ELSEVIER

An interpretive framework for assessing freshwater mussel taxonomic abundances in zooarchaeological faunas

Traci Popejoy [a, *], Steve Wolverton [a], Lisa Nagaoka [a], Charles R. Randklev [b]

[a] University of North Texas, Department of Geography, 1155 Union Circle #305279, Denton, TX 76203-5017, USA
[b] Institute of Natural Renewable Resources, College Station, TX 77843, USA

ABSTRACT

Zooarchaeological freshwater mussel remains provide information about past environments, faunal communities, and human behaviors. However, one challenge of using archaeological assemblages of animal remains is differential preservation such that bones and shells of some taxa are more vulnerable to processes that destroy or remove them from the record over time. Thus, remains of some species of freshwater mussels may be underrepresented in terms of presence/absence data as well as abundance compared to the life or death assemblages. Evaluating the representativeness of assemblages before using such data to answer zooarchaeological and paleozoological research questions is common practice in archaeology, particularly for vertebrate remains. However, little research has focused on evaluating representativeness for molluscan assemblages. In this paper, three processes that potentially influence archaeomalacological data are addressed: mussel life history strategies, shell identifiability, and shell robusticity. Expectations about taxonomic abundances in unionid zooarchaeological assemblages are framed and assessed using two datasets from sites from the Leon River in central Texas. As expected, shell robusticity and identifiability influence zooarchaeological abundance data; differences in life history strategy can be used to interpret past stream environments. The expectations derived in this paper can be used as interpretive tools for understanding factors that influence archaeomalacological taxonomic abundance data.

© 2016 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

Freshwater mussel (hereafter unionid) remains are prevalent in many zooarchaeological faunas and have been used to study past human behavior, environments, and animal ecology (Matteson, 1960; Klippel et al., 1978; Spurlock, 1981; Parmalee et al., 1982; Parmalee and Bogan, 1986; Bogan, 1990; Warren, 1991; Parmalee and Polhemus, 2004; Peacock, 2005, 2012; Williams et al., 2008; Randklev et al., 2009, 2010; Haag, 2012; Randklev and Lundeen, 2012; Miller et al., 2014). Paleozoological and zooarchaeological unionid presence/absence data are often used as evidence of shifts in human subsistence or biogeographic distributions of taxa during prehistory (Baker, 1936; Parmalee and Klippel, 1974; Warren, 1975; Peacock and Chapman, 2001; Peacock, 2012). Taxonomic abundance data from zooarchaeological assemblages can provide additional data with which to approach these types of questions

(e.g., studies of human behavior through foraging theory (Botkin, 1980; Mannino and Thomas, 2002; Braje et al., 2007; Morrison and Hunt, 2007; Singh and McKechnie, 2015)). Abundance data are also used in paleoenvironmental studies, for conservation purposes, or to assess environmental changes in species abundance as an alternative hypothesis to change in human subsistence (Matteson, 1960; Klippel et al., 1978; Casey, 1986; Peacock et al., 2005; Peacock and Seltzer, 2008; Randklev et al., 2010; Randklev and Lundeen, 2012; Miller et al., 2014; Campbell and Braje, 2015). Because taxonomic abundance data are used to address a wide variety of research and conservation questions, it is important to understand potential influences on the structure of such data.

Zooarchaeological data have been used to inform unionid conservation since 1909, when Ortmann wrote, "The Destruction of the Fresh-Water Fauna in Western Pennsylvania". Many studies since have discussed how zooarchaeological data can be used to improve mussel conservation (Matteson, 1960; Klippel et al., 1978; Spurlock, 1981; Parmalee et al., 1982; Parmalee and Bogan, 1986; Bogan, 1990; Warren, 1991; Randklev and Lundeen, 2012; Miller et al., 2014). While these studies set the groundwork for using

zooarchaeological data for unionid conservation, many studies do not address shell preservation. Parmalee et al. (1982) notes *Anodonta* species were "well established locally in … most of the reservoirs" but absent in zooarchaeological assemblages (pg. 87). Bogan (1990) addressed this lack of *Anodonta* species as a 'cultural bias' due to prehistoric peoples not sampling habitats other than riffles/shoals, which is a valid hypothesis. Parmalee and Bogan (1986) discussed difficulties associated with the identification of archaeological mussel valves, and cite sculpture as a diagnostic feature that improves identification. This paper seeks to add to this literature by addressing problems presented by Parmalee et al. (1982), Parmalee and Bogan (1986) and Bogan (1990) and by attempting to understand how three factors influence the presence and abundance of unionids in zooarchaeological assemblages.

Abundance data produced from zooarchaeological assemblages are influenced by many different forces, such as the interplay of abiotic and biotic factors at various spatial and temporal scales across the prehistoric landscape, differential preservation of shells, preferences of prehistoric people who incorporated unionids in their diets, and/or differential identifiability of some remains over others (Kidwell and Flessa, 1995; Poff, 1997; Kosnik et al., 2009; Wolverton et al., 2010; Peacock et al., 2012). These influences are alternative mechanisms that might drive patterns in taxonomic abundance and thus impact the results of zooarchaeological studies (Grayson, 1987; Lyman, 1994, 2012). Before burial, the cultural preferences of where prehistoric humans harvested mussels influenced the taxonomic composition of the deposited assemblage (Lyman, 1984; Peacock et al., 2012). After the shells are deposited in the lithosphere, differential diagenesis can influence abundance based on shell size, species, and soil moisture (Muckle, 1985). In addition, different types of excavation can influence the sample studied by zooarchaeologists (Nagaoka, 1994, 2005). The excavated assemblages from which zooarchaeological data are produced may pass through many filters prior to analysis, which includes aggregation into a deposited assemblage, time in the lithosphere, constraints on sampling, and analysis by zooarchaeologists, each potentially resulting in forms of data loss or addition (see Clark and Kietzke, 1967, p. 117; Meadow, 1980, p. 67; Lyman, 1994, pp. 12–40).

Three distinctive mechanisms that conceivably influence taxonomic composition and abundance data are addressed in this article: variable unionid life history strategies and their influence on population abundances, identifiability of shells, and preservation potential of shells from different unionid taxa. Life history strategies play an integral role in constructing ecological communities (Pianka, 1970, 1972; Southwood, 1977, 1988) and, thus, potentially influence taxonomic abundances in zooarchaeological data (Kidwell and Rothfus, 2010; Kidwell, 2013). In addition, differences in accuracy and precision of taxonomic identification can directly affect zooarchaeological mussel abundance (Gobalet, 2001); easily identified taxa are more likely to be accurately and precisely identified than hard-to-identify taxa. In addition to identifiability and abundance related to life history ecology, zooarchaeological taxonomic abundance data may be affected by differential preservation of shells from one taxon over another based on a species' shell phenotype (Wolverton et al., 2010). Together these factors have complex but predictable influences on zooarchaeological freshwater mussel taxonomic abundance data; thus, an interpretive framework that provides general expectations about which species ought to and ought not to be abundant can aid research in zooarchaeology and paleozoology that focuses on unionids. Rank order continua of life history strategy, identifiability (based on sculpture), and preservation potential are developed for taxa encountered in two zooarchaeological datasets from the Leon River of Texas and help frame expectations about aspects of taphonomy, ecology, and human behavior.

1.1. Unionid life history ecology

Life history strategies describe a species' differential allocation of energy based on the rate of population growth and reproductive ecology (Fisher, 1930; MacArthur and Wilson, 1967; Pianka, 1970). Life history should indirectly affect species abundance in zooarchaeological assemblages because reproductive ecological strategies influence their abundance in living communities (Southwood, 1977, 1988; Kidwell, 2001; Kidwell and Rothfus, 2010). Typically, Pianka's r versus K selection gradient is used to define life history strategies among different species (Pianka, 1970, 1972; Southwood, 1977, 1988). Although unionids are generally categorized as long lived and slow growing, they exhibit a wide range of variability in life history characteristics (Haag, 2012; Vaughn, 2012). In this study, unionid life history strategies are categorized into three types that are based on Winemiller and Rose's (1992) three endpoint continuum: opportunistic, periodic, and equilibrium strategies (see also Dillon, 2000; Grime, 2001; Haag, 2012). The opportunistic strategy is similar to Pianka's r-selection; such mussel species are characterized by a short life span, early maturity, and high fecundity (number of offspring). Equilibrium selected mussels live long and mature late, similar to Pianka's K-selection. Periodic selected mussels are "characterized by moderate to high growth rate, low to intermediate life span [low] age at maturity, and [low] fecundity" (Haag, 2012, p. 211). Periodic species are adapted to habitats that experience cyclical environmental variability, intermittently producing conditions conducive to successful reproduction (Winemiller and Rose, 1992; Haag, 2012). Stream position and habitat influence the abundance of different life history strategists in riverine biotic communities (Southwood, 1977, 1988; Haag, 2012; Mims and Olden, 2012). Haag (2012, p. 282) constructs a conceptual model that predicts the abundance of unionid taxa with different life history strategies based on biotic and abiotic factors for small, medium and large-sized rivers. Small, low order streams are predicted to experience high disturbance frequency and low habitat diversity and high competition for host fish and as result should be dominated by periodic and opportunistic species. Medium sized streams experience less disturbance and as a result have more habitat diversity, and competition for host fish is also reduced due to the fact that fish diversity increases with stream size. These factors cause higher relative abundance of periodic and equilibrium species. Large, high order rivers tend to be fairly stable in terms of disturbance and have high habitat diversity and very low potential for host competition as a result equilibrium species tend to proportionately more abundant in large order streams. Throughout the river, lentic mesohabitats (areas of still water such as pools, backwater or depositional areas along stream margins) should have high abundance of opportunistic species. Therefore, consideration of the type of stream, disturbance frequency, and potential habitat is important for understanding life history composition of faunal assemblages. For the small to medium sized Leon River, we expect periodic and equilibrium species to be most abundant, unless lentic mesohabitats were the focus of mussel gathering by prehistoric humans.

1.2. Identifiability

Differences in identifiability of shells between species relate to two factors: distinctiveness of shell morphology and preservation potential related to shell fragmentation. One way that zooarchaeologists account for differences in identifiability and also bolster confidence in data quality is to fully describe identification criteria (Driver, 1992, 2011; Wolverton, 2013). Zooarchaeological specimens are often fragmented and eroded, making identifications difficult, which is exacerbated by the fact that shell phenotype (e.g.,