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Prey body size and anthropogenic resource depression: The decline of prehistoric fishing at Chelechol ra Orrak, Palau

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ABSTRACT

Prior investigation at the Chelechol ra Orrak site (3000/1700–0 BP) in Palau's Rock Islands revealed a decline in fishing and increased reliance on small-bodied, inshore and littoral molluscs, commensurate with evidence for declining foraging efficiency and prey switching that signal potential resource depression. Yet, standard markers for 'overfishing', such as diet-breadth expansion, increased taxonomic richness, and a switch to exploitation of offshore waters, are lacking at the site, undermining the case for anthropogenic resource (exploitation) depression as a cause of the observed patterning. Broad scale climate change similarly fails to account for these shifts. To investigate these conflicting patterns we performed a mean/median size analysis of two parrotfish (Scaridae) taxa, *Scarus* and *Chlorurus*, among the most commonly recovered fish at the site. Results indicate that *Scarus* size remains unchanged through 1500 years of exploitation, while *Chlorurus* become larger, substantiating previous findings for sustainable resource use at Orrak. With these results in mind, we critically evaluate prey size change as a metric for anthropogenic exploitation depression, noting that size diminution, in particular, may arise epiphenomenally due to multiple causes unrelated to human predation pressure. Results have broader implications for the detection and attribution of resource depression in studies of human paleoecology.

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1. Introduction

Recent, heightened concern with methodology and interpretation in the analysis of archaeofish assemblages from the Pacific (Anderson, 2013; Butler, 1994; Lambrides and Weisler, 2013, 2015; Nagaoka, 1994; Olmo, 2013; Ono and Addison, 2013; Ono and Clark, 2012; Ono and Intoh, 2011; Vogel, 2005) is undergirded by the explicit recognition that these aspects of archaeological investigation have direct bearing on reconstructions of subsistence, foraging strategies, capture technologies, gender roles in foraging, anthropogenic ecological impacts, human responses to environmental change, and more (e.g., Allen, 1992, 2002; Anderson, 2013; Butler, 1994, 2001; Leach and Boocock, 1993; Leach and Davidson, 2001; Morrison and Addison, 2009; Vogel and Anderson, 2012). Identification of resource depression in fish assemblages, in particular, requires considered and careful evaluation as certain cultural practices and sociopolitical developments can mimic the appearance of human instigated resource depression (e.g., Allen, 2012; Daniels, 2009; Whitaker and Byrd, 2014). Derived from evolutionary ecology, the term 'resource depression' describes a situation in which prey numbers decline on the landscape, or in the seascape in the case of fish or other marine taxa, and may be caused by a number of factors (Charnov et al., 1976). Most archaeological studies of resource depression are concerned with anthropogenic exploitation depression (*sensu* Charnov et al., 1976), in which prey numbers decrease because human predation exceeds the level at which the target taxon can sustain its population (e.g., Broughton, 1994, 1997; Butler, 2001; Codding et al., 2010; Lupo, 2007; Nagaoka, 2000, 2002); for archaeological studies examining behavioral depression see Whitaker, 2010; Wolverton et al., 2012; also Broughton, 2002). Because this form of resource depression carries implications for the sustainability of resource exploitation, human responses to environmental change, niche construction, the origins of domestication, as well as potential applied value in conservation biology (Broughton et al., 2010; Codding and Bird, 2015; Gremillion et al., 2014; Lupo, 2007; Lyman and Cannon, 2004; Smith, 2015; Wolverton and Lyman, 2012 and papers therein; Zeder, 2012, 2014, 2015), it is important that determinations of exploitation depression be grounded in secure evidence. A decrease in the abundance of

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high-ranked prey—where rank is determined by the energetic (or some other currency) return rate of prey in accordance with foraging theory (Kaplan and Hill, 1992; Stephens and Krebs, 1986)—and increases in the abundance of lower-ranked prey often flag potential resource depression in the archaeological record and trigger follow up investigation. However, habitat destruction, disease, biotic and abiotic environmental factors, and even the methods used to quantify or recover zooarchaeological remains can lead to scenarios where the relative abundance of high-ranked taxa in the archaeological record appear to fall (with the potential statistical effect of making others appear to increase in relative importance). Abundance data alone, therefore, are insufficient to substantiate exploitation depression, and other lines of evidence are required to corroborate such findings.

Among the indicators employed by archaeologists to further support cases of exploitation depression are quantitative measures (richness [NTAXA], diversity, and evenness) that reflect diet breadth expansion through the addition of new prey or patches (Jones, 2004; Lupo, 2007; Nagaoka, 2001; Smith et al., 2014), the exploitation of more distant patches (Binford, 1978; Bird and Bliege Bird, 1997; Bird et al., 2002; Broughton, 1995; Cannon, 2000, 2003; Nagaoka, 2005; Smith et al., 2014), or the intensified use/increased processing of existing prey (Binford, 1981; Broughton, 1995; Lech et al., 2011; Nagaoka, 2005; Wolverton et al., 2008). A change in the mean size of a prey taxon is also widely used to assess the effect of human predation pressure in the past, especially for taxa of indeterminate growth such as many fish and mollusc species (e.g., Ash et al., 2013; Blick, 2007; Erlandson et al., 2008, 2011; Giovas et al., 2010, 2013; Jerardino, 1997; Masse et al., 2006; Milner et al., 2007; Ono and Clark, 2012; Turrero et al., 2014; Wing, 2001; Wing and Wing, 1995; see Codding et al., 2014 and Thomas, 2015 for recent reviews on molluscs). Such studies are fairly routine despite potential complicating factors (Broughton, 2002; Campbell, 2008; Claassen, 1998; Fenberg and Roy, 2007, 2012; Giovas et al., 2010, 2013; Mannino and Thomas, 2002; Shin et al., 2005), perhaps because effects like a size decrease are analytically simple to measure, visually satisfying in their graphic presentation, and intuitively appealing in their underlying logic.

Here we present a case study from the Chelechol ra Orrak rockshelter in the northern Rock Islands of Palau, where changing absolute relative abundances of fish and molluscs, the latter focused increasingly on a single small bivalve, *Atactodea striata*, suggest prey switching commensurate with exploitation depression in fish. In contrast to our expectations, we did not find evidence for impacts on fish or molluscan prey taxa that could be linked to intense predation pressure in previous studies of these trends (Fitzpatrick et al., 2011; Giovas et al., 2010). This study examines the issue further through a size analysis of one of the most frequently recovered fish taxa at the site, parrotfish (Scaridae), and considers these results in relation to a critical review of prey size change in the archaeological record, its causes, and significance.

2. Theoretical background: Relationship of taxon size to biology, ecology, and predation

Expectations for change in the mean size of an animal under predation pressure derive from the biological relationship between taxon age and growth and predictions about return-rate maximizing behavior in human hunters. For three primary reasons, as exploitation exceeds a certain threshold, the mean size of a taxon is generally expected to decline. First, body size and age are usually correlated, particularly for species that continue to grow throughout life. Increased predation pressure makes it less likely that individuals of a given taxon will survive to older ages, lowering the mean age of the population and, concomitantly, the mean size—fewer older individuals over time effectively results in fewer larger individuals. Depending on species life history and ecology, however, an increase in mean age is also possible (Broughton, 2002; Claassen, 1998; Giovas et al., 2010; Mannino and Thomas, 2002). Second, foraging theory in combination with the body-size proxy predicts that larger individuals within a taxon might be preferentially targeted by hunters (Fenberg and Roy, 2007). To the extent that this happens, larger individuals decline in number. As this occurs, smaller individuals should increasingly contribute to the diet.

Lastly, human predation essentially constitutes a form of selection. If larger individuals within a taxon are consistently removed from the breeding population, phenotypically smaller individuals may come to predominate over time (Fenberg and Roy, 2007; Law and Stokes, 2005). This effect, termed fisheries-induced evolution, has been demonstrated in modern field, controlled, and simulation experiments with fish (Hilborne and Minte-Vera, 2008; Kuparinen and Hutchings, 2012; Reznick et al., 1990, 1997, 2002; see also Jørgensen et al., 2007; Kuparinen and Merilä, 2007; Law, 2007 with respect to global fisheries impacts), but whether localized human exploitation on a preindustrial scale is sufficient to produce such outcomes is unclear.

The predation effects outlined here will shift prey population size structure downward so that a greater number of smaller individuals and fewer large individuals compose the population. Archaeologically, detection of this phenomenon is based on evaluation of animal size through the application of allometric formulas to the measurement of a specific skeletal/exoskeletal part (Reitz and Wing, 2008; Reitz et al., 1987) or the direct measure of a skeletal/exoskeletal element, where this can be shown to be reliably correlated with overall body size (e.g., Campbell and Braje, 2015; Seymour, 2004; Wing, 2001; Zohar et al., 1997). However, prey size declines in the archaeological record should not automatically be assumed to reflect the effects of human exploitation since size change may be epiphenomenal to other process. The time and space averaging of archaeological assemblages (Lyman, 2008) can potentially yield such patterning, for example, when prey populations characterized by distinctive mean sizes are distributed in different patches on the landscape and are exploited by foragers from a central place to which they are returned. In this context, the palimpsest of zooarchaeological remains may appear to suggest size change through time, when in fact it reflects spatial or environmental variation in prey populations.

As a further consideration, there are a number of instances where the 'decreasing size' rule of thumb may be violated. For instance, removal of predators or competitors of a species may positively influence size. This has been demonstrated in controlled studies of nerite snails (Underwood, 1976), and appears to have occurred in nerites exploited by prehistoric people on Nevis in the West Indies (Giovas et al., 2013). By contrast, intensified intra-specific competition in sea urchins has been shown to provoke a size increase in aristotle's lantern (the urchin's feeding apparatus), relative to the test—an effect which for at least some taxa is reversible and seasonally correlated with food availability (Ebert et al., 2014; Levitan, 1991). Thus, life history, behavior, and ecological variables specific to a taxon must be considered when making predictions about the directionality of size change resulting from resource depression (Claassen, 1998; Giovas et al., 2010; Leach and Davidson, 2001; Thakar, 2011).

It is critical to recognize that when archaeologists use prey length, width, or mass as a measure of intensified human exploitation they are essentially using size as a proxy for prey age—that is, survivorship in the population. This is the true target variable of interest. However, body size is the product of both age and growth rate, and a change in growth rate can produce a change in size even if survivorship does not change. For this reason, a number of

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