Prey Body Size and Anthropogenic Resource Depression: The Decline of Prehistoric Fishing at Chelechol ra Orrak, Palau

Christina M. Giovas^{1,2}, Scott M. Fitzpatrick², Osamu Kataoka³, Meagan Clark²

¹School of Social Science, University of Queensland, Brisbane St Lucia, Australia

²Department of Anthropology, University of Oregon, Eugene OR, USA

³College of International Language and Communications, Kansai Gaidai University, Osaka, Japan

Corresponding author: Christina M. Giovas

Corresponding Address:

School of Social Science

University of Queensland

Michie Building (#9)

Brisbane St Lucia, QLD 4072

Australia

Phone: (+61 7) 336 54928

Email: c.giovas@uq.edu.au

Permanent Address:

School of Social Science

University of Queensland

Michie Building (#9)

Brisbane St Lucia, QLD 4072

Australia

Phone: (+61 7) 336 54928

Email: c.giovas@uq.edu.au

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 heavily exploited 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.

Keywords: Resource depression; foraging theory; body size change; Micronesia; parrotfish (Scaridae); lower pharyngeal grinder

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., Anderson 2013; Allen 1992, 2002; 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; Coddling 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; Coddling 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 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) reflecting 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 Coddington et al. 2014 and Thomas 2015 for recent reviews on molluscs). Such studies are fairly routine despite potential complicating factors (Broughton 2002; Claassen 1998; Campbell 2008; 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 the most heavily exploited fish taxon, parrotfish (Scaridae), and considers these results in relation to a critical review of prey size change in the archaeological record, its causes, and significance.

THEORETICAL BACKGROUND: RELATIONSHIP OF TAXON SIZE TO BIOLOGY, ECOLOGY, AND PREDATION

Expectations for change in the mean size of prey 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 has been demonstrated in modern field, controlled, and simulation experiments with fish (fisheries-induced evolution) (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, behavioral, 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).

Critical to recognize is 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 archaeological researchers have recognized the need to evaluate size-at-age data, not simply size alone, to assess the relationship of growth rate to observed size changes (Campbell 2008; Claassen 1998; Faulkner 2009; Giovas et al. 2010, 2013; Mannino and Thomas 2001, 2002; Milner et al. 2007; Roy et al. 2003; Turrero et al. 2014). Unfortunately, independent control on prey age can be difficult to establish archaeologically (but see Turrero et al. 2013, 2014). Ultimately, whether a mean size change in a prey population takes the form of a decrease or an increase will depend on species life history and ecology in addition to the specific attributes of human interaction with that prey. Because of this, it is important to have an empirical or ecologically informed basis for the predicted direction of size change when looking at exploitation

depression. With this in mind we now turn to the archaeofish case study from the Chelchol ra Orrak site in Palau.

RESEARCH BACKGROUND

Palau Environment and Archaeology

The Palauan archipelago comprises several hundred islands located in the northwest tropical Pacific (Fig. 1). Several of the larger islands are primarily volcanic, but the majority are the result of uplifted reef systems and locally referred to as “Rock Islands”. Over time these karstic formations have weathered into steep and jagged pit and pinnacle topography, which are now surrounded by extensive shallow, fringing, and barrier reef complexes (Tupper et al. 2015, ReefBase). Palau is well known for its ecological diversity, particularly with respect to the marine environment, but also many endemic terrestrial and freshwater species. More than 1500 marine fish species are known from Palau, and the archipelago supports the most diverse marine fish, stony coral, and freshwater fish taxa in Micronesia (Colin 2009; Donaldson 2002; Donaldson and Myers 2002; Froese and Pauly 2015, FishBase; Myers 1999). There are also similar levels of diversity for marine plants and most invertebrate groups (Colin 2009).

Archaeological evidence currently suggests that Palau was initially settled between ca. 3300-3000 BP (Clark 2005; Fitzpatrick 2003a) as part of the larger movement of Austronesian horticulturists expanding out from somewhere in Island Southeast Asia. There are few sites that date to this earlier time period, but the smaller limestone islands were not necessarily peripheral to inhabitants as once thought given that the earliest unequivocal dates come from Ulong (Clark 2005) and Orrak (Fitzpatrick 2003a), two Rock Islands separated by 30 km in straight line distance. It is likely that the coastal margins of the bigger islands, particularly Babeldaob, were also settled contemporaneously, although the evidence for this has proven elusive. Nonetheless, it is clear that these larger islands were pivotal in

cultural development, as can be seen by the construction of dozens of earthworks and terraces beginning around 2400 BP, coupled with the intensification of dryland agriculture (Liston 2009). It appears that villages during this time were relatively small with simple stone architecture and earthworks. Beginning by about 800 BP, there is a movement of populations to the coast with evidence for elaborate stonework, including residential and special use platforms, pathways, docks, bathing areas, and other features, and a focus on wetland taro cultivation.

Research Focus and Zooarchaeological Background

The site of Chelechol ra Orrak is located in Palau's northern Rock Islands. Previous analysis of archaeological fish remains from the site indicated a decline in reef herbivores and increase in omnivorous and piscivorous fish after ca. 1300 BP, while taxonomic richness, and Shannon diversity and evenness, remain relatively stable (Fitzpatrick et al. 2011). The most significant observed trend, however, was for a decline by an order of magnitude in the abundance of fish between early occupation (Phase II, 1400 – 1240 BP: NISP = 2038, MNI 298) and subsequent periods (Phase III, 1290 – 720 BP: NISP = 391, MNI = 107; Phase IV, 500 – 0 BP: NISP = 175, MNI = 85) (Fitzpatrick and Kataoka 2005; Fitzpatrick et al. 2011) (Table 1). Similar declines in fishing have been recorded elsewhere in the Pacific, Caribbean, and other locations where they have been variously ascribed to climate change (e.g., the "AD 1300 Event") (Nunn 1999, 2000; Ono and Intoh 2011), technological shifts, or allocation of energy to other economic pursuits, such as agriculture or the adoption of intensive dairy farming (e.g., Allen 2002; Cramp et al. 2014; Giovas 2013).

Because of an absence of evidence within the fish assemblage for diet breadth expansion or changes in patch exploitation (e.g., increased capture of more distant offshore fish, such as tunas [Scombridae]) at Chelechol ra Orrak, we suggested the observed fishing trends were inconsistent with expectations for human-induced resource depression and that causal triggers likely lay elsewhere. We

further proposed that these mechanisms possibly related to an increased focus on agriculture that lead fishing to be de-emphasized due to opportunity cost associated tradeoffs (Fitzpatrick et al. 2011). Subsequent analysis of the molluscan assemblage from the site presented intriguing complications to this assessment. First, the archaeomalacological research indicated intensification of specific molluscan resources after ca. 1700 BP, and especially after ca. 1200/1000 BP, coinciding roughly with the period of declining fish remains at Orrak (i.e., after ca. 1290/1240 BP). These trends were driven almost exclusively by increases in the small marine snail, *Gibberulus* (formerly *Strombus*) *gibberulus* (ca. 2.9% molluscan NISP and 6.9% molluscan MNI in the period between 3000 – 1700 BP; 4.9% molluscan NISP and 12.0% molluscan MNI between 1700 – 1000 BP), and, in particular, the small bivalve *A. striata* (ca. 32% molluscan NISP and 40% molluscan MNI between 3000 – 1700 BP; ca. 40% molluscan NISP and 52% molluscan MNI between 1700 – 1000 BP; and ca. 63% molluscan NISP and 63% molluscan MNI between 1200/1000 – 0 BP; Giovas et al. n.d.). Together they hinted that the anticipated diet breadth expansion by Orrak foragers may have bypassed fish entirely to focus on lower-ranking molluscs easily collected from nearshore and littoral habitats. At the same time, a study of size change in *G. gibberulus*, the most heavily exploited gastropod taxon, demonstrated a mean increase in snail shell size over time, suggesting that heightened exploitation was not sufficiently intense to suppress mean snail longevity (Giovas et al. 2010). Thus, at least molluscan foraging at the site appeared sustainable, although it remains to be determined why such small taxa (*G. gibberulus* maximum length = 7 cm, common length = 5 cm; *A. striata* maximum length = 4 cm, common length = 2.5 cm) (Poutiers 1998a, 1998b) were targeted when larger taxa (e.g. *Tridacna* spp.) were presumably available and how this might relate to changing subsistence and sociopolitical systems in Palauan prehistory.

Against this complex backdrop, the meaning of the changes in fishing appeared less clear—within the fish assemblage, evidence for exploitation depression was lacking, but when these data were considered in combination with the molluscan assemblage, a pattern for patch switching and

incorporation of lower-ranking prey consistent with resource depression appeared to emerge. In order to determine whether predation pressure by occupants at Chelechol ra Orrak had a negative impact on fish populations in the surrounding waters, we undertook analysis of changing parrotfish (Scaridae) size through time at the site. Here we present the results of this analysis based on mean width of the dental plate of the lower pharyngeal bone (grinder), a highly derived element of the branchial skeleton which forms the lower grinding surface of the pharyngeal mill apparatus (Bellwood 1994). The lower pharyngeal dental plate has been demonstrated to correlate with parrotfish mass (Seymour 2004) and has previously been employed in similar studies to assess size changes in this taxon (e.g., Blick 2007; Carder et al. 2007; Masse et al. 2006; Ono and Clark 2012). Empirical studies of modern Pacific and Caribbean fisheries support a correlation between increased fishing pressure and a decline in body size in parrotfish (Bellwood et al. 2011; Hawkins and Roberts 2003; Vallès and Oxenford 2014).

We focus on Scaridae in this study because: 1) it is the most abundant taxon by NISP and MNI for each Phase (Table 1) of the last 1400 years BP; 2) previous analysis demonstrated a statistically significant decline in scarid NISP after ca. 1300 BP; and 3) the robustness of the scarid lower pharyngeal grinder lends itself to good preservation, facilitating reliable measurement. Because this common reef taxon appears to have been heavily exploited at the site, we expect that if Orrak occupants were ‘overfishing’ local fish stocks, it should be evident as a statistically significant decline in mean width of the lower pharyngeal grinder (LPG) of scarid species. We discuss our results in terms of their implications for understanding long-term trends in subsistence strategies at Chelechol ra Orrak and the wider significance for studies of human foraging and resource depression in the past.

Chelechol ra Orrak (B:IR-1:23)

Chelechol ra Orrak (“Beach of Orrak”) is a rockshelter found along the western edge of the small limestone island of Orrak, which is situated in Airai Bay just off the southeast coast of the largest island

of Babeldaob. Orrak is primarily surrounded by sand flats leading out to shallow coral reefs, with the southern edge lying adjacent to the main barrier reef system that drops substantially in depth (Fig. 2). While the site was known as a location where the Yapese came to quarry their famous stone money (Fitzpatrick 2003b), it had not been investigated in detail until 2000 when Fitzpatrick conducted excavation there as part of his dissertation fieldwork into Yapese-Palauan exchange systems and discovered occupation refuse dating back to as early as 1700, and earlier human remains that dated between ca. 3000 and 1700 BP (Fitzpatrick 2003a; Nelson and Fitzpatrick 2006). Three additional field seasons in 2002, 2007, and 2012 demonstrated that after use as a burial ground, the site was occupied post-1700 BP up until the recent historic period.

In total, 10 m² have been excavated from 11 test units (nine 1.0 × 1.0 and two 1.0 × 0.50m²), from in and around the center of the site. Test Units 1-4 were excavated in 2000, while the other seven units (E2/S1, E3/S1, E2/S2, E1/S4, E2/S4, E1/S5, and E2/S5) were excavated later (Fig. 3). All units were wet-screened through 1/8" (3.2 mm) mesh, with the exception of E2/S4 which was wet screened using nested 1/4" (6.4 mm) and 1/16" (1.6 mm) mesh. Stratified deposits in these nine units are fairly complex, with evidence of mixing in some of the lower layers due to repeated burial activities, some of which displaced earlier burials, and in the upper 0-20 cm due to engineering activities associated with stone money quarrying (Fitzpatrick 2003b) and more recent activities. In some units, thin anthropogenic depositions are visible from what appears to be repeated fires and cooking. These uppermost layers (1-7), which are generally 0-50 cmbs, mostly date post-cal 1700 BP (but possibly earlier) and consist of a mixture of calcareous sand and silty loam intermixed with limestone and coral rock and dense faunal refuse and artifacts. Burial deposits dating from ca. 3000-1700 BP are composed primarily of coralline sand (Layers 8-10, generally 50 cm and below) and occasionally capped with limestone rocks.

To date, investigations at Orrak have identified the burials of more than 35 individuals, recovered a variety of artifacts manufactured from bone, stone, and shell, and yielded a large

assemblage of faunal material composed primarily of fish, gastropod, and bivalve remains (Fitzpatrick 2003a, 2003b; Fitzpatrick and Kataoka 2005; Fitzpatrick and Nelson 2008; Fitzpatrick et al. 2011; Giovas et al. 2010). The abundance of shell and fish bone at Chelechol ra Orrak suggests a heavy dietary reliance on marine-based protein, findings which are consistent with results from preliminary stable isotope analysis indicating human bone collagen enriched in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Krigbaum and Fitzpatrick 2009).

ANALYTIC METHODS

Scarid Identification and Measurement

Parrotfish are so-called because of their distinctive, beak-like mouth adapted for herbivorous grazing of hard substrates. They are chiefly tropical, marine fish usually found in association with reefs where they play an important role in the formation of coral sand through their feeding behavior, which consists primarily of scraping algae from dead coral substrates and ingesting coralline algae and, in some cases, coral polyps (Bellwood et al. 2011). Hard calcareous matter ingested with food is ground into sand by the pharyngeal mill to aid digestion and then excreted. Parrotfish are typically active in the day, with some species enveloping themselves in a mucoid sack during nocturnal rest for predator protection (Videler et al. 1999). These colorful fish pass through sequential stages of hermaphroditism and color phases, ending in a brightly patterned terminal, or supermale, phase associated with larger attained size (Bellwood 2001; Froese and Pauly 2015). Parrotfish protogyny carries important implications for size analyses. If fishing pressure is sufficient to prevent fish from growing large enough to undergo sex change, populations may become non-reproductive unless they can counteract the effect by transforming sex earlier or through external recruitment (Hawkins and Roberts 2003). Pacific scarid species range in size, but many commonly grow to ca. 40 – 50 cm total length. The largest species *Bolbometopon muricatum*, reaches a maximum of 130 cm total length and up to 46 kg (Froese and Pauly

2015). Parrotfish are generally found at depths of 1 – 40 m and caught using nets and traps or by spearing, as hooking the hard, beak-like mouth can be difficult (Butler 1994; Froese and Pauly 2015; Johannes 1981; Keegan 1986; Prokop et al. 2006).

We follow Seymour's (2004) example in which size analysis is based on lower-level (genus or species) identification due to inter-generic/family differences in allometric relationships between element size and overall fish size. Palauan waters host 34 species of parrotfish in seven genera: *Bolbometopon* (1 sp.); *Calotomus* (2 spp.); *Cetoscarus* (1 sp.); *Chlorurus* (6 spp.); *Hipposcarus* (1 sp.); *Leptoscarus* (1 sp.); and *Scarus* (22 spp.) (Froese and Pauly 2015, FishBase). Of these taxa, only *Hipposcarus* was not identified in the Orrak archaeofish assemblage. Scarid LPGs were identified to genus relying on anatomical characteristics illustrated and described in Bellwood (1994). While the lower pharyngeal grinder is a robust element, the keel and lateral horns, which bear diagnostic morphology, are prone to fragmentation, potentially impeding lower level taxonomic identification. Therefore, only specimens that could be identified below the family level were included in this study, resulting in a total sample of 103 LPGs. This number includes 28 additional specimens which were not included in the original zooarchaeological analysis (Fitzpatrick and Kataoka 2005; Fitzpatrick et al. 2011), but were drawn from unanalyzed faunal material from the same archaeological contexts recovered in 2012 to augment sample size.

The width of specimen dental plates was measured to a hundredth of a millimeter using Absolute Digimatic vernier calipers. Width is recorded as the greatest distance between the lateral edges at the posterior margin of the grinding plate (Fig. 4). Specimens with missing or incomplete landmarks were not measured. Taxa with a *confer* designation were assigned to the particular genus indicated. Width was recorded a second time after completing all initial measurements and the two values averaged for use in evaluation. In general, there was very little difference between first and second measurements, on the order of 1-2 mm. Measurements for each genus were aggregated by

Phase (Phase II, 1400 – 1240 BP; Phase III, 1290 – 720 BP; Phase IV, 500 – 0 BP) and statistical analysis was conducted using Systat 13 and SPSS 13 software.

RESULTS

While 103 scarid LPG specimens in six genera—*Bolbometopon*, *Calotomus*, *Cetoscarus*, *Chlorurus*, *Leptoscarus*, *Scarus*—were measured, only those belonging to *Chlorurus* ($n = 29$) and *Scarus* ($n = 64$) were sufficiently abundant to permit statistical analysis. Therefore, we focus on these two taxa in our reporting. Descriptive statistics and boxplots for LPG width in these genera are presented for Phases II – IV in Table 2 and Figures 5 and 6. Despite the relatively greater abundance of measurable *Scarus* and *Chlorurus* LPGs compared to other parrotfish genera, absolute sample size is small.

Mean LPG width for *Scarus* drops somewhat between Phase II and III, from 6.26 mm to 5.91 mm, before rebounding to 7.11 mm in Phase IV, the final period of site occupation. In contrast, *Chlorurus* mean LPG width exhibits a gradual increase over time, from 5.77 mm in Phase II, to 7.87 mm in Phase III, and finally, 8.03 mm in Phase IV (Fig. 5 and 6). For both *Scarus* and *Chlorurus*, visual inspection of the data combined with Shapiro-Wilk tests reveal non-normality in the datasets for Phase III (*Scarus*: $W = 0.918$, $p = 0.019$, $df = 32$; *Chlorurus*: $W = 0.825$, $p = 0.010$, $df = 14$), with high skewness and kurtosis in some of the samples and the presence of a small number of outliers (Table 2). Sample sizes are small and standard data transformations were only partly effective in correcting issues of non-normality and homoscedasticity, therefore, we decided to bootstrap the samples and assess changes in LPG width using the median as a measure of central tendency.

Chlorurus and *Scarus* datasets were bootstrapped based on 10,000 sampling events to obtain the 80%, 95%, and 99% confidence intervals of the median. Results are presented in Table 3 and Figures 7 and 8. At each level of confidence, overlapping intervals indicate instances where median LPG width does not statistically differ between phases. As can be seen from Figure 7, *Scarus* median LPG width in

Phase III and IV overlaps with that of Phase II at the 80%, 95%, and 99% levels, indicating no statistical difference in these pairwise comparisons. There is no evidence to support size change in *Scarus* due to high predation levels in Phase II at Orrak. Importantly, this indicates that the previously detected, statistically significant decline in *Scarus* relative abundance between Phases II and III (Fitzpatrick et al. 2011) is not accompanied by a size diminution that would be expected if exploitation depression was at the root of observed foraging shifts. It should be noted that 80% and 95% confidence intervals for median LPG width between Phases III and IV do not overlap, suggesting a size increase in *Scarus* in later prehistory. This effect, however, disappears at the 99% confidence level.

For *Chlorurus*, confidence intervals for Phase III overlap with those of Phases IV at the 80% and 95% levels and Phase II and IV at the 99% level (Fig. 8). However, the median width of *Chlorurus* specimens from Phase IV is statistically distinct from that of Phase II even at the 99% confidence level, and indicates that exploited *Chlorurus* specimens become larger over time at Orrak. A Kruskal-Wallis test of mean LPG width supports this finding ($\chi^2 = 11.533$, $p = 0.003$, $df = 2$) showing a moderate to strong effect size ($\eta^2 = 0.41$).

These results suggest a meaningful change in the size of *Chlorurus* at the site over time, at least within the analyzed archaeological sample. The extent to which this reflects an increase in the average size of *Chlorurus* specimens fished by Orrak occupants or is representative of a size increase in *Chlorurus* populations in the waters surrounding Orrak are open questions. Based on the data presented here, *Scarus* does not appear to undergo any significant size change through the course of 1400 years of occupation at Chelechol ra Orrak.

DISCUSSION

Work by several researchers has established the potential for anthropogenic resource depression in Palauan zooarchaeological assemblages. For instance, based on evidence for intensified fishing after 1000 BP of offshore pelagic and outer reef species, such as tuna (Scombridae) and sharks (Carcharhinidae), Ono and Clark (2012) argue residents of Ulong Island increasingly targeted these zones as nearshore resources were depleted. Preliminary evidence for a decrease in mean *Scarus* sp. size between 3100 – 500 cal BP and the rarity of formerly abundant, large tridacnid clams after ca. 2700 BP, provide provisional support for a model of local resource depletion and exploitation depression relatively early in site history. Masse et al. (2006) similarly recorded a size decrease in *Scarus* sp. at Uchularois Cave in the Ngemelis Island Group between AD 640 and AD 1450, concomitant with size declines in the large-eyed bream (*Monotaxis granduoculis*) and *G. gibberulus*. These patterns are attributed to increased fishing/harvest pressure as a result of intensified occupation of the Rock Islands during the stonework village era, ca. AD 1200-1450. Drawing on Nunn's (1999, 2000) hypothesized 'AD 1300 Event', Masse et al. (2006) suggested anthropogenic impacts may have been aggravated by worsening climate conditions associated with the Little Ice Age (ca. AD 1300-1500). However, evidence for the latter is equivocal (Fitzpatrick 2010a; see also Nunn and Hunter-Anderson 2010; Fitzpatrick 2010b), as is the link between human impacts and stonework village construction in the Rock Islands, which has recently been called into question based on recalculations of ΔR that push radiocarbon dates for this period to after AD 1450 (Clark et al. 2006; Petchey and Clark 2010; Snyder et al. 2011).

While the size changes in exploited taxa and prey and patch switching documented for Uchularois Cave and Ulong Island illustrate the potential of prehistoric Palauan populations to significantly impact prey populations, they stand in marked contrast to the lack of evidence for anthropogenic exploitation depression at Chelechol ra Orrak, despite nearly two millennia of sustained use of the latter site. The decline in fishing and increased emphasis on nearshore/littoral molluscan resources (i.e., *G. gibberulus* and *A. striata*) (Giovas et al. n.d.) are not accompanied by an anticipated

size decline in scarid taxa that would make this scenario consistent with a resource depression model and foraging theory expectations. Instead, the results of the analysis conducted here indicate that *Scarus* size remains relatively unchanged over site history, while *Chlorurus* median size actually increases. Since empirically established expectations for Scaridae dictate a length and mass decrease under intensified fishing pressure (Bellwood et al. 2011; Hawkins and Roberts 2003; Vallès and Oxenford 2014), *Chlorurus*' size gain defies easy explanation. Interestingly, *Chlorurus* is not unique in exhibiting this effect at Chelechol ra Orrak; as noted above a size increase over time has been previously documented for humped conch at the site (Giovas et al. 2010).

Why does *Chlorurus* become larger over time at Chelechol ra Orrak? Prior to addressing this question, it should be noted that it is unknown to what extent the size data in the analyzed samples are representative of the archaeological parrotfish population, the prehistoric parrotfish catch, or the natural parrotfish population which inhabited the waters surrounding Orrak in the past. From a theoretical standpoint, given that virtually all forms of fishing are size-selective and that taphonomic processes and archaeological recovery methods tend to bias against smaller specimens we can expect there to be degrees of mismatch between the mean/median size of each of these nested 'populations'. This fact should be borne in mind when interpreting possible causes of size change in archaeofauna since it impacts the scale of inference, that is, the degree to which size data in the measured sample can be extended to make meaningful inferences about taxon size in any of the nested populations under consideration. With this in mind, potential explanations fall into three broad categories, those arising from analytic bias, those related to the fishing behavior of Orrak residents, and those related to ecological variables. Hypothesized explanations for *Chlorurus* size increase should also plausibly account for size stasis in *Scarus*.

The most likely source of analytic bias in this case stems from the potential for smaller, more easily fragmented lower pharyngeal bones to be more readily excluded from the sample of measured

elements. This would not explain, however, why those larger, more robust elements that exceed this size threshold become either more plentiful or larger over time (bearing in mind that scarid NISP and MNI decline in each Phase). Variation in screening methods could also produce an artificial size increase. As noted above, one unit, E2/S4 was screened with nest 1/4" (6.4 mm) and 1/16" mesh (1.6 mm), rather than the standard 1/8" (3.2 mm) employed in all other units. However, no measured LPGs derive from this unit.

Explanations drawing on human behavior are varied, but a few are particularly worth considering. A change in fishing technology involving a shift toward larger gauge nets or traps for instance, would produce a *de facto* size increase in the *Chlorurus* assemblage by reducing the number of smaller individuals captured. Technological changes, however, would be expected to have similar effects on *Scarus* as well, since the same capture technologies would probably have been employed across the parrotfish family. Alternatively, the increase in *Chlorurus* size could relate to prey or patch switching within the genus. Five of the six species of *Chlorurus* recorded in Palauan waters range between 31 to 50 cm in maximum total length, with the sixth, *Chlorurus microrhinus*, reaching 70 cm (Froese and Pauly 2015, FishBase). A targeted shift toward fishing of larger *Chlorurus* species over time could produce the observed size increase in the zooarchaeological assemblage. Similarly, a shift to more distant patches could also yield a size increase in *Chlorurus* through time as such areas would be less impacted by human foraging and would be farther away from protected inshore waters where juveniles tend to be found.

Unfortunately, archaeological data that could inform these hypothesized behavioral explanations is lacking, and the ethnographic record as an alternative line of evidence is somewhat equivocal with respect to the specific prey recognized by Palauans and the technologies used to fish these. In general, the ability to target certain taxa in fishing is based on the intersection of a series of variables, including time of day, month or year; tides; weather; ecological zone; the logistical position of

the fisherman (e.g., boat, swimming, etc.); the communal or solitary nature of the endeavor; fish behavior; bait used; and of course, the fishing gear employed (Butler 1994; Johannes 1981; Keegan 1986; Ono and Addison 2013). A knowledgeable fisherman can exploit these elements to his or her advantage in order to pursue specific taxa, although these taxa do not necessarily correspond directly to Linnaean species. In the case of parrotfish, traditional Palauan fishing knowledge does distinguish a general category of (green) parrotfish (*buitiliang*) that aligns roughly with the scarid family, but at the same time, fishers recognize and target certain species, such as the impressively large green humphead parrotfish¹ (*Bolbometopon muricatus*, or *kemedukl* in Palauan). Notably, however, they also make less fine-grained distinctions for other fish taxa based on such attributes as behavior (Johannes 1981). As an example of the latter, both *Chlorurus stronglycephalus* and *Cetoscarus pulchellus* are known by the same Palauan term *hoa*, meaning “missing”—a reference to their ability to escape a hook (Johannes 1981). For the most part, behavioral similarities (e.g., similar spawning aggregation behavior, nighttime envelopment in a mucoid sac, resistance of the ‘beak’ to hook and line fishing) between many species within the parrotfish family would have meant that traditional Palauan capture techniques for scarids, which involved nets and traps, would have been less discriminatory at the species or genus level (hand spears were also used for scarids, in which case fishermen could have been more selective, but for the relatively small specimens [ca. 150 g] in the Orrak assemblage net and trap fishing is virtually assured). As such, it is unclear that altered fishing strategies, whether the changes involved gear or the particular patches exploited, could produce a size increase in *Chlorurus*, but not *Scarus*. In addition, the fact that fishing as an activity declines overall in favor of the collection of specific molluscan taxa (*G. gibberulus* and *A. striata*) gathered from shallow water and littoral zones, suggests increased foraging of patches closer to, not more distant from the site.

¹ The humphead is the largest parrotfish in the world reaching up to 1.3 m total length and 46 kg (Froese and Pauley 2015). Traditionally, it was most productively targeted after the new moon, using hand spears at night when fish were resting in very shallow water at low tide (Johannes 1981).

It is tempting to assume that the observed size increase in *Chlorurus* represents a size rebound following release from predation pressure due to the decline in fishing in Phase III, after ca. 1290/1240 BP. Since the significant increase (at the 99% CI) in median LPG width is not recorded until Phase IV, i.e., after ca. 500 BP, this leaves the predicament of explaining why it took more than seven centuries for parrotfish stocks to recover following a reduction in fishing activities. It is possible the size increase in Phase III represents an incremental upward adjustment in size that captures this recovery process—particularly if we relax the confidence intervals to 95% where *Chlorurus* median LPG width for Phase II and III do not overlap—and that stock recovery was a slow process spread out over centuries to a millennium. It is difficult to support this conclusion, however, in the absence of any data first demonstrating size reduction as a result of predation pressure.

If mean/median size increase in archaeological *Chlorurus* reflects a genuine trend in the size structure of the natural population in Orrak's marine environment, this pattern could be accounted for by any variable which affects parrotfish growth, survivorship, or recruitment. For instance, growth rate and size in fish have been linked to sea temperatures, availability of food, and the presence of competitors (Blanchard et al. 2005; Shin et al. 2005; Vallès and Oxenford 2014). Amelioration of any of these conditions for *Chlorurus* could, theoretically, foster enhanced rates of growth and larger size in individuals, pushing upwards the mean/median size of the population. This could occur without any changes in mortality rates. Equally possible, a size increase in *Chlorurus* could arise from changes in survivorship that allow individuals to live longer, thereby attaining larger body sizes. This scenario is similar to the rebound effect that would be experienced with the cessation of fishing, but need not be anthropogenic in origin. Release from predation might occur if non-human predators of parrotfish, such as moray eels (Winn and Bardach 1959), declined naturally on the reef and could potentially be corroborated archaeologically if predators can be shown to decrease through time in the archaeofish assemblage. Interestingly, moray eels are present in the Chelechol ra Orrak assemblage and exhibit a

statistically significantly increase in abundance between Phase II and Phase III (Fitzpatrick et al. 2011) (although they are generally less than 3% of total fish NISP or MNI in any period), suggesting that human removal of predators could also potentially drive *Chlorurus* size increase.

Finally, since instances of unusually high juvenile recruitment have been shown to depress the mean size of fish populations due to the flood of smaller individuals entering the population (Vallès and Oxenford 2014), declines in recruitment would be expected to have the opposite effect, shifting the population age structure toward older and larger individuals. While catching fewer parrotfish overall in later prehistory, Orrak fishers would be drawing from this pool of larger individuals, raising the mean/median size of the archaeological *Chlorurus* assemblage. This scenario, however, presents the further complication of determining how and why juvenile recruitment might be negatively impacted—a range of environmental and anthropogenic causes are possible. More problematic, however, is the difficulty involved in archaeological testing of this hypothesis. One final important consideration is that we do not know to what extent size fluctuations might occur naturally in *Chlorurus* or other scarid populations. It may be that size increases or decreases over time are a normal phenomenon even in the absence of human predation.

The results of this study corroborate previous findings for the absence of exploitation depression in the Orrak fish assemblage, but unfortunately leave the pattern of fishing strategies pursued at the site still largely unexplained. While our discussion of possible causes remains inconclusive at this stage, it does present multiple, potentially productive avenues for further investigation into the nature of marine resource exploitation in Palau and the basis for its variability over the long sweep of history. One area in particular that we suggest needs further careful investigation is the possible link between changing marine resource use and larger sociopolitical and economic shifts taking place in the region. Major developments such as the rise of stonework villages and defensive architecture and the advent of pondfield cultivation may have precipitated changes in resource use by altering opportunity

costs and foraging constraints, changing how and where Palauans chose to allocate time and energy in the acquisition of resources. Whitaker and Byrd (2014) have made a similar argument in suggesting that social circumscription, not resource depression, is responsible for the Late Holocene intensification of the small-bodied (ca. 2-3 cm) bivalve *Donax gouldii* and gastropod *Cerithidea californica* along coastal southern California and the San Francisco Bay Area. In their model, aggressive territorial control of coastal resources was precipitated by population packing, reduced mobility, and diminishing ability of women to forage independently of children with ongoing population growth. Increased exploitation of the low-ranking and low-risk *D. gouldii* and *C. californica* is explained by the ready availability of these species within the circumscribed territories and their amenability to collection by the elderly and mothers with small children.

Although beyond the scope of this paper to evaluate in full here, similar dynamics may be responsible for some of the observed change in the Orrak fish and mollusc assemblage in Palau. Table 4 summarizes the major developments in Liston's (2009) chronology of sociopolitical developments in Palau and Snyder et al.'s (2011) reconstruction of settlement systems in relation to landscape use and anthropogenic impacts for comparison against the observed trends in marine resource use at Chelechol ra Orrak after ca. 2400 BP. The onset of fishing declines and shift to piscivorous taxa is roughly correlated with the beginning of the Transitional Era, ca. 1200 – 700 BP, which is associated with a pattern of dispersed villages along the coast, greater settlement of the Rock Islands, and a shift away from use of the interior of larger volcanic islands like Babeldoab. In the centuries following, villages become increasingly nucleated, with evidence for increased territoriality and possible aggression apparent in the construction of stonework villages that incorporate natural landscape features into defensive posturing. While increased proximity to the coast might be expected to encourage fish exploitation, and no doubt did in some instances, at Orrak continued fishing declines are correlated with these developments, and it might be that here, as in the case study investigated by Whitaker and Byrd

(2014), social circumscription driven by greater territoriality and warfare played a causal role. Orrak is separated by a 500 m channel from the large volcanic island of Babeldaob, where dense coastal occupations arose in the period after 1200 BP. The proximity of several such settlements to Chelechol ra Orrak and their influence may explain why the changes in faunal exploitation here are so different from what has been found on Ulong (Ono and Clark 2012) and Ngemelis (Masse et al. 2006).

Interestingly, the intensification of the small-bodied taxa *A. striata* and *G. gibberulus* at Orrak appears to begin before the Transitional Era, that is prior to observed fishing declines, suggesting that explanatory models incorporating women's foraging may be an important component to understanding resource exploitation dynamics in Palau. The ways in which risk, foraging constraints, and tradeoffs are differentially managed by male and female foragers have been studied extensively in traditional societies. In these contexts subsistence shellfishing is frequently conducted by women who benefit by being able to secure a reliable, although less prestigious, lower energetic return food source for their families while simultaneously caring for young children who accompany them (Bird 1999; Bird and Bliege Bird 1997; Bliege Bird 2007; Brown 1970; Codding et al. 2011; Daniels 2009; Meehan 1982; Moss 1993). In Palau, mollusc collection is customarily performed by women, while fishing is the traditional domain of men (Matthews 1992). If this division of labor held in the past, it is possible that the decline in fishing and intensification of molluscs, particularly *A. striata*, may be due to distinct, but not unrelated developments that caused men to largely abandon fishing or shift this activity elsewhere, while women came to increasingly use the Orrak as a location from which to exploit certain molluscan taxa in greater numbers. Evaluation of this possibility will require further investigation and data that address developments in other settlements around Airai Bay and, in particular, the stonework village of Airai just across the sea channel separating Orrak Island from Babeldaob. The past sociopolitical relationship of Airai village to Orrak is unclear, but the latter may have been used as logistical foraging base by Airai residents to conduct fishing and shellfishing forays.

CONCLUSION

The reasons for *Chlorurus*' size increase over time at Chelechol ra Orrak remain elusive. To address this issue multiple lines of evidence, including paleoclimate records and details of population abundance and size structure for other zooarchaeological taxa, need to be combined with increased archaeological understanding of sociopolitical and economic developments occurring more broadly in Airai Bay and their impact on foraging behavior. Future research focused on known, but as yet uninvestigated Rock Island sites in close proximity to Orrak should help to elucidate the extent to which other locations in the immediate area exhibit diachronic patterns in marine foraging similar to those of Chelechol ra Orrak and the processes driving them. Based on the data presented here, it does appear that despite nearly two millennia of fishing at the Chelechol ra Orrak, prehistoric Palauans did not cause exploitation depression in fish populations. One of the more heavily fished taxa, Scaridae does not exhibit evidence for the size declines expected with predation pressure. Instead, our analysis indicates members of the parrotfish genus *Scarus* remain relatively consistent in size over the course of site occupation, while members of *Chlorurus* actually become larger. This pattern stands in marked contrast to evidence for resource depression observed prehistorically at other locations in Palau, especially Uchularois Cave during where a size decline in *Scarus* is recorded for the same approximate time period (Masse et al. 2006). Variability in the record for anthropogenic impacts suggests human ecodynamics at any given location are dependent on site specific processes influenced by local environmental and cultural factors and should inject a cautionary note about always assuming foraging of island environments will be unsustainable.

Elsewhere we have argued that the complexity and multi-scalar nature of human-environment interactions is too easily overlooked and may lead to premature identification of anthropogenic environmental impacts (Fitzpatrick et al 2011; Giovas 2013; Giovas et al. 2010). The Chelechol ra Orrak

zooarchaeological assemblage illustrates this possibility well. The decline in large bodied fish, overall drop in fishing, and increase in small, low-ranking inshore/littoral molluscan taxa over time are consistent with the prey and patch switching that accompanies resource depression. Deeper investigation into this issue employing scarid size analysis refutes this proposition and verifies our previous finding for an absence of resource depression at Orrak based on static fish richness and the persistence of higher trophic level fish in the catch (Fitzpatrick et al. 2011). The Orrak case thus demonstrates the potential to overlook other processes of interest when certain patterns in the faunal record are too readily assigned to human foraging pressure prior to fully vetting alternative explanations and echoes other recent work highlighting the impact of analytical scale on interpretations of resource depression (e.g., Otaola et al. 2015).

While it may yet be that the foraging shifts seen at Orrak arise from environmental impacts initiated by humans themselves, perhaps through a series of ecological cascades (see discussion in Giovas et al. 2010), without empirical foundation in multiple archaeological indicators, this argument cannot be made. We suggest that premature identification of resource depression, that is, conclusions based on equivocal or singular evidence (e.g., diet-breadth expansion alone), can distort our understanding of human paleoecology and the nuanced complexity of human-environment interactions in the past. With mounting evidence for long-term sustainable use of marine resources from a variety of insular and coastal settings (Carder et al. 2007, 2012; Giovas 2013; Giovas et al. 2013; Grouard 2001; Whyte et al. 2005), it is clear that humans did not necessarily cut a swath of ecological destruction wherever they went in the past. Viewing anthropogenic environmental impacts along a continuum of severity and incorporating models of ecosystem resilience (Campbell and Butler 2010; Folke et al. 2004; Nyström et al. 2000; Rick 2011; Reitz 2014)—recognizing animals in the archaeological record bring to bear their own ecology and life history variables—frees us from exclusive preoccupation with whether effects such as resource depression can be detected, and instead allows us to focus on more productive

questions concerning the nature and scale of those impacts, the processes through which they arose, and their long-term consequences.

ACKNOWLEDGEMENTS

This research was supported by grants to Fitzpatrick from the National Science Foundation (SBR-0001531), the Center for Asian and Pacific Studies at the University of Oregon, and a Sigma Xi Grant-in-Aid for Research. We wish to thank the Palau Bureau of Arts & Culture for their long-time and ongoing support of research in Palau, as well as Cai Yan and Dick Drennan who provided statistical software assistance. Thanks go to reviewers whose comments helped to clarify various aspects of the paper. A portion of this research was conducted by Giovas while a Visiting Scholar with the Center for Comparative Archaeology at the University of Pittsburgh.

References

- Allen, M.S., 1992. Temporal variation in Polynesian fishing strategies: The Southern Cook Islands in regional perspective. *Asian Perspectives* 31, 183-204.
- Allen, M.S., 2002. Resolving long-term change in Polynesian marine fisheries. *Asian Perspectives* 41, 195-202.
- Allen, M.S., 2012. Molluscan foraging efficiency and patterns of mobility amongst foraging agriculturalists: a case study from northern New Zealand. *Journal of Archaeological Science* 39, 295-307.
- Anderson, A., 2013. The antiquity of sustained offshore fishing. *Antiquity* 87, 879-885.
- Ash, J., Faulkner, P., Brady, L.M., Rowe, C., 2013. Morphometric reconstructions and size variability analysis of the surf clam, *Atactodea* (=Paphies) *striata*, from Muralag 8, southwestern Torres Strait, northern Australia. *Australian Archaeology* 77, 82-93.
- Bellwood, D.R., 1994. A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidei), with a revision of genera. *Records of the Australian Museum Supplement* 20.
- Bellwood, D.R., 2001. Scaridae. In: Carpenter, K.E., Neim, V.H. (Eds.), *The Living Marine Resources of the Western Central Pacific, Volume 6 Bony Fishes Part IV (Labridae to Latimariidae) Estuarine Crocodiles, Sea Turtles, Sea Snakes and Marine Mammals*. Food and Agricultural Organization of the United Nations, Rome, pp. 3468-3492.
- Bellwood, D.R., Hoey, A.S., Hughes, T.P., 2011. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B*. doi:10.1098/rspb.2011.1906.
- Binford, L.R., 1978. *Nunamiut Ethnoarchaeology*. Academic Press, New York.
- Binford, L.R., 1981. *Bones: Ancient Men and Modern Myths*. Academic Press, New York.
- Bird, R., 1999. Cooperation and conflict: the behavioral ecology of the sexual division of labor. *Evolutionary Anthropology* 8, 65-75.
- Bird, D.W., Bliege Bird, R., 1997. Contemporary shellfish gathering strategies among the Meriam of the Torres Strait Islands, Australia: testing predictions of a central place foraging model. *Journal of Archaeological Science* 24, 39-63.
- Bird, D.W., Richardson, J.L., Veth, P.M., Barham, A.J., 2002. Explaining shellfish variability in middens on the Meriam Islands, Torres Strait, Australia. *Journal of Archaeological Science* 29, 457-469.
- Blanchard, J.L., Dulvy, N.K., Jennings, S., Ellis, J.R., Pinnegar, J.K., Tidd, A., Kell, T.L., 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *Journal of Marine Science* 62, 405-411.
- Blick, J., 2007. Pre-Columbian impact on terrestrial, intertidal, and marine resources, San Salvado, Bahamas (A.D. 950-1500). *Journal for Nature Conservation* 15, 174-183.
- Bliege Bird, R., 2007. Fishing and the sexual division of labor among the Meriam. *American Anthropologist* 109, 442-451.
- Broughton, J.M., 1994. Declines in mammalian foraging efficiency during the late Holocene, San Francisco Bay, California. *Journal of Archaeological Science* 13, 371-401.
- Broughton, J.M., 1995. Resource depression and intensification during the late Holocene, San Francisco Bay: Evidence from the Emeryville Shellmound vertebrate fauna. PhD Dissertation, University of Washington, Seattle.
- Broughton, J.M., 1997. Widening diet breadth, declining foraging efficiency, and prehistoric harvest pressure: Ichthyofaunal evidence from the Emeryville Shellmound, California. *Antiquity* 71, 845-862.

- Broughton, J.M., 2002. Prey spatial structure and behavior affect archaeological tests of optimal foraging models: Examples from the Emeryville Shellmound vertebrate fauna. *World Archaeology* 34, 60-83.
- Broughton, J.M., Cannon, M.D., Bartelink, E.J., 2010. Evolutionary ecology, resource depression, and niche construction theory: Applications to central California hunter-gatherers and Mimbres-Mogollon agriculturists. *Journal of Archaeological Method and Theory* 17, 371-421.
- Brown, J.K., 1970. A note on the division of labor by sex. *American Anthropologist* 72, 1073-1078.
- Butler, V.L., 1994. Fish feeding behaviour and fish capture: the case for variation in Lapita fishing strategies. *Archaeology in Oceania* 29, 81-90.
- Butler, V.L., 2001. Changing fish use on Mangaia, Southern Cook Islands: resource depression and the prey choice model. *International Journal of Osteoarchaeology* 11, 88-100.
- Campbell, B., Braje, T.J., 2015. Estimating California mussel (*Mytilus californianus*) size from hinge fragments: A methodological application in historical ecology. *Journal of Archaeological Science* 58, 167-174.
- Campbell, G., 2008. Beyond means to meaning: Using distributions of shell shapes to reconstruct past collecting strategies. *Environmental Archaeology* 13, 111-121.
- Campbell, S.K., Butler, V.L., 2010. Archaeological evidence for resilience of Pacific Northwest salmon populations and the socioecological system over the last ~7,500 years. *Ecology and Society* 15. <http://www.ecologyandsociety.org/vol15/iss1/art17/>.
- Cannon, M.D., 2000. Large mammal relative abundance in Pithouse and Pueblo period archaeofaunas from Southwestern New Mexico: resource depression among the Mimbres-Mogollon? *Journal of Anthropological Archaeology* 19, 317-347.
- Cannon, M.D., 2003. A model of central place forager prey choice and an application to faunal remains from the Mimbres Valley. *Journal of Anthropological Archaeology* 22, 1-25.
- Carder, N., Crock, J.G., 2012. A pre-Columbian fisheries baseline from the Caribbean. *Journal of Archaeological Science* 34, 588-599.
- Carder, N., Reitz, E.J., Crock, J.G., 2007. Fish communities and populations during the post-Saladoid period (AD 600/800-1500), Anguilla, Lesser Antilles. *Journal of Archaeological Science* 34, 588-599.
- Charnov, E.L., Orians, G.H., Hyatt, K., 1976. Ecological implications of resource depression. *The American Naturalist* 110, 247-259.
- Claassen, C., 1998. *Shells*. Cambridge University Press, Cambridge.
- Clark, G.R., 2005. A 3000-year culture sequence from Palau, western Micronesia. *Asian Perspectives* 44, 349-380.
- Codding, B.F., Bird, D.W., 2015. Behavioral ecology and the future of archaeological science. *Journal of Archaeological Science* 56, 9-20.
- Codding, B.F., Bliege Bird, R., Bird, D.W., 2011. Provisioning offspring and others: risk-energy trade-offs and gender differences in hunter-gatherer foraging strategies. *Proceedings of the Royal Society* 282. doi:10.1098/rspb.2010.2403.
- Codding, B.F., Porcasi, J.F., Jones, T.L., 2010. Explaining prehistoric variation in the abundance of large prey: a zooarchaeological analysis of deer and rabbit hunting along the Pecho Coast of California. *Journal of Anthropological Archaeology* 29, 47-61.
- Codding, B.F., Whitaker, A., Bird, D.W., 2014. Global patterns in the exploitation of shellfish. *Journal of Island and Coastal Archaeology* 9, 145-149.

- Colin, P.L., 2009. Marine Environments of Palau. Indo-Pacific Press, San Diego.
- Cramp, L.J.E., Jones, J., Sheridan, A., Smyth, J., Whelton, H., Mulville, J., Sharples, N., Evershed, N.P., 2014. Immediate replacement of fishing with dairying by the earliest farmers of the northwest Atlantic archipelagos. *Proceedings of the Royal Society B* 281: 20132372.
- Daniels, P.S., 2009. A Gendered Model of Prehistoric Resource Depression: A Case Study on. PhD Dissertaion, Univeristy of Washington, Seattle.
- Donaldson, T.J., 2002. High islands versus low islands: a comparison of fish faunal composition of the Palau Islands. *Environmental Biology of Fishes* 65, 241-248.
- Donaldson, T.J., Myers, R.F., 2002. Insular freshwater fish faunas of Micronesia: Patterns of species richenss and similarity. *Environmental Biology of Fishes* 65, 139-149.
- Ebert, T.A., Hernández, J.C., Clemente, S., 2014. Annual reversible plasticity of feeding structures: cyclical changes of jaw allometry in a sea urchin. *Proceedings of the Royal Society B* 281, 20132284.
- Erlandson, J.M., Braje, T.J., Rick, T.C., Kennett, D.J., Dwyer, N., Ainis, A.F., Vellanoweth, R.L., Watts, J., 2011. 10,000 years of human predation and size changes in the owl limpet (*Lottia gigantea*) on San Miguel Island, California. *Journal of Archaeological Science* 38, 1127-1134.
- Erlandson, J.M., Rick, T.C., Braje, T.J., Steinberg, A., Vellanoweth, R.L., 2008. Human impacts on on ancient shellfish: a 10,000 year record from San Miguel Island, California. *Journal of Archaeological Science* 35, 2144-2152.
- Faulkner, P., 2009. Focused, intense and long-term: evidence for granular ark (*Anadara granosa*) exploitation from late Holocene shell mounds of Blue Mud Bay, northern Australia. *Journal of Archaeological Science* 36, 821-834.
- Fenberg, P.B., Roy, K. 2007. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology* 17, 209-220.
- Fenberg, P.B., Roy, K., 2012. Anthropogenic harvesting pressure and changes in life history: Insights from a rocky intertidal limpet. *American Naturalist* 180, 200-210.
- Fitzpatrick, S.M., 2003a. Early Human Burials in the Western Pacific: Evidence for a c.3000 year old Occupation on Palau. *Antiquity* 77, 719-731.
- Fitzpatrick, S.M., 2003b. Stones of the Butterfly: An Archaeological Investigation of Yapese Stone Money Quarries in Palau, Western Micronesia. PhD Dissertation, University of Oregon, Eugene.
- Fitzpatrick, S.M., 2010a. A critique of the 'AD 1300 Event', with particular reference to Palau. *Journal of Pacific Archaeology* 1, 168-173.
- Fitzpatrick, S.M., 2010b. Defending the defensible or offending the sensible? A response to Nunn & Hunter-Anderson. *Journal of Pacific Archaeology* 2(1), 100-105.
- Fitzpatrick, S.M., Kataoka, O., 2005. Prehistoric fishing in Palau, Micronesia, evidence from the Northern Rock Islands. *Archaeology in Oceania* 40, 1-13.
- Fitzpatrick, S.M., Nelson, G., 2008. From limestone caves to concrete graves: 3000 years of mortuary practice in the Palauan archipelago of western Micronesia. *International Journal of Osteoarchaeology* 18, 439-457.
- Fitzpatrick, S.M., Giovas, C.M., Kataoka, O., 2011. Temporal trends in prehistoric fishing in Palau, Micronesia over the last 1500 years. *Archaeology in Oceania* 46, 6-16.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution and Systematics* 35, 557-581.

- Froese, R., Pauly, D., 2015. www.fishbase.org, version (04/2015).
- Giovas, C.M., 2013. Foraging Variability in the Prehistoric Caribbean: Multiple Foraging Optima, Resource Use, and Anthropogenic Impacts on Carriacou, Grenada. PhD Dissertation, University of Washington, Seattle.
- Giovas, C.M., Clark, M., Fitzpatrick, S.M., Stone, J., 2013. Intensifying collection and size increase of the tessellated nerite snail (*Nerita tessellata*) at the Coconut Walk Site, Nevis, northern Lesser Antilles, AD 890-1440. *Journal of Archaeological Science* 40, 4024-4038.
- Giovas, C.M., Fitzpatrick, S.M., Clark, M., Abed, M., 2010. Evidence for size increase in an exploited mollusc: humped conch (*Strombus gibberulus*) at Chelechol ra Orrak, Palau from ca. 3000 – 0 BP. *Journal of Archaeological Science* 37, 2788-2798.
- Giovas, C.M., Fitzpatrick, S.M., Caruso, A., n.d. Prehistoric Mollusc Exploitation at the Chelechol ra Orrak Rockshelter (Palau, Micronesia) Demonstrates Intensification of a Nearshore Clam (*Atactodea striata*). Manuscript in revision.
- Gremillion, K.J., Barton, L., Piperno, D.R., 2014. Particularism and the retreat from theory in the archaeology of agricultural origins. *Proceedings of the National Academy of Sciences* 111 (17), 6171-6177.
- Grouard, S., 2001. Faunal remains associated with Late Saladoïd and Post- Saladoïd occupations at Anse à la Gourde, Guadeloupe, West Indies, preliminary results. *Archaeofauna* 10, 71-98.
- Hawkins, J.P., Roberts, C.M., 2003. Effects of fishing on sex-changing Caribbean parrotfishes. *Biological Conservation* 115, 213-226.
- Hilborne, R., Minte-Vera, C.V., 2008. Fisheries-induced changes in growth rates in marine fisheries: are they significant? *Bulletin of Marine Science* 83, 95-105.
- Jerardino, A., 1997. Changes in shellfish species composition and mean shell size from a Late-Holocene record of the west coast of South Africa. *Journal of Archaeological Science* 24, 1031-1044.
- Johannes, R.E., 1981. Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia. University of California Press, Berkely.
- Jones, E.L., 2004. Dietary evenness, prey choice, and human-environment interactions. *Journal of Archaeological Science* 31, 307-317.
- Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, B.S., Brander, K., Ernande, B., Gårdmark, A.G., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.D., 2007. Managing evolving fish stocks. *Science* 318, 1247-1248.
- Kaplan, H., Hill, K., 1992. The evolutionary ecology of food acquisition. In: Smith, E.A., Winterhalder, B. (Eds.), *Evolutionary Ecology and Human Behavior*. Aldine de Gruyter, New York, pp. 167-201.
- Keegan, W.F., 1986. The ecology of Lucayan Arawak fishing practices. *American Antiquity* 51, 816-825.
- Krigbaum, J., Fitzpatrick, S.M., 2009. Reconstructing Palau Paleodiet through Stable Isotope Ratio Analysis of Human Bone. Paper presented at the Pacific Archaeology 2009 Conference, Palau, Micronesia.
- Kuparinen, A., Merilä, J., 2007. Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution* 22, 652–659.
- Kuparinen, A., Hutchings, J.A., 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proceedings of the Royal Society B* 279, 2571-2579.
- Lambrides, A.B.J., Weisler, M.I., 2013. Assessing protocols for identifying Pacific island archaeological fish remains: the contribution of vertebrae. *International Journal of Osteoarchaeology* 25, 838-848. doi: 10.1002/oa.2354.

- Lambrides, A.B.J., Weisler, M.I., 2015. Applications of vertebral morphometrics in Pacific Island archaeological fishing studies. *Archaeology in Oceania* 50, 53-70.
- Law, R., 2007. Fisheries-induced evolution: present status and future directions. *Marine Ecology Progress Series* 335, 271–277.
- Law, R., Stokes, K., 2005. Evolutionary impacts of fishing on target populations. In: Norse, E.D., Crowder, L.B (Eds.) *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, Washington, D.C., pp. 232-246.
- Leach, F.B., Boocock, A.S., 1993. Prehistoric Fish Catches in New Zealand. *British Archaeological Reports International Series* 584. Harian Books Ltd, Oxford.
- Leach, F.B., Davidson, J., 2001. The use of size-frequency diagrams to characterize prehistoric fish catches and to assess human impact on inshore fisheries. *International Journal of Osteoarchaeology* 11, 150-162.
- Lech, V., Betts, M.W., Maschner, H.G.D., 2011. An analysis of seal, sea lion, and sea otter consumption patterns on Sanak Island, Alaska: an 1800-year record on Aleut consumer behavior. In: Braje, T.J., Rick, T.C. (Eds.), *Human Impacts on Seals, Sea Lions and Otters: Integrating Archaeology and Ecology in the Northeast Pacific*. University of California Press, Berkeley, pp. 111-128.
- Levitan, D.R., 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. *Marine Biology* 111, 431-435.
- Liston, J., 2009. Cultural chronology of earthworks in Palau, western Micronesia. *Archaeology in Oceania* 44, 56-73.
- Lupo, K.D., 2007. Evolutionary foraging models in zooarchaeological analysis: recent applications and future challenges. *Journal of Archaeological Research* 15, 143-189.
- Lyman, R.L., 2008. *Quantitative Paleozoology*. Cambridge University Press, Cambridge.
- Lyman, R.L., Cannon, K., (Eds.), 2004. *Zooarchaeology and Conservation Biology*. University of Utah Press, Salt Lake City.
- Mannino, M.A., Thomas, K.D., 2001. Intensive Mesolithic exploitation of coastal resources? Evidence from a shell deposit on the Isle of Portland (Southern England) for the impact of human foraging on populations of intertidal rocky shore molluscs. *Journal of Archaeological Science* 28, 1101-1114.
- Mannino, M.A., Thomas, K.D., 2002. Depletion of a resource? The impact of prehistoric human foraging on intertidal mollusc communities and its significance for human settlement, mobility and dispersal. *World Archaeology* 33, 452-474.
- Masse, W.B., Liston, J., Carucci, J., Athens, J.S., 2006. Evaluating the effects of climate change on environment, resources depletion, and culture in the Palau Islands between AD 1200 and 1600. *Quaternary International* 151, 133-143.
- Matthews, E., 1992. *The role of women in the fisheries of Palau*. MSc Thesis, Corvallis, Oregon, Oregon State University.
- Meehan, B., 1982. *Shell Bed to Shell Midden*. Australian Institute of Aboriginal Studies, Canberra.
- Milner, A., Barrett, J., Welsh, J., 2007. Marine resource intensification in Viking Age Europe: The molluscan evidence from Quoygrew, Orkney. *Journal of Archaeological Science* 34, 1461-1462.
- Morrison, A., Addison, D.J., 2009. Examining causes and trends in marine trophic level change: 1500 years of fish exploitation at Fatu-ma-Futi, Tutuila Island, American Sāmoa. *Journal of Island and Coastal Archaeology* 4, 177-194.

- Moss, M., 1993. Shellfish, gender, and status on the Northwest Coast: reconciling archaeological, ethnographic, and ethnohistoric records of the Tlingit. *American Anthropologist* 95, 631-652.
- Myers, R.F., 1999. *Micronesian Reef Fishes*. 3rd. Coral Graphics, Barrigada, Guam.
- Nagaoka, L., 1994. Differential recovery of Pacific Island fish remains: Evidence from the Moturakau. *Asian Perspectives* 33, 1-17.
- Nagaoka, L., 2000. *Resource Depression, Extinction, and Subsistence Change in Southern New Zealand*. PhD Dissertation, University of Washington, Seattle.
- Nagaoka, L., 2001. Using diversity indices to measure changes in prey choice at the Shag River Mouth site, New Zealand. *International Journal of Osteoarchaeology* 11, 101-111.
- Nagaoka, L., 2002. The effects of resource depression on foraging efficiency, diet breadth, and patch use in Southern New Zealand. *Journal of Anthropological Archaeology* 21, 419-442.
- Nagaoka, L., 2005. Declining foraging efficiency and moa carcass exploitation in southern New Zealand. *Journal of Archaeological Science* 32, 1328-1338.
- Nelson, G.C., Fitzpatrick, S.M., 2006. Preliminary investigations of the Chelechol ra Orrak cemetery, Republic of Palau: I, skeletal biology and paleopathology. *Anthropological Science* 113, 1-12.
- Nunn, P.D., 1999. *Environmental Change in the Pacific Basin: Chronologies, Causes, and Consequences*. Wiley, London.
- Nunn, P.D., 2000. Illuminating sea-level fall around AD 1220-1510 (730 – 440 cal yr BP) in the Pacific islands: implication for environmental change and cultural transformation. *New Zealand Geographer* 56, 46-54.
- Nunn, P.D., Hunter-Anderson, R., 2010. Defending the Defensible: a Rebuttal of Scott Fitzpatrick's (2010) Critique of the AD 1300 Event Model with Particular Reference to Palau. *Journal of Pacific Archaeology* 2, 92-99.
- Nyström, M., Folde, C., Moberg, F., 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends in Evolutionary Ecology* 15, 413-417.
- Olmo, R.K., 2013. New flesh for old bones: using modern reef fish to understand midden remains from Guam, Mariana Islands. In: Ono, R., Morrison, A., Addison, D. (Eds.) *Prehistoric Marine Resource Use in the Indo-Pacific Region*. Terra Australis 39. ANU E Press, Canberra, pp. 1-33.
- Ono, R., Addison, D., 2013. Historical ecology and 600 years of fish use on Atafu Atoll, Tokelau. In: Ono, R., Morrison, A., Addison, D. (Eds.) *Prehistoric Marine Resource Use in the Indo-Pacific Region*. Terra Australis 39. ANU E Press, Canberra, pp. 59-83.
- Ono, R., Clark, G., 2012. A 2500-year record of marine resource use on Ulong Island, Republic of Palau. *International Journal of Osteoarchaeology* 22, 637-654.
- Ono, R., Intoh, M., 2011. Island of pelagic fishermen: temporal changes in prehistoric fishing on Fais, Micronesia. *Journal of Island and Coastal Archaeology* 6, 255-286.
- Otaola, C., Wolverton, S., Giardina, M.A., Neme, G., 2015. Geographic scale and zooarchaeological analysis of Late Holocene foraging adaptations in western Argentina. *Journal of Archaeological Science* 55, 16-25.
- Petchey, F., Clark, G., 2010. A marine reservoir correction value (ΔR) for the Palauan Archipelago: Environmental and oceanographic considerations. *Journal of Island and Coastal Archaeology* 5, 236-252.
- Poutiers, J.M., 1998a. Bivalves (Acephala, Lamellibranchia, Pelecypoda). In: Carpenter, K.E., Neim, V.H. (Eds.), *The Living Marine Resources of the Western Central Pacific*. Volume 1: Seaweeds, Corals,

- Bivalves and Gastropods. Food and Agricultural Organization of the United Nations, Rome, pp. 123-362.
- Poutiers, J.M., 1998b. Gastropods. In: Carpenter, K.E., Neim, V.H. (Eds.), The Living Marine Resources of the Western Central Pacific. Volume 1: Seaweeds, Corals, Bivalves and Gastropods. Food and Agricultural Organization of the United Nations, Rome, pp. 363-648.
- Prokop, F.P., Hawkins, B.T., Wilson, W., 2006. The Australian Fishing Guide. Australian Fishing Network, Croydon, Victoria.
- Reitz, E.J., 2014. Continuity and resilience in the central Georgia Bight (USA) fishery between 2760 BC and AD 1580. *Journal of Archaeological Science* 41, 716-731.
- Reitz, E.J., Wing, E.S., 2008. *Zooarchaeology*. 2nd. Cambridge University Press, Cambridge.
- Reitz, E.J., Quitmyer, I.R., Hale, H.S., Scudder, S.J., Wing, E.W., 1987. Application of allometry to zooarchaeology. *American Antiquity* 52, 304-317.
- Reznick, D.N., Bryant, M.J., Bashey, F., 2002. r and K-selection revisited: the role of population regulation in life-history evolution. *Ecology* 83, 1509-1520.
- Reznick, D.N., Bryga, H., Endler, J.A., 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346, 357-359.
- Reznick, D.N., Shaw, F.H., Rodd, F.H., Shaw, R.G., 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275, 1934-1937.
- Rick, T.C., 2011. Weathering the storm: coastal subsistence and ecological resilience on Late Holocene Santa Rosa Island, California. *Quaternary International* 239, 139-146.
- Roy, K., Collins, A.G., Becker, B.J., Begovic, E., Engle, J.M., 2003. Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecology Letters* 6, 205-211.
- Seymour, K., 2004. Empirical data for archaeological fish weight analyses. In: Emery, K.F. (Ed.), *Maya Zooarchaeology: New Directions in Methods and Theory*. University of California, Los Angeles Monograph 51. Cotsen Institute of Archaeology, Los Angeles, pp. 159-173.
- Shin, Y.J., Rochet, M.-J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science* 64, 384-396.
- Smith, B.D., 2015. A comparison of niche construction theory and diet breadth models as explanatory frameworks for the initial domestication of plants and animals. *Journal of Archaeological Research* 23, 216-262.
- Smith, C.B., Ebert, C.E., Kennett, D.J., 2014. Human ecology of shellfish exploitation at a prehistoric fishing-farming village on the Pacific coast of Mexico. *Journal of Island and Coastal Archaeology* 9, 183-202.
- Snyder, D.M., Masse, W.B., Carucci, J., 2011. Dynamic settlement, landscape modification, resource utilisation and the value of oral traditions in Palauan archaeology. In: Liston, J., Clark, G., Alexander, D. (Eds.), *Pacific Island Heritage: Archaeology, Identity and Community*. Terra Australis 35. ANU E Press, Canberra, pp. 155-180.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton, N.J.
- Thakar, H.B., 2011. Intensification of shellfish exploitation: evidence of species-specific deviation from traditional expectations. *Journal of Archaeological Science* 38, 2596-2605.
- Thomas, K.D., 2015. Molluscs emergent, part II: themes and trends in the scientific investigation of molluscs and their shells as past human resources. *Journal of Archaeological Science* 56, 159-167.

- Tupper, M., Tan, M.K., Tan, S.L., Radius, M.J., Abdullah, S., 2015. ReefBase: A Global Information System on Coral Reefs. <http://www.reefbase.org>. Last accessed December 8, 2015.
- Turrero, P., Hórreo, J.L., López, B., Arbizu, I.G., Pola, M., Gracia-Vázquez, E., 2013. Chronological changes in Upper Paleolithic fisheries revealed by museum archival material. *Palaios* 28, 228-232.
- Turrero, P., García-Vázquez, E., García de Leaniz, C., 2014. Shrinking fish: comparisons of prehistoric and contemporary salmonids indicating decreasing size at age across millennia. *The Royal Society Open Science* 1, 140026.
- Underwood, A.J., 1976. Food competition between age-classes in the intertidal *Nerita atramentosa* Reeve (Gastropoda, Prosobranchia). *Journal of Experimental Marine Biology and Ecology* 23, 145-154.
- Vallès, H., Oxenford, H.A., 2014. Parrotfish size: a simple yet useful alternative indicator of fishing effects on Caribbean reefs? *PLoS One* 9, e86291.
- Videler, H., Geertjes, G.J., Videler, J.J., 1999. Biochemical characteristics and antibiotic properties of the mucous envelope of the queen parrotfish. *Journal of Fish Biology* 54, 1124-1127.
- Vogel, Y., 2005. Ika. MA Thesis, University of Otago, Dunedin.
- Vogel, Y., Anderson, A.J., 2012. Prehistoric fishing on Rapa Island. In: Anderson, A.J., Kennett, D.J. (Eds.), *Taking the High Ground: The Archaeology of Rapa, a Fortified Island in Remote Polynesia*. Terra Australis 37. ANU E Press, Canberra, pp. 115-133.
- Whitaker, A.R., 2010. Prehistoric behavioral depression of cormorant (*Phalacrocorax* spp.) on the northern California coast. *Journal of Archaeological Science* 37, 2562-2571.
- Whitaker, A.R., Byrd, B.F., 2014. Social circumscription, territoriality, and the Late Holocene intensification of small-bodied shellfish along the California Coast. *Journal of Island and Coastal Archaeology* 9, 150-168.
- Whyte, T.R., Berman, M.J., Gnivecki, P.L., 2005. Vertebrate archaeofaunal remains from the Pigeon Creek Site, San Salvador Island, the Bahamas. In: Buckner, S.D., McGrath, T.A. (Eds.), *Proceedings of the Tenth Symposium on the Natural History of the Bahamas*. Gerace Research Center, Ltd., San Salvador, Bahamas, pp. 165-177.
- Wing, E.S., 2001. The sustainability of resources used by Native Americans on four Caribbean islands. *International Journal of Zooarchaeology* 11, 14-23.
- Wing, E.S., Wing, S.R., 1995. Prehistoric Ceramic Age adaptation to varying diversity of animal resources along the West Indian Archipelago. *Journal of Ethnobiology* 15, 119-148.
- Winn, H.E., Bardach, J.E., 1959. Differential food selection by moray eels and a possible role of the mucous envelope of parrot fishes in reduction of predation. *Ecology* 40, 296-298.
- Wolverton, S., Lyman, R.L. (Eds.), 2012. *Conservation Biology and Applied Zooarchaeology*. University of Arizona Press, Tuscon.
- Wolverton, S., Nagaoka, L., Densmore, J., Fullerton, B., 2008. White-tailed deer harvest and pressure and within bone nutrient exploitation during the mid to late Holocene in southeast Texa, USA. *Before Farming* 2, article 3.
- Wolverton, S., Nagaoka, L., Don, P., Kennedy, J.H., 2012. On behavioral depression in white-tailed deer. *Journal of Archaeological Method and Theory* 19, 462-489.
- Zeder, M.A., 2012. The Broad Spectrum Revolution at 40: resource diversity, intensification, and an alternative to optimal foraging explanations. *Journal of Anthropological Archaeology* 31, 241-264.

- Zeder, M.A., 2014. Alternative to faith-based science. *Proceedings of the National Academy of Sciences, USA* 111 (28), E2827.
- Zeder, M.A., 2015. Core questions in domestication research. *Proceedings of the National Academy of Sciences* 112(11), 3191-3198.
- Zohar, I., Dayan, T., Spanier, E., 1997. Predicting grey triggerfish body size from bones. *International Journal of Osteoarchaeology* 7, 150-156.

Table and Figure Captions

Table 1 Quantification of fish remains from Chelechol ra Orrak (after Fitzpatrick et al. 2011).

Table 2 Descriptive statistics for *Scarus* and *Chlorurus* lower pharyngeal grinder width (mm).

Table 3 Bootstrap results for *Scarus* and *Chlorurus* lower pharyngeal grinder width (mm) based on 10,000 sampling events.

Table 4 Chronological framework of sociopolitical developments, settlement patterning, and landscape use in Palau in relation to marine resource exploitation trends recorded at Chelechol ra Orrak, as summarized by Liston (2009) and Snyder et al. (2011).

Figure 1 Map of Island Southeast Asia and Micronesia showing the location of Palau

Figure 2 Map of Palau showing the location of the Chelechol ra Orrak site on Orrak Island.

Figure 3 Map of Chelechol ra Orrak site illustrating location of excavation units.

Figure 4 Left: the lower pharyngeal grinder of a modern *Scarus* specimen illustrating the measurement points for the maximum width of the posterior dental plate (photo by C.M. Giovas); right: an archaeological *Scarus* lower pharyngeal grinder from Chelechol ra Orrak illustrating the typical preservation level of the dental plate width dimension in measured specimens (photo by M. Clark).

Figure 5 Box and whisker plot for mean lower pharyngeal dental plate width of *Scarus* sp. at Chelechol ra Orrak.

Figure 6 Box and whisker plot for mean lower pharyngeal dental plate width of *Chlorurus* sp. at Chelechol ra Orrak.

Figure 7 Bootstrapped confidence intervals for median *Scarus* lower pharyngeal grinder plate width at 80%, 95%, and 99% confidence levels.

Figure 8 Bootstrapped confidence intervals for median *Chlorurus* lower pharyngeal grinder plate width at 80%, 95%, and 99% confidence levels.

Table 1

Taxon	Common Name	Phase II (Layer 7)				Phase III (Layers 4-6)			
		NISP	%NISP	MNI	%MNI	NISP	%NISP	MNI	%MNI
Chondrichthyes (cartilaginous fishes)									
Elasmobranchii sharks and rays		74	3.6	6	2.0	41	10.5	8	7.5
Actinopterygii (bony ray-finned fishes)									
Acanthuridae	surgeonfishes	371	18.2	15	5.0	47	12.0	5	4.7
Balistidae	leatherjackets	113	5.5	26	8.7	27	6.9	9	8.4
Belonidae	needlefishes	0	0.0	0	0.0	1	0.3	1	0.9
Carangidae	jacks	12	0.6	4	1.3	3	0.8	3	2.8
Diodontidae	porcupinefishes	111	5.4	3	1.0	22	5.6	4	3.7
Haemulidae	grunts	1	0.0	1	0.3	1	0.3	1	0.9
Holocentridae	squirrelfishes	31	1.5	8	2.7	10	2.6	6	5.6
Kyphosidae	sea chubs	1	0.0	1	0.3	0	0.0	0	0.0
Labridae	wrasses	182	8.9	39	13.1	34	8.7	10	9.3
Lethrinidae	emperors	168	8.2	35	11.7	21	5.4	10	9.3
Lutjanidae	snappers	16	0.8	7	2.3	7	1.8	3	2.8
Mugilidae	mulletts	0	0.0	0	0.0	0	0.0	0	0.0
Mullidae	goatfishes	42	2.1	13	4.4	8	2.0	3	2.8
Muraenidae	moray eels	15	0.7	8	2.7	10	2.6	3	2.8
Ostraciidae	boxfishes	79	3.9	3	1.0	9	2.3	4	3.7
Scaridae	parrotfishes	639	31.4	103	34.6	103	26.3	23	21.5
Scorpaenidae	scorpionfishes	68	3.3	2	0.7	0	0.0	0	0.0
Serranidae	sea basses	109	5.3	21	7.0	46	11.8	13	12.1
Siganidae	rabbitfishes	6	0.3	3	1.0	1	0.3	1	0.9
Total Identified		2038		298		391		107	

Table 2

	<i>Scarus</i>			<i>Chlorurus</i>		
	Phase II	Phase III	Phase IV	Phase II	Phase III	Phase IV
n	24	32	8	9	14	6
Mean	6.26	5.91	7.11	5.77	7.87	8.03
Median	6.23	5.78	6.95	5.33	7.56	7.80
Variance	4.28	3.03	0.85	1.16	4.45	0.41
Std. deviation	2.07	1.74	0.92	1.08	2.11	0.64
Minimum	2.67	3.46	6.00	4.64	5.45	7.32
Maximum	10.72	11.41	8.52	8.07	13.96	8.98
Range	8.05	7.95	2.52	3.43	8.52	1.66
Skewness	0.33	1.21	0.66	1.29	1.95	0.73
Kurtosis	-0.14	2.04	-0.57	1.56	5.12	-1.07

Table 3

		<i>Scarus</i>			<i>Chlorurus</i>		
		Phase II	Phase III	Phase IV	Phase II	Phase III	Phase IV
Mean		6.26	5.91	7.11	5.77	7.87	8.02
Median		6.26	5.70	6.99	5.51	7.54	7.93
80% CI of median	Upper	6.82	6.00	7.64	6.23	8.14	8.30
	Lower	5.58	5.11	6.59	5.03	6.85	7.63
95% CI of median	Upper	7.22	6.37	7.75	6.23	8.38	8.64
	Lower	5.23	4.86	6.51	5.03	6.50	7.56
99% CI of median	Upper	7.44	6.43	8.43	6.61	8.59	8.81
	Lower	4.92	4.78	6.16	4.95	6.34	7.47

Table 4

Date cal BP	Liston (2009)	Snyder et al. (2011)	Chelechol ra Orrak Marine Resource Trends
ca. 3100 - 2400 BP	Expansion Era: coastal settlement, inland use for horticulture; population growth; burials in limestone caves.		ca. 3000 - 1700 BP: Orrak Rockshelter burials; molluscan resource use dominated by <i>Atactodea striata</i> clams and <i>Gibberulus gibberulus</i> .
ca. 2400 - 1200 BP	Earthwork Era: growth and decline of large earthworks in volcanic island interiors; chiefly power and territorial districts; intensive interior settlement; dryland cultivation; later coastal and Rock Islands settlement.	Nucleated villages; erosion and soil depletion associated with earthwork construction and horticulture.	ca. 1700 BP: transition of Orrak Rockshelter from use as cemetery site to permanent occupation/consistent use.
ca. 1500 - 1200 BP	Late Earthwork Era: movement out of interior of larger volcanic islands to coasts and Rock Islands; decline of districts and earthwork construction and use; inland cultivation continues; emergence of ring-ditch palisades suggests conflict and defense.	Nucleated villages leading to dispersed settlement pattern.	Phase II (ca. 1400-1240): fishing important, dominated by herbivorous reef taxa (e.g., Scaridae, Acanthuridae). <i>A. striata</i> and <i>G. gibberulus</i> abundance increases ca. 1700-1000 BP, while other molluscs generally decrease; <i>G. gibberulus</i> increases in size.
ca. 1200 - 700 BP	Transitional Era: little evidence for cultural activity; Rock Islands occupation; limited use of interior; potential overharvesting of inshore resources.	Settlement pattern of dispersed villages; anthropogenic impacts broadly distributed over landscape; dependence on lagoon resources leads to depletion.	Phase III (ca. 1290-720 BP): decrease in fishing, relative decline in herbivores and increase in piscivores (e.g., Serranidae, Lamniformes / Elasmobranchii); <i>Chlorurus</i> exhibits a size increase, although this is probably not statistically significant. Continuing increase in <i>A. striata</i> clams, decrease in bivalve and gastropod collection; continued size increase in <i>G. gibberulus</i> .
ca. 700 - 150 BP	Stonework Village Era: compact complexes of coastal villages behind defensive barriers of mangrove forests and terraces; monumental stone architecture and paving; warfare; extensive wet and dryland agriculture; taro pondfield cultivation.	Nucleated villages; population aggregation into compact villages, leaving idle villages and coastal locations elsewhere and facilitating environmental recovery; intensive exploitation of taro swamp gardens.	Phase IV (ca. 500-0 BP): continued decrease in fishing, relative increase in omnivorous/benthic carnivorous taxa (e.g. Lethrinidae, Labridae); <i>Chlorurus</i> size increase continues, with fish of this species being significantly larger in Phase IV than Phase II. Continuing increase in <i>A. striata</i> clams, decrease in bivalve and gastropod collection; continued size increase in <i>G. gibberulus</i> .

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8