



A biometric technique for assessing prehistoric freshwater mussel population dynamics (family: Unionidae) in north Texas

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ABSTRACT

Biometry is useful for a suite of analyses relevant to zooarchaeology, which include analysis of mortality profiles, taphonomy, paleoecology, among other purposes. Here, size-age prediction models are developed for 10 freshwater mussel species found in north Texas to develop a method for studying paleo-environmental conditions. Shell length is often used to evaluate the structures of modern mussel populations, but its use on paleozoological specimens is not feasible because complete shells rarely preserve. Instead, pallial line-to-lateral teeth length (PLL) and pseudocardinal teeth-to-pallial line length (PSP) are evaluated as proxy measures for shell length. Linear regression models based on PLL and PSP using modern mussels demonstrate that they are accurate proxies of shell length for multiple species from a variety of habitats. In addition, ontogenetic-age structures for a modern sample and for two late Holocene assemblages from north Texas are developed using PLL and PSP. These techniques are useful tools for evaluating past ecological conditions of freshwater mussel populations when large samples are available for study, which expands analytical potential of zooarchaeological studies of prehistoric unionid remains.

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1. Introduction

Biometry of zooarchaeological remains is becoming an increasingly important tool for analyzing human subsistence during prehistory and for studies of paleoecology. In North America, biometric methods have not witnessed the same popularity in zooarchaeology as in the Old World (e.g. Davis, 1981; Dayan et al., 1991; Stiner et al., 1999, 2000; von den Driesch, 1976; Zeder, 2001, 2006), though this is starting to change (see discussion in Wolverton, 2008 in reference to vertebrate faunas). Notable exceptions include analysis of freshwater mussel faunas in areas of the Southeast (e.g. Peacock, 2000; Peacock and Chapman, 2005; Peacock and Mistak, in press; Peacock and Seltzer, 2008; Warren, 1975; Williams and Fradkin, 1999; see also Erlandson et al., 2008 for marine shellfish). In this paper we expand upon a method for determining freshwater mussel size distributions originally developed by Warren (1975) and apply the method to zooarchaeological shellfish remains from sites on the Trinity and Brazos River drainages in north Texas (Fig. 1). The method is important because it enables zooarchaeologists to use size estimates from fragmentary

mussel specimens to assess size-age distributions that usually rely on full shell-length measurements in modern ecological studies. In addition, because the method works for multiple unionid species from a variety of habitats, it has general utility for zooarchaeological application.

Modern studies of freshwater mussel communities often involve quantitative analyses using size-age distributions. Shell length is frequently used as a proxy for age and is measured as the greatest length between the anterior and posterior margins of the shell. Age-classes are determined based on shell lengths and are graphically represented in histograms (e.g. Christian et al., 2005; Haag and Warren, 2007; Miller and Payne, 1988, 1993; Miller et al., 1994; Outeiro et al., 2008; Payne and Miller, 1989, 2000). Modern mussel assemblages with consistent recruitment display positively skewed, unimodal frequency distributions. The shapes of such distributions are described as inverted “tear-drops” (Miller and Payne, 1993; Peacock, 2000). A distribution of this shape corresponds to a moderately long-lived unionid community whose growth slows with age (Miller and Payne, 1993). The size demography for such a population is expected to comprise a small number of juveniles, grading into a large portion of the population that is non-growing and sexually mature, which tapers off to a few large, old individuals (Bauer, 2001a; Miller and Payne, 1993; Peacock, 2000). It is important to note that unionid juveniles like other r-selected species are initially hyperabundant, but mortality and difficulty in sampling for both early and late juvenile stages results

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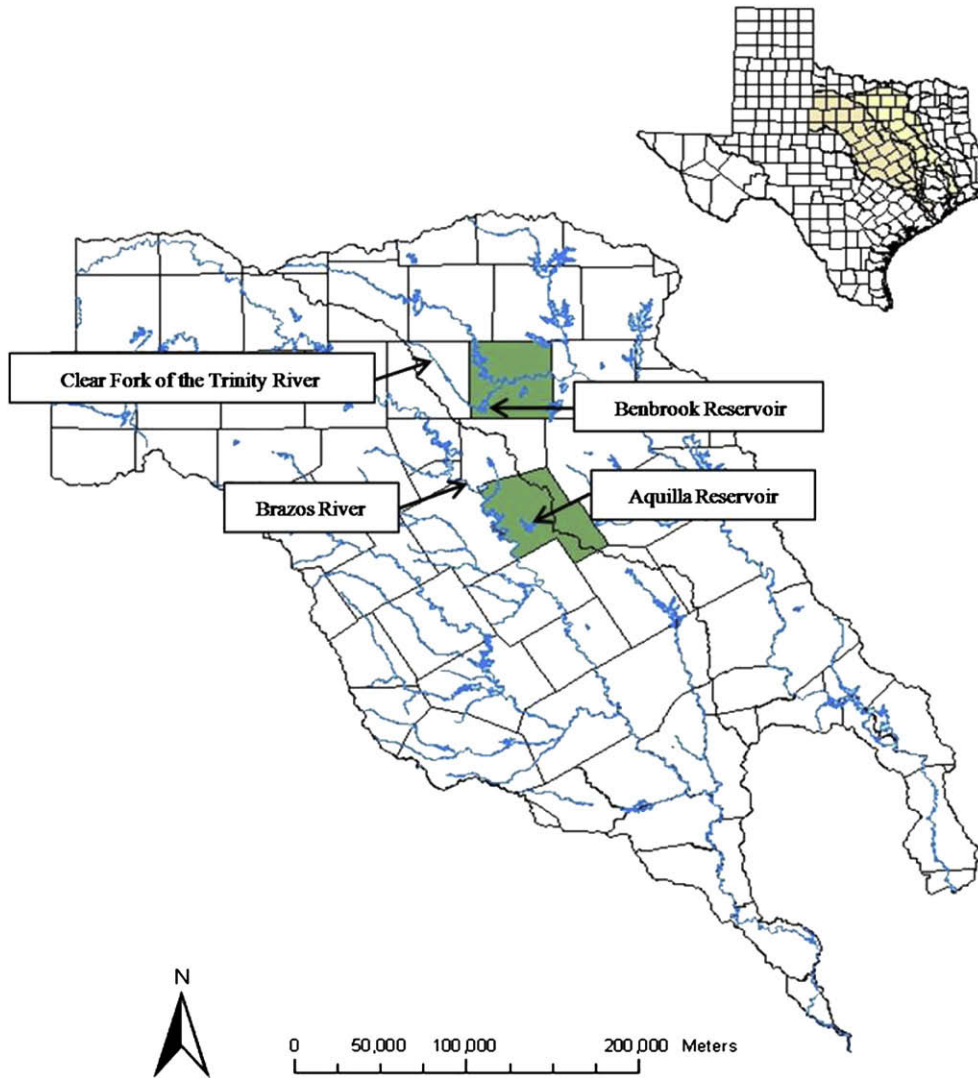


Fig. 1. Map of the Trinity River drainage and the lower portion of the Brazos River drainage. Shaded counties indicated areas where archaeological sites are found.

in only a small portion of this segment of the population depicted in the “tear-drop distribution” (Bauer, 2001a; Christian et al., 2005; Jansen et al., 2001; Matteson, 1955; Miller and Payne, 1988; Payne and Miller, 2000; Read, 1954). In addition, it is important to realize that the *actual range of sizes* in zooarchaeological assemblages *may not be helpful* in terms of studying prehistoric mussel ecology because size can vary phenotypically and genetically through time in a population. Of more interest is the *shape* of the size-age distribution, which relates to mussel population structure.

Zooarchaeological unionid remains are often highly fragmented and poorly preserved. As a result determining different age-size classes for a range of species identified in fossil assemblages is difficult because shell length requires complete specimens. To accommodate problems with fragmentation and preservation, Warren (1975) provided two measurements of interest, pallial line-to-lateral teeth length (PLL) as a proxy for shell height, and the distance between the posterior margin of the anterior pedal retractor scar and the anterior margin of the posterior adductor muscle scar (APR–PAS) as an analogue for shell length (Fig. 2). Unlike conventional shell measurements, Warren’s (1975) biometric techniques use a smaller portion of the shell and thus, are more easily applied to fragments. Peacock (2000) expanded on Warren’s (1975) biometric method, using PLL as an estimate of shell length (Fig. 3). Peacock (2000) investigated the correlation between

shell length and PLL in *Pleurobema decisum* (L. Lea, 1831), which has lateral teeth running parallel to the pallial line. Many other unionid species lack such ideal morphology for application of PLL and thus new measurements are required for broader application in zooarchaeology. For example, species belonging to the genus *Pyganodon* lack both lateral and pseudocardinal teeth, while

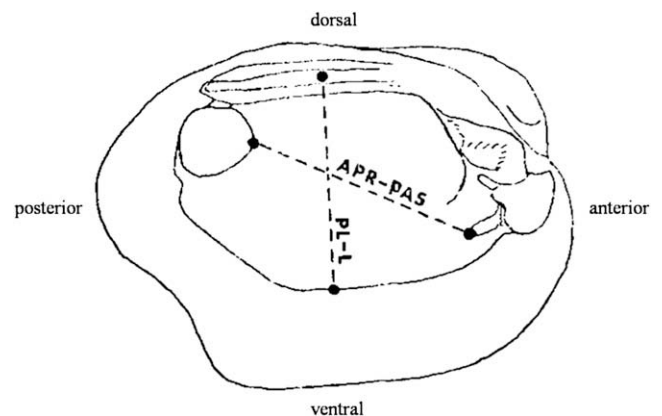


Fig. 2. Left valve PLL and APR–PAS measurements (after Warren, 1975: p. 48).

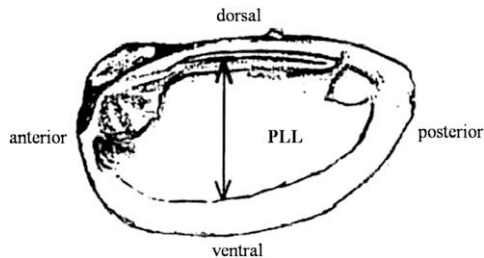


Fig. 3. Right valve PLL measurement for *P. decisum* (after Peacock, 2000: p. 192).

individuals in the genus *Truncilla* often have pallial lines that disappear posteriorly and lateral teeth that curve so severely that it is difficult to take straight-line measurements. To compound matters, environmental differences both within and between stream and lake settings can produce ecophenotypes that alter shell morphology (e.g. Ball, 1922; Bauer, 2001b; Eagar, 1978; Howells et al., 1996; Ortmann, 1920; Scholz and Hartman, 2007; Watters, 1994) and may skew PLL measurements. Based on previous work, it is unclear whether or not the high degree of scaling between shell length and PLL observed in *P. decisum* holds for other freshwater mussel species, how it varies between different species, and whether this measurement is predictive for the same species taken from different habitats (e.g. lakes or rivers). In this paper, we apply PLL and a new measurement (see below) to multiple species from a variety of modern and prehistoric settings.

Given the potential advantages of and challenges to a broader use of proxy measures for sizing mussel remains, the aims of this paper are: (1) to develop a new measurement, pseudocardinal teeth-to-pallial line length (PSP), for application to species and

fragments for which PLL is difficult to apply; (2) to develop correlative models using stepwise regression to test the strength with which PLL and PSP predict shell length in modern species from north Texas. Models are created for mussels inhabiting both lake and stream conditions to test whether or not these measurements predict shell length in a variety of habitats. And (3) to produce PLL and PSP frequency distribution graphs for one prehistoric unionid species from Late Holocene archaeological sites on Hackberry Creek (Brazos River drainage) and the Clear Fork of the Trinity River (Trinity River drainage) to demonstrate the zooarchaeological utility of this approach.

2. Materials and methods

Modern individuals of 10 freshwater mussel species were selected for analysis using PLL and PSP because those species occurred in north Texas during the late Holocene. Modern samples are reference collection specimens from north Texas (Fig. 4) curated in the Joseph Britton Freshwater Mussel Collection, located in the Elm Fork Natural Heritage Museum, Denton Texas. The 10 unionid species include *Amblema plicata* (Say, 1817), *Lampsilis hydiana* (I. Lea, 1838), *Lampsilis teres* (Rafinesque, 1820), *Plectomerus dombeyanus* (Valenciennes, 1827), *Potamilus purpuratus* (Lamarck, 1819), *Quadrula apiculata* (Say, 1829), *Quadrula mortoni* (Conrad, 1835), *Toxolasma texasensis* (I. Lea, 1857), *Truncilla truncata* (Rafinesque, 1820), and *Unio merus tetralasmus* (Say, 1831). Freshwater mussels from the Late Holocene assemblages on the Clear Fork of the Trinity River and Hackberry Creek were identified using field guides (Howells et al., 1996; Parmalee and Bogan, 1998) and modern reference specimens, and problems of synonymy were rectified using Serb et al. (2003), and Turgeon et al. (1998). Sample sizes for each species are reported in Tables 1 and 2.

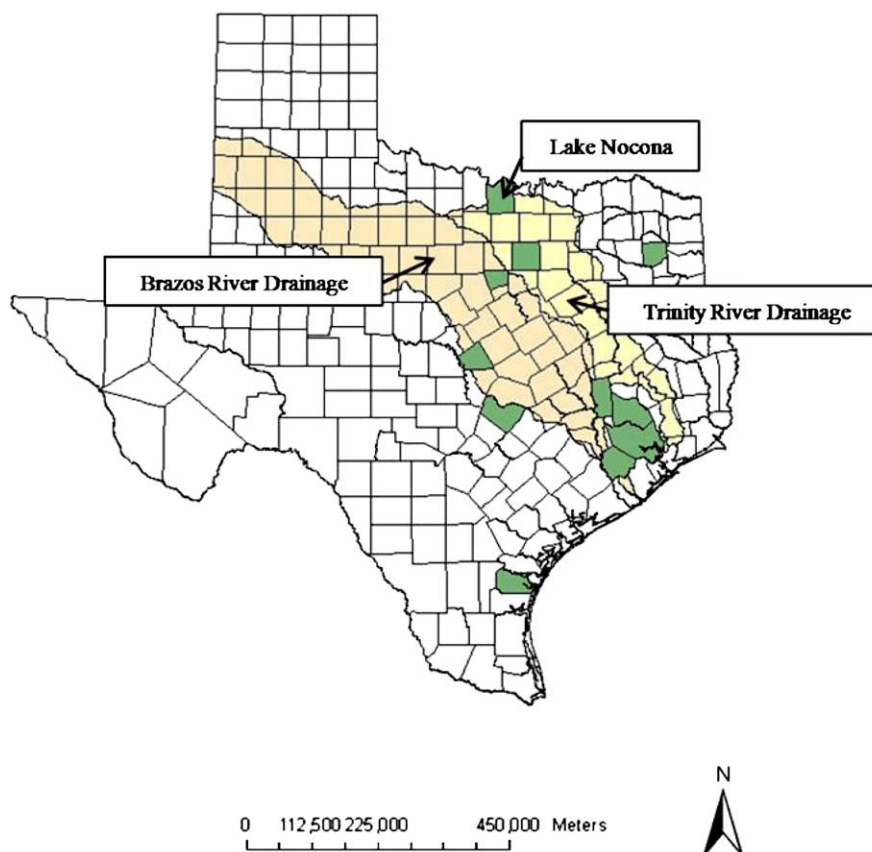


Fig. 4. Map of Texas with Brazos and Trinity River drainage. Shaded counties indicated areas where contemporary mussels were sampled.

Table 1
Coefficient of determination for morphometric equations using left valves for estimation of shell lengths using PLL and PSP measurements

Species	Metric	Valve	n	r ²	μ	95% Conf. int. ±	SE	CV (%)	Water body	County
<i>A. plicata</i>	PLL	L	14	0.99	35.9	4.6	2.4	24.5	Lotic	Montgomery, TX
	PSP	L	14	0.98	30	4	2.1	25.7		
	PLL	L	23	0.96	45.8	3.3	1.7	17.5	Lentic	Tarrant, TX
	PSP	L	23	0.88	36.6	2.5	1.3	17		
<i>L. hydiana</i>	PLL	L	24	0.93	26.4	2.1	1.1	20.1	Lotic	Lampasas, TX
	PSP	L	24	0.95	22.1	1.6	0.8	18.1		
<i>L. teres</i>	PLL	L	14	0.78	35.1	2.1	1.1	11.4	Lotic	Fort Bend, TX
	PSP	L	14	0.83	32.8	2.4	1.2	13.7		
	PLL	L	26	0.83	32.4	1.4	0.7	11.4	Lentic	Tarrant, TX
	PSP	L	26	0.86	28.7	1.4	0.7	12.5		
<i>P. dombeyanus</i>	PLL	L	12	0.88	42	4.6	2.3	19.3	Lotic	Miller, AR
	PSP	L	12	0.89	38	4.6	2.3	21.3		
<i>P. purpuratus</i>	PLL	L	21	0.93	54.8	4	2	17	Lotic	Hood, TX
	PSP	L	21	0.91	50.4	4.2	2.1	19.4		
	PLL	L	18	0.98	51.5	5.3	2.7	22.1	Lentic	Tarrant, TX
	PSP	L	18	0.87	39.9	4.4	2.3	24.1		
<i>Q. apiculata</i>	PLL	L	46	0.94	40.8	2.5	1.3	21.1	Lentic	Harris, TX
	PSP	L	46	0.91	38.1	2.3	1.2	21		
	PLL	L	47	0.9	40.9	1.6	0.8	13.7	Lentic	Tarrant, TX
	PSP	L	47	0.89	38.3	1.4	0.7	12.5		
<i>Q. mortoni</i>	PLL	L	43	0.88	31	1.4	0.7	14.8	Lotic	Montgomery, TX
	PSP	L	43	0.9	28.2	1.2	0.6	14.2		
	PLL	L	23	0.9	30.6	1.6	0.8	13.1	Lentic	Tarrant, TX
	PSP	L	23	0.84	27.1	1.5	0.8	13.3		
<i>T. texasensis</i>	PLL	L	17	0.93	16.5	1.2	0.6	15.8	Lotic	Lampasas, TX
	PSP	L	17	0.92	14.5	1.1	0.6	15.9		
	PLL	L	17	0.95	15.5	1.4	0.7	18.7	Lentic	Upshur, TX
	PSP	L	17	0.85	14.3	1.2	0.6	18.2		
<i>T. truncata</i>	PLL	L	19	0.76	28.3	2	1	15.5	Lentic	Tarrant, TX
	PSP	L	19	0.81	25.5	1.8	1	15.7		
<i>U. tetralasmus</i>	PLL	L	40	0.82	35.6	1.6	0.8	14.3	Lotic	Tarrant, TX
	PSP	L	40	0.77	32.9	1.4	0.7	13.7		
	PLL	L	15	0.93	30.7	2.4	1.2	15.3	Lotic	Nueces, TX
	PSP	L	15	0.94	28.9	2.3	1.2	15.6		

In all cases, $p < 0.05$ for F statistic. Descriptive statistics for frequency data is also given: coefficient of variation (CV), standard error (SE), and sample mean (μ).

To demonstrate that a tear-drop shaped size-age histogram depicts a recruiting population, PLL measurements are applied to a modern (non-Museum) sample of mussels [*Potamilus ohioensis* (Rafinesque, 1820)] from Lake Nocona in north Texas (Fig. 4). Age-size histograms are used to demonstrate that this proxy measure is useful for illustrating recruitment in a portion of the Lake Nocona population. Similarly, age-size histograms are produced for two zooarchaeological samples (Fig. 1): the first site (41TR170) is on the Clear Fork of the Trinity River and dates to roughly 1450 to 1270 BP based on radiocarbon dates of ash deposits (Lintz et al., 2008). The second zooarchaeological sample is from a site (41HI115) on Hackberry Creek, which dates to 2300 to 1100 BP based on uncorrected radiocarbon dates using soil humates and mussel shell found at the site (Brown et al., 1987).

Shell length for *P. ohioensis* and the 10 other north Texas freshwater mussel species from the Elm Fork Heritage Museum collection was measured as the greatest length between the anterior and posterior end of each articulated mussel (Fig. 5). PLL measurements were taken by determining the distance between the center of the two left lateral teeth and the pallial line. The line measured should be perpendicular to the lateral teeth, extending at an angle to the pallial line (Fig. 5A). For right valves, measurements were taken as the perpendicular line between the center of the lateral tooth and measured to the pallial line (Fig. 5B). Right and left valves from the same species were aggregated for the Lake Nocona and the archaeological case studies. Recorded measurements were then analyzed to determine if PLL is an accurate proxy for shell length. Size-age histograms were constructed for *P. ohioensis* to demonstrate

the utility of the PLL methodology on a known recruiting population.

In addition, PSP measurements were developed because often the entire posterior portion of the shell is missing in archaeological contexts, which limits the utility of PLL. PSP was taken on left and right valves, and measured as the straight-line distance between the posterior dorsal apex of the pseudocardinal teeth and the pallial line (Fig. 5). PSP measurements were not recorded during the survey of Lake Nocona. All measurements were obtained to the nearest 0.01 mm and were taken using Mitutoyo CD-8" CX digital calipers.

We constructed stepwise regression models to determine whether or not PLL and PSP are strong predictors of shell length across multiple species. Wilcoxon rank sum tests were used to determine whether or not coefficients of determination differ significantly on right and left valves and in lake and stream settings across these species. SPSS version 16.0 was used to compare coefficients of determination, and to construct both regression models and frequency histograms.

3. Results

Linear regressions for 10 modern (museum) unionid species from both lentic and lotic habitats across Texas indicate that shell length and PLL/PSP measurements are highly correlated (Tables 1 and 2). The coefficients of determination using both measurements for all 10 unionids are high (≥ 0.73). *L. teres*, *T. truncata* and *U. tetralasmus* had the lowest coefficients of determination, with r^2

Table 2
Coefficient of determination for morphometric equations using right valves for estimation of shell lengths using PLL and PSP measurements

Species	Metric	Valve	n	r ²	μ	95% Conf. int. ±	SE	CV (%)	Water body	County
<i>A. plicata</i>	PLL	R	16	0.99	36.7	4.3	2.2	24	Lotic	Montgomery, TX
	PSP	R	16	0.96	32	3.9	2	24.7		
	PLL	R	21	0.93	45.8	3.7	1.9	19	Lentic	Tarrant, TX
	PSP	R	21	0.78	39.8	3.1	1.6	18.1		
<i>L. hydiana</i>	PLL	R	24	0.87	25.9	2	1	19.3	Lotic	Lampasas, TX
	PSP	R	24	0.9	21.3	1.7	0.9	20.2		
<i>L. teres</i>	PLL	R	14	0.8	35.7	2.2	1.1	11.8	Lotic	Fort Bend, TX
	PSP	R	14	0.84	30.7	2.1	1.1	13.4		
	PLL	R	25	0.84	32.6	1.5	0.7	11.3	Lentic	Tarrant, TX
	PSP	R	25	0.86	27.3	1.3	0.7	12.1		
<i>P. dombeyanus</i>	PLL	R	12	0.89	42.7	4.4	2.2	18	Lotic	Miller, AR
	PSP	R	12	0.88	36	3.9	2	19.2		
<i>P. purpuratus</i>	PLL	R	20	0.96	54.7	4.1	2.1	17	Lotic	Hood, TX
	PSP	R	20	0.92	49.8	4.2	2.1	19.3		
	PLL	R	17	0.97	51.7	5.5	2.8	22.4	Lentic	Tarrant, TX
	PSP	R	17	0.87	39.7	4.7	2.4	24.7		
<i>Q. apiculata</i>	PLL	R	46	0.94	41.1	2.4	1.2	20.4	Lentic	Harris, TX
	PSP	R	46	0.91	37.8	2.4	1.2	22		
	PLL	R	47	0.89	41.5	1.6	0.8	13.5	Lentic	Tarrant, TX
	PSP	R	47	0.86	37	1.3	0.7	12.7		
<i>Q. mortoni</i>	PLL	R	43	0.89	30.2	1.3	0.7	14.2	Lotic	Montgomery, TX
	PSP	R	43	0.86	28.7	1.2	0.6	13.6		
	PLL	R	22	0.9	30	1.5	0.8	12.3	Lentic	Tarrant, TX
	PSP	R	22	0.86	27.8	1.5	0.7	12.6		
<i>T. texasensis</i>	PLL	R	17	0.94	16.2	1.3	0.7	16.7	Lotic	Lampasas, TX
	PSP	R	17	0.93	13.2	1.1	0.6	18.2		
	PLL	R	16	0.84	15.6	1.4	0.7	18.6	Lentic	Upshur, TX
	PSP	R	16	0.86	13.2	1.4	0.7	21.2		
<i>T. truncata</i>	PLL	R	20	0.73	27.2	1.8	0.9	15.1	Lentic	Tarrant, TX
	PSP	R	20	0.75	26.2	1.7	0.9	14.9		
<i>U. tetralasmus</i>	PLL	R	40	0.85	35.5	1.5	0.8	14.1	Lotic	Tarrant, TX
	PSP	R	40	0.77	30.6	1.5	0.7	15.4		
	PLL	R	15	0.94	31.5	2.6	1.3	16.2	Lotic	Nueces, TX
	PSP	R	15	0.96	27.7	2	1	14.4		

In all cases, $p < 0.05$ for F statistic. Descriptive statistics for frequency data is also given: coefficient of variation (CV), standard error (SE), and sample mean (μ).

values at 0.78, 0.73, and 0.77 ($p < 0.05$ for all three cases), respectively. Conversely, *A. plicata* ($r^2 = 0.99$, $p < 0.05$), and *P. purpuratus* ($r^2 = 0.98$, $p < 0.05$) had the highest coefficients of determination. Slight differences in r^2 were also documented

between left and right valves, and water body type (e.g. lentic or lotic) for independent samples of same species (Tables 1 and 2). Wilcoxon signed rank tests revealed no significant difference between r^2 values for left or right valves or for lake and stream settings for each species (Table 3).

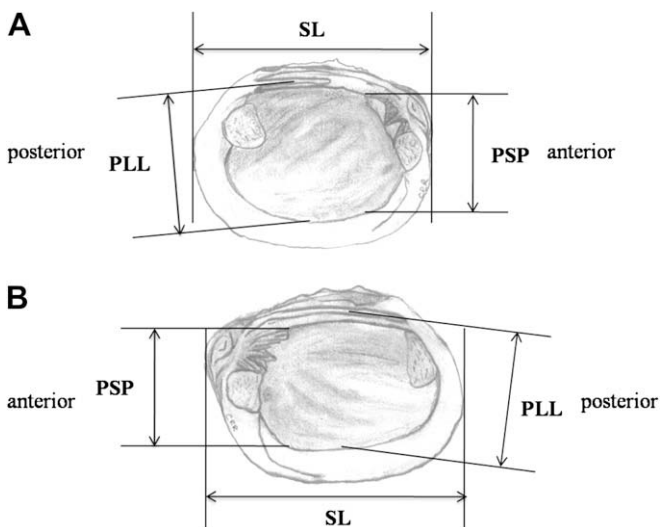


Fig. 5. (A) Left valve PLL (pallial line-to-lateral teeth length), PSP (pseudocardinal teeth-to-pallial line length), and SL (shell length) measurements for *A. plicata*, (B) right valve PLL (pallial line-to-lateral teeth length), PSP (pseudocardinal teeth-to-pallial line length) and SL (shell length) measurements for *A. plicata*.

3.1. Modern Case Study: Lake Nocona

A total of 49 *P. ohiensis* articulated shells were examined from Lake Nocona using PLL. As with the other modern north Texas species, PLL proved to be an accurate predictor for shell length, with $r^2 = 0.90$ ($p < 0.05$) (Fig. 6). Shell length for *P. ohiensis* ranged from a minimum of 68.4 mm to a maximum of 154.5 mm, with the mean shell length recorded at 130.8 ± 2.6 mm (mean \pm SE). PLL

Table 3
Statistical results comparing coefficient of determination for left versus right valves

Metric	Comparison	n	Wilcoxon (p-value)	Z
PLL	Left vs. right valve	17	0.82	-0.22
PSP	Left vs. right valve	17	0.17	-1.37
PLL	Lotic vs. lentic- (left valve)	8	0.83	-0.21
	Lotic vs. lentic- (right valve)	8	0.4	-0.84
PSP	Lotic vs. lentic- (left valve)	8	0.18	-1.33
	Lotic vs. lentic- (right valve)	8	0.13	-1.52

Includes comparison of left and right valves based on habitat (e.g. lentic or lotic). Non-parametric Wilcoxon signed rank test was used for both comparisons.

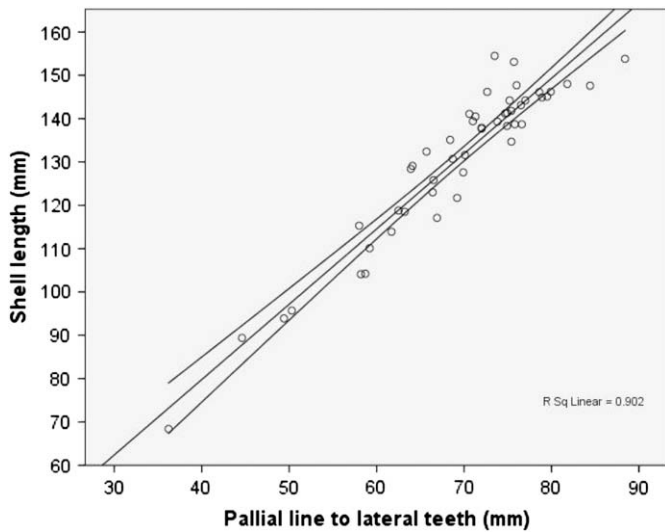


Fig. 6. Scatterplot of shell length vs. pallial line length on modern *Potamilus ohioensis* from Lake Nocona, Montague County, Texas. Confidence intervals are $\pm 95\%$.

measurements ranged from a minimum of 36.2 mm to a maximum of 88.4 mm, with the mean at 69.4 ± 1.4 mm. For both shell length and PLL measurements, coefficient of variation was low ($CV \leq 14.5\%$). Graphed PLL and SL measurements for *P. ohioensis* each produced a unimodal “tear-drop” shaped frequency distribution (Fig. 7). Live unionids including juveniles and adults were observed in great abundance at the location where spent valves were taken. Unfortunately, these specimens were analyzed prior to development of PSP.

3.2. Prehistoric Case Study

41TR170 on the Clear Fork of the Trinity River contained 27 measurable specimens, which were analyzed using PLL. PLL ranged from a minimum of 25.5 mm to a maximum of 50.5 mm, with the mean length recorded at 35.7 ± 1.3 mm. A total of 147 *A. plicata* valves were measured from 41HI115 on Hackberry Creek. Only PSP measurements were taken due to preservation problems hindering PLL measurements on shells from this assemblage. PSP ranged from

a minimum of 21.1 mm to a maximum of 50.1 mm, with the mean PSP recorded at 35.4 ± 0.5 mm. Regardless of the method used coefficients of variation for PLL and PSP were low ($CV \leq 19.3\%$). PLL and PSP analyses on prehistoric *A. plicata* from the Clear Fork of the Trinity River and Hackberry Creek produced “tear-drop” shaped frequency distributions (Fig. 8A and 8C). However, the distribution of *A. plicata* from the prehistoric assemblage near the Clear Fork of the Trinity River is not a unimodal distribution (Fig. 8A). This is likely the result of small sample size ($n = 27$) rather than a preponderance of multiple cohorts in this assemblage. It is interesting to note that when PLL measurements are used to predict shell length a more distinct tear-drop shape is produced (Fig. 8B). PSP and predicted SL measurements for prehistoric *A. plicata* from Hackberry Creek are both “tear-drop” in shape (Fig. 8C and 8D). At both archaeological sites the range of variability in size of *A. plicata* and the shape of its frequency distribution suggest representation of a full set of age cohorts (Fig. 8).

4. Discussion

Our results indicate that shell length is highly correlated with both PLL and PSP measurements for all species examined (Tables 1 and 2). Modern studies of Lake Nocona demonstrate that a “tear-dropped” distribution characterizes unionid populations that are recruiting (Fig. 7). Analysis of the 10 modern (museum) species suggests that small sample size and habitat (lakes and streams) have minimal impact on r^2 values. Five of the contemporary mussels examined had at least one measurement with sample sizes less than or equal to 16 individuals (Tables 1 and 2). PLL measurements (left valves) for *L. teres* ($n = 14$) and *A. plicata* ($n = 14$) produced r^2 values of 0.78 ($p < 0.05$), and 99% ($p < 0.05$), respectively. Peacock (2000), assessing bias in archaeological shell assemblages correlated shell length with PLL measurements ($r^2 = 0.90$) using only 16 individuals of *P. decisum*. Habitat and biogeography also appear to have little effect on r^2 values (Tables 1 and 2). Additionally, if PLL and PSP are used to predict shell length, habitat should be evaluated to ascertain the most predictive model. For example, *A. plicata* produced higher coefficient of determinations for lotic sites compared to lentic (Table 1). However, what is noteworthy is that regardless of species, samples size or habitat, PSL and PSP measurements are predictive for shell length and thus can be used to evaluate long term trends in prehistoric unionid demography.

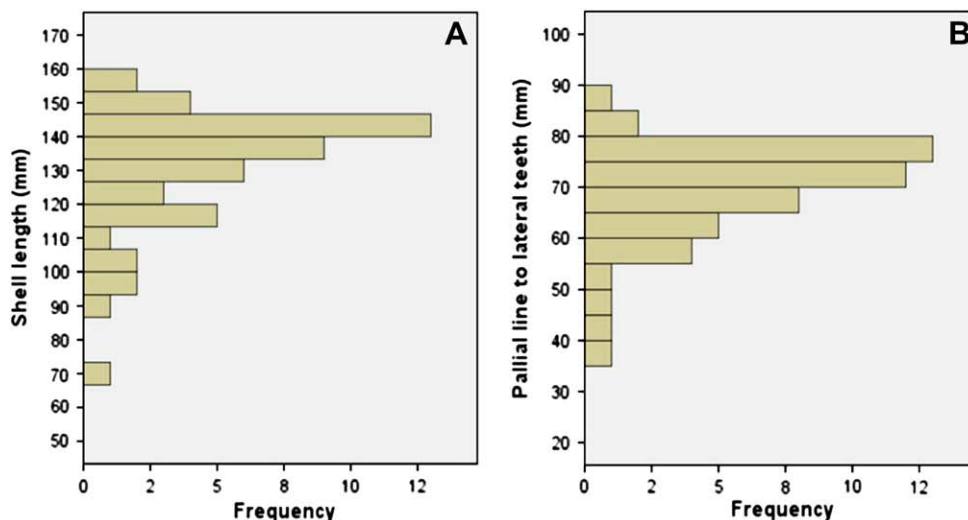


Fig. 7. Size-age distributions using frequency distribution histograms for modern *Potamilus ohioensis* ($n = 47$). (A) Size-age distribution using shell length, and (B) size-age distribution using PLL measurements.

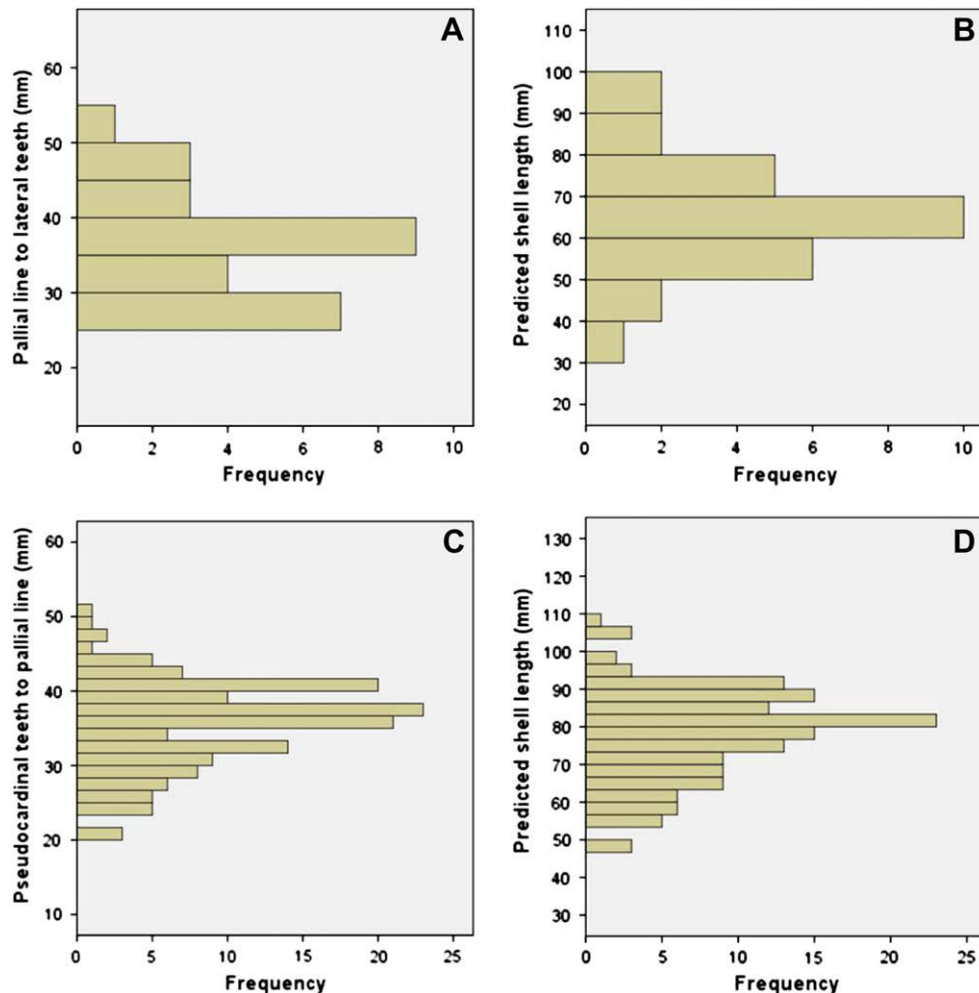


Fig. 8. Size-age distributions using frequency distribution histograms of PLL and PSP for prehistoric samples of *Amblema plicata* from the Clear Fork of the Trinity River (sample 41TR170) ($n = 27$) and Hackberry Creek (sample 41HI115) ($n = 147$). (A) PLL distributions at the Clear Fork of the Trinity River, (B) predicted shell length distributions using PLL measurements at the Clear Fork of the Trinity River, (C) PSP distributions at Hackberry Creek, and (D) predicted shell length distributions using PSP measurements at Hackberry Creek.

Prehistoric PLL and PSP histograms for *A. plicata* follow what would be expected from a recruiting modern population in the Clear Fork of the Trinity River and Hackberry Creek (Fig. 8). Individuals of *A. plicata* at both archaeological sites appear to be smaller than what has been recorded in modern populations. Using stepwise regression, the mean predicted shell length for *A. plicata* excavated from the Clear Fork of the Trinity River (based on lotic data from Montgomery County) is 66.2 ± 2.6 mm and the maximum shell length is 94.8 mm. Using the same model for the Hackberry Creek sample, the mean predicted shell length for *A. plicata* is 77.8 ± 0.9 mm and the maximum shell length is 107.8 mm. Mauldin (1972) surveying Eagle Mountain Reservoir (West Fork of the Trinity River) reported a maximum shell length of 105 mm and a mean ($n = 16$) shell length of 78.2 mm for *A. plicata*. The maximum and mean lengths predicted from the Clear Fork site are less than that reported by Mauldin (1972), and both archaeological sites are substantially less than the maximum shell length (148 mm) reported for modern *A. plicata* in Texas (Howells et al., 1996). It is important to note that we did not measure shell length for modern populations of *A. plicata* from the Clear Fork of the Trinity River and Hackberry Creek. However, previous studies have also documented smaller mussel shells from archaeological sites compared to those collected in modern times (e.g. Klippel et al., 1978; Parmalee, 1988; Peacock and Chapman, 2005; Peacock and Mistak, in press; Warren, 1975). Smaller size may relate to a variety

of causes, such as higher population density, poor quality habitat and thus low growth rate, reduction in food availability, or selective harvest of larger older individuals by human foragers that reduced average age and size (e.g. Stiner et al., 1999, 2000; see also discussion in Peacock, 2000 for unionids).

The lentic systems studied in this paper represent human-made reservoirs, and there were no lakes in north Texas during the prehistoric late Holocene. However, broadly defined lentic systems also include backwater areas, sloughs, pools and other slow-moving microhabitats within river systems. As a result, our data may not apply as a direct analogue for north Texas streams, but they do show convincingly that our biometric method can be applied across multiple habitats. Nonetheless, whether or not the method can be applied successfully in other regions needs to be assessed on a case-specific basis.

5. Conclusion

Freshwater mussels unlike many animal remains are well suited to withstand the test of time, but like many other animal remains they rarely survive intact (Lyman, 1994). Prehistoric mussel remains are ideal for describing past historical conditions and changes in biodiversity as a result of modern impacts (Evans, 1969; Matteson, 1958, 1960; Morey and Crothers, 1998; Parmalee, 1994; Parmalee and Hughes, 1993, 1994; Parmalee and Klippel, 1986; Parmalee and

Polhemus, 2004; Parmalee et al., 1980, 1982; Peacock and Mistak, in press; Theler, 1991; Warren, 1975, 1991). Quantitative analysis with regards to shell length can provide insights into both demography and recruitment of a population (e.g. Christian et al., 2005; Haag and Warren, 2007; Miller and Payne, 1988, 1993; Miller et al., 1994; Outeiro et al., 2008; Parmalee et al., 1980; Payne and Miller, 1989, 2000; Peacock, 2000; Peacock and Chapman, 2005; Peacock and Seltzer, 2008; Warren, 1975). In addition to understanding prehistoric recruitment, PLL and PSP may offer these additional advantages: first, using PLL and PSP measurements, highly fragmented samples can be used to obtain shell-size data, thus increasing sample size and statistical validity of paleozoological studies. Second, bias in preservation can be assessed by comparing mean sizes of whole shell lengths versus predicted shell lengths from fragmented shells. Jerardino and Navarro (2008) comparing mean limpet sizes between actual and predicted shell lengths for limpet species, found that fragmentation during preservation affected mainly large shells and smaller shells less. Using only whole specimens in this case would have led to the underestimation of shell size in these coastal middens. Given the high degree of correlation between shell length and PLL/PSP, these biometric equations can serve as useful tools for evaluating past ecological conditions of freshwater mussel populations, and thus expand analytical potential of zooarchaeological studies of prehistoric unionid remains.

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