related to the conditions of their environment. Additional studies of other species in different systems will undoubtedly be insightful for better understanding environmental controls on mussel growth.

## Conclusion

The alarming collapse of freshwater mussel assemblages worldwide should inspire increased effort to understand the ecology of these animals and the environmental challenges they face. Globally, lakes host numerous mussel populations and may be preferred habitat for some species (Nedeau et al. 2009, Haag 2012). Lakes impose divergent environmental challenges for mussels in comparison to fluvial environments, and we know very little about the ecology of lake-dwelling mussels, their responses to changing environmental conditions, or the ecosystem services they provide. Here, we show that the growth of mussels in lakes can be dynamic, can be highly variable between individuals, and may be correlated to landscape-scale environmental changes unique to lake systems. Further investigation of the ecology and life history of lake-dwelling mussels is important for developing a broader understanding these enigmatic animals.

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Author contributions: ALR conceived of the study. VLB and ALR collected and processed the samples. VLB conducted the analyses. VLB, with ALR and EHS, wrote the manuscript.

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