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Reconstructing prehistoric fishing zones in Palau, Micronesia using fish remains: A blind test of inter-analyst correspondence

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Abstract: Archaeologists routinely reconstruct the types of marine environments fished by past human societies in order to understand economic systems, foraging behaviour, maritime technology and seafaring abilities. These reconstructions are based on ecological data provided by archaeofish identifications, but can be problematic where coarse-grained designations, such as inshore or pelagic, are used, or the influence of fish behaviour and life history traits on movement between habitats is overlooked. In tropical waters, intra-family diversity complicates habitat reconstruction by precluding lower-level taxonomic identifications that provide precise habitat information (e.g. surge channels, dropoffs). Consequently, a single generalised habitat may be imposed on fishes that could be caught in multiple environments, thereby eroding the reliability of fishing zone reconstructions. This study employs the archaeofish assemblage from Chelechol ra Orrak (c. 3000–0 BP), Palau to examine the analytical impact of these variables on fishing habitat reconstruction based on a blind assessment of taxon-derived environmental data by two analysts. We assesses how analysts' variable decision protocols for the handling of imprecise environmental data impact resulting habitat exploitation profiles. Our results address the issue of spatial resolution in habitat information gleaned from fish assemblages like Orrak's, with important implications for the interpretation of foraging practices and maritime adaptations.

Résumé: Très souvent les archéologues reconstituent les types de milieux marins pêchés par les sociétés humaines du passé pour comprendre les systèmes économiques, le comportement alimentaire, la technologie maritime et les capacités maritimes. Ces reconstructions sont basées sur des données écologiques fournis par les identifications des poissons archéologiques, mais cela peut être problématique lors des désignations générales, tels que les eaux côtières ou pélagiques sont utilisés, ou l'influence du comportement des poissons et les caractéristiques de l'histoire de la vie en mouvement entre les habitats sont ignorés. Dans les eaux tropicales, la diversité intrafamiliale complique la reconstruction de l'habitat en excluant le niveau inférieur des identifications taxonomiques qui fournissent des informations plus précises de l'habitat (i.e., les canaux de surtension, des tombants). Par conséquent, un seul habitat généralisé peut être imposée sur des poissons qui pourraient être pris dans multiples milieux, affaiblissant ainsi la fiabilité des reconstructions de la zone de pêche. Cette étude utilise l'agglomérat des poissons archéologiques de Chelechol ra Orrak (environ 3000-0 BP), Palau pour examiner l'impact analytique de ces variables de la reconstruction de l'habitat de la pêche, basée sur une évaluation aveugle des données environnementales taxon-dérivées par deux analystes. Nous évaluons comment les variables, décision-protocoles des analystes dans le traitement des données environnementales imprécises impactent les résultats des profils de l'exploitation de l'habitat. Nos résultats portent sur la question de la résolution spatiale de l'information de l'habitat, extraite à partir de l'amas de poissons comme l'Orrak, avec des implications importantes pour l'interprétation des pratiques de recherche de nourriture et des adaptations maritimes.

Introduction

In a recent issue of Antiquity, several authors engaged in a spirited exchange over the interpretative significance of scombrid (tuna and mackerel family) fish bones recovered from the c.42 ka site of Jerimalai Rock Shelter on Timor in South-East Asian (Anderson 2013a,b; Bailey 2013; Erlandson 2013; O'Connor & Ono 2013; see also O'Connor et al. 2011). At issue was whether the archaeological presence of these particular bones could justifiably be attributed to the practice of offshore pelagic fishing, given the family-level identification of fish remains. The Scombridae encompass species found in both oceanic and neritic (over the continental shelf) waters, including species known to travel close to shore during seasonal migrations (Collette 2001). Assignment of Jerimalai's scombrid remains to one or the other habitat – offshore or inshore – thus bears critically on the level of technological sophistication, maritime skills and risk-taking behaviour present at an early date in human history.

The debate is provocative, but our intent here is not to review the merits of the various arguments involved. Rather, we take up one of the key issues highlighted by Anderson (2013a) in his discussion, namely the difficulty posed by higher-level taxonomic identifications (family and above) for the reconstruction of fishing zones based on taxonomic analogy. This difficulty has long been recognised for the Pacific, as well as other areas (Butler 1994; Fitzpatrick et al. 2011; Lambrides & Weisler 2016; Olmo 2013; Ono 2010; Reitz 2004; Wake 2004), and is particularly problematic for tropical and subtropical regions where fish families tend to be especially rich in genera and species. In this paper, we investigate the impact of identification level on the reconstruction of specific fishing environments using an archaeofish assemblage from the Chelechol ra Orrak site (c.3000–0 calBP) in Palau's Rock Islands, Micronesia. In particular, we address the spatial resolution of such reconstructions – the degree to which broad environmental

zones can be narrowed down to specific habitats or microhabitats based on the level of taxonomic identification. Spanning the later 1400 years of site occupation, the Orrak fish assemblage comprises species, genus, family, order and subclass identifications of fishes. Our analysis pairs this heterogeneity with a blind inter-analyst comparison to evaluate the effect of interacting taxonomic identification and analytical protocols on resulting interpretations of fishing behaviour and marine habitat exploitation over time.

The Palauan marine environment and fish

Palau is an archipelago of several hundred volcanic and limestone islands lying in western Micronesia (Figure 1). Situated in the north-western tropical Pacific, the islands are renowned for their well-developed fringing and barrier reef complexes and marine biodiversity, especially for fish (Donaldson 2002; Golbuu et al. 2007; Goldberg et al. 2008). Palauan waters contain an estimated 1500–1700 native marine species (Froese & Pauly 2016; Goldberg et al. 2008). These are found in a range of environments, including mangrove, estuary, lagoon, reef, channel, pelagic and benthic settings, and occur over a variety of substrates, such as mud, sand, seagrass, rubble, coral and pavement (Myers 1989, 1999). Reef fish are particularly abundant in Palau, accounting for more than 1300 species (Froese & Pauly 2016; Myers 1999). Myers (1999) divides Micronesian reefs and near shore areas into zones, which vary in characteristics of substrate, temperature, water depth, tidal exposure, wave or surge action, and light penetration. As depicted in Figure 2, these typically comprise coastal bays (where rivers enter the sea), lagoons, channels, reef flats and seaward reefs. Lying beyond these is the pelagic zone, or the open-water column, often graded by depth; for example, epipelagic (0–200 m), mesopelagic (200–1000 m) and so on. Major zones can be further subdivided into specific habitats such as mangroves, tidal pools, turbid inner lagoons, slopes and dropoffs (Battista et al. 2007; Myers 1999). Pelagic habitats may either

be neritic (occurring over the continental shelf to a depth of about 200 m) or oceanic, referring to offshore waters beyond the continental shelf.

While some fish tend to inhabit specific habitats, others may range widely across a variety of habitats or zones based on daily feeding routines, spawning behaviour, or the need for shelter or protected waters during vulnerable resting periods and juvenile life stage. For instance, the yellowbanded sweetlips (*Plectorhinchus lineatus*) occupies lagoons and coral rich areas of the outer reef slopes during the day. At night, it moves over shallow reef flats to forage for crustaceans. Other species, such as *Ctenochaetus striatus*, *Acanthurus triostegus* and *Monotaxis grandoculis*, will aggregate in large groups at the mouths of channels or the base of reef slopes to spawn at certain times of the lunar month (Myers 1999). Importantly, the relationship between fish ethology and habitat is not always consistent across species of the same family. This is readily illustrated in the behaviour of juvenile porcupine fish (*Diodon* spp.); young *D. hystrix* are pelagic, while *D. liturosus* juveniles typically inhabit shallow lagoons (Myers 1999).

Ethnographically, reefs and associated habitats, such as lagoons, have played an important role in traditional Palauan society, underpinning subsistence, providing resources to generate small-scale market income and reifying Palauan identity (Johannes 1981; Matthews 1992). Archaeological evidence indicates that marine resources were similarly important in the past (Masse et al. 2006; Ono & Clark 2012), including at the study site of Chelechol ra Orrak, where cultural deposits provide evidence for 1400 years of sustained fishing and mollusc exploitation (Fitzpatrick & Kataoka 2005; Fitzpatrick et al. 2011; Giovas et al. 2010, 2016).

The nature and impact of past human interaction with Palau's marine environments varied across space (Clark 2005; Fitzpatrick & Kataoka 2005; Fitzpatrick et al. 2011; Giovas et al. 2010, 2016; Koshiba et al. 2014; Masse et al. 2006; Ono & Clark 2012). For example, based on the changing

taxonomic composition of the fish assemblage, Masse et al. (2006) document an emphasis on inshore fishing areas in the prehistoric Rock Islands, with a shift over time from the use of droplines (suitable for squirrelfish (Holocentridae), snapper (Lutjanidae), sea breams (Monotaxidae) and emperorfish (Lethrinidae) to the use of nets and basket traps (suitable for wrasses (Labridae) and porcupinefish (Diodontidae)). The authors also note declines in skipjack tuna (*Katsuwonus pelamis*), a species typically assigned to the offshore pelagic zone. On Ulong Island, Ono and Clark (2012; see also Clark 2005) record intensified fishing of offshore pelagic and outer reef species, such as tuna and sharks (Carcharhinidae), after 1000 calBP, which they attribute to a need to exploit areas beyond the reef with the depletion of inshore resources. Johannes' (1981: 108-9) investigation of traditional Palauan ecological knowledge, however, relates that certain tuna species, such as skipjack and yellowfin (*Thunnus albacares*), were known by fishermen to travel between offshore and inshore waters on a daily cycle influenced by currents, seasons and phases of the moon. The trends noted by Ono and Clark (2012) may, therefore, have another explanation if tunas were caught inshore. At Orrak, where a decline in absolute fish abundance is recorded in later site history, studies show no reductions in fish and mollusc size, suggesting sustainable resource use throughout occupation (Giovas 2013; Giovas et al. 2016). The present study was conducted in part to determine if fine-grained data about fishing areas could be obtained to understand better the historical ecology of Orrak.

Chelechol ra Orrak lies on the western shore of Orrak Island, situated near the mouth of mangrove-fringed Airai Bay, which drains the 28.5 km^2 Ngerikiil watershed of Babeldaob Island (Figure 1). On its north end, Orrak is separated from Babeldaob by a narrow channel. On its western side, the island is flanked by fringing reefs interspersed with lagoons and areas of shallow sand and seagrass beds that extend several kilometres from the coast. The main outlet channel of Airai Bay lies to

the east, while deeper waters separate Orrak from a major barrier reef system just over 3 km to the south. How closely Orrak's past marine environment mirrors contemporary structure is unknown. This is often the case in studies of prehistoric fishing, however, and it explains why the archaeological presence of specific fishes is frequently used to reconstruct habitat/fishing zones available in the past. Such studies depend on analogy with contemporary fish ethology, biology and ecology, a bridging assumption that we also employ in this investigation.

The archaeological background

The site of Chlechol ra Orrak consists of a series of smaller caves and rock shelters extending along the western side of Orrak Island in the northern Rock Islands of Palau

(Figure 1). The site was originally identified as a Yapese stone money quarry and first excavated in 2000 (Fitzpatrick 2003a), but continued work at the site over several field seasons also revealed evidence for human burials dating between c.3000 and 1700 calBP, overlaid by dense occupation refuse (Fitzpatrick 2003b; Nelson & Fitzpatrick 2006).

Chelechol ra Orrak has been excavated over five field seasons (2000, 2002, 2007, 2012 and 2015) in a series of 1.0×1.0 m ($n = 14$) and 0.5×1.0 m ($n = 2$) units organised thus far in two different blocks (northern and southern) across the central part of the largest rock shelter, covering a total surface area of 15 m^2. The site stratigraphy is complex, with burial deposits composed of loose coral sand generally found between 50 cmbs to at least 110 cmbs. Deeper deposits turn to a much harder, consolidated calcrete due to tidal action that intrudes into the units at depths below 1 m. In some areas, larger limestone rocks appear to have been used to cap the coral sand matrix, post-burial. The upper 50 ± 10 cm is an undulating series of temporary occupational episodes (see Fitzpatrick 2003b: Figures 2 and 4). Some parts of the site (e.g. unit E1S4) clearly show numerous

sequential deposits indicative of frequent and repeated burning, presumably from fires used for cooking.

All units were wet-screened using 1/8 in (3.2 mm) mesh, with the exception of E2/S4 and W1S1, where nested 1/4 in (6.4 mm) and 1/16 in (1.6 mm) mesh was used to recover smaller site constituents. Excavation of the burials has identified 28 complete or partial individuals, with at least 20 more represented among the thousands of isolated bones and bone fragments recovered from the site. The artefact record includes abundant stone, shell and bone objects and a rich zooarchaeological assemblage. The sheer abundance of fish bone and molluscs at Chelechol ra Orrak (Fitzpatrick 2003a, b; Fitzpatrick & Kataoka 2005; Fitzpatrick & Nelson 2008; Fitzpatrick et al. 2011; Giovas et al. 2010), as well as preliminary stable isotope analysis of human bone collagen indicating enrichment of $\delta^{15}N$ and $\delta^{13}C$ (Krigbaum & Fitzpatrick 2009), indicates a dietary emphasis by site occupants on marine-based protein.

Methods

This study employs data from archaeofish analysis performed by Kataoka and reported in Fitzpatrick and Kataoka (2005) and Fitzpatrick et al. (2011; see also Giovas et al. 2016). Analytical methods are detailed in these publications. In the original study, fish remains were identified to the family level and higher using a suite of elements. For bony fish, these are the premaxilla, maxilla, dentary, articular, quadrate and certain elements diagnostic to specific fishes, such as the pharyngeal mills of wrasses (Labridae), bucklers of surgeonfish (Acanthuridae) and the distinctive vertebrae of scombrids; for cartilaginous fish, these are the vertebrae, caudal spine (rays), and teeth and dermal denticles (sharks). Remains were quantified using NISP (total = 2604) and MNI (total = 490) across three temporal periods: Phase II (Layer 7, c.1400–1240 calBP), Phase III (Layers 4–6, 1290–720 calBP) and Phase IV (Layers 1–3, 500–0 calBP). In this present analysis, several of

the original identifications were resolved to the genus and species level by Kataoka to provide finer-grained environmental data where possible (Table 1). Two of the authors (CMG and ABJL) conducted the fishing zone environmental reconstructions based on this updated dataset. Since the purpose of this investigation was to evaluate how differences in environmental reconstruction protocols used by archaeologists impact resulting reconstructions and interpretations, the environmental analysis was conducted as a blind study. CMG and ABJL each received the dataset with instructions to extract environmental data related to general environments/specific habitats fished, but did not discuss with each other the significance of the taxonomic identifications, the methods employed or the published resources relied upon until analysis and associated quantifications were completed. As such, the two reconstructions reported below were conducted independently and disparities in the results reflect analyst decision-making with respect to the assemblage, not any inherent characteristics of the assemblage. The methods employed by each analyst, designated A and B, and the respective results are reported below, followed by a comparison of the two analyses and a discussion of the underlying reasons for any observed disparities.

Analyst A: methods and results

Information on specific habitats occupied by fish –including characteristics of substrate and water depth –along with details of feeding, spawning movements and juvenile fish behaviour were collected for all relevant Palauan species, relying on Myers (1999) as a primary source. FishBase was used to generate a species checklist for Palau (Froese & Pauly 2016; see also references within the checklist) to delimit the species that could potentially be identified in the fish assemblage and augment habitat information from Myers (1999) as needed. Species-level habitat information was aggregated and synthesised for genus, family and order designations for the list of identified fishes

at Orrak (Table 1) Kataoka's analysis includes higher-level identifications where lower-level (genus or species) attributions are theoretically possible if the species checklist is used to eliminate non-resident fish and to narrow the list of potential candidates to which fish remains can be assigned. For example, Kataoka's identification of Rajiformes can be refined to *Rhynchobatus djiddensis* because this is the sole representative of this order in Palau (Myers 1999). Analyst A made these refinements wherever possible to enhance the resolution of the habitat information obtained. These instances (n = 5) are indicated in the "Taxon" column of Table 2, where the lower-level (species or genus) attributions appear in parentheses. Because fish identified to the level of order subsume so many potential species, the number of habitats, substrate types, etc. that could be represented become so many that the classification is effectively useless for extracting environmental information. This is also the case for a number of fish families (Table 2).

Aggregated environmental information for each identified taxon was consolidated into a series of zones/habitat types (e.g. "Lg–R–RF–SR–RS–Chn", or "lagoon, generalised reef, reef flat, seaward reef, reef slope, channels"; see Supplement 1) that were deemed representative, based on semi-quantitative assessment of the frequency of each type. Resulting data were used to define six environmental areas in which the fish in question could be obtained: shore to reef flat; seagrass beds to reef; lagoon to outer seaward reef; shore to outer seaward reef; and offshore pelagic (Table 2). These categories vary in their spatial extent (as measured on a inshore inshore gradient) as a function of fish identification level and the behaviour of the fish themselves; families encompassing species that occupy many habitats, for example, are assigned to broader environmental categories. A seventh category, constituting about 8.4% of total assemblage MNI, was designated for taxa whose habitat types were too many to permit inclusion in any specific category. With the exception of offshore pelagic fishes, the resulting environmental categories are

not mutually exclusive, as specific types of habitat, such as sand flats, may occur in more than one category (Supplement 1 lists habitats included in each category). Instead, they represent the minimum range of marine area that would need to be fished in order for the identified taxa assigned to that particular environmental category to appear in the Orrak assemblage. For example, the presence of *Calatomus* and *Leptoscarus* among Orrak's fish remains requires only fishing of seagrass beds and reef areas (Table 2), but to account for the occurrence of other taxa, fishermen would have needed to range more widely.

Excluding the no-designation category, the shore to outer seaward reef zone is the most spatially extensive environmental zone reconstructed. Across all phases, 10–12% MNI of fishes fall into this broad category (Table 2 and Figure 3). However, most of the assemblage (⁓66–82% total MNI, depending on phase) can be accounted for by fishing of lagoon and reef areas, including reef flat, reef slopes, dropoffs and channels. While spatially extensive, this category does exclude some habitats, such as mangroves, estuaries, sandy shallows along the shore and offshore pelagic zones, suggesting that Orrak was not regularly used to logistically forage Airai Bay or areas beyond the reef.

Several temporal trends in fishing are apparent. There is a marked decline of 16% total MNI in fish representing the lagoon to outer reef category across the three phases (Table 2 and Figure 3). Over the same 1400-year period, representation of shore to reef flat and shore to seaward reef categories increases by approximately 2–3% total MNI. While these gains are small, in the case of the former, they represent more than a threefold increase in relative abundance and may be accounted for by increased fishing of guitarfish (Rajiformes/*Rhynchobatus djiddensis*) and emperor bream (Lethrinidae). Emperor bream may be found in many of the same habitats as fish assigned to the lagoon to outer reef category, but certain species and juveniles within the family

frequent nearshore areas such as mangroves (Myers 1999). Their increased presence in the assemblage may signify more time spent fishing this area, as might also be the case with guitarfish, which inhabits brackish and marine waters of shallow estuaries and inshore areas (Sommer et al. 1996). As noted above, refined identification of rajiforms to *Rhynchobatus djiddensis* permitted inclusion of those skeletal remains in this study. Left at the order level, this fish would have been excluded, and detection of increased fishing of inshore, estuarine habitats would not have occurred.

Lastly, evidence for fishing of offshore pelagic sharks (Lamniformes) appears for the first time in Phase IV, in the final 500 years of site use (Table 2 and Figure 3). In a previous publication (Giovas et al. 2016), we remarked on the absence of evidence for pelagic fishing. Here, a small (5.9% total MNI), but notable, pelagic fishing component is registered because contemporary species checklists (Froese & Pauly 2016) were used to refine the lamniform identifications to two pelagic-oceanic shark species, the shortfin mako (*Isurus oxyrinchus*) and the pelagic thresher (*Alopias pelagicus*). While occasionally these sharks may be found close inshore (Mundy 2005; Sommer et al. 1996), their absence in Phases II and III and their sudden appearance in Phase IV is better explained by a shift to pelagic fishing later in site history rather than fortuitous capture in inshore waters, as the latter would be expected to occur randomly across all phases. Still, caution is warranted in this interpretation. Other pelagic fishes, such as tuna, were not detected, and the sample size is small (NISP = 6, MNI = 5; pronounced size differences in vertebrae were used to calculate MNI). Additional verification is needed, focusing on lower-level identification of the elements in question and size analysis of vertebral specimens to rule out potential inshore-dwelling juveniles. Palauans traditionally fish sharks by luring them with bait or underwater vibrations. They are then caught using a noose or a wooden hook large enough that the teeth cannot sever the line (Johannes 1981).

Overall, Analysis A indicates a predominant fishing focus on lagoon to outer reef zones, areas that may be readily exploited within ~500 m of the site (Figure 1). By the final phase, however, Chelechol ra Orrak occupants had apparently expanded the environmental zones fished to include shoreline habitat and deeper, open waters beyond the reef. These conclusions rest on the assumption that fish behaviour and ecology have not changed through time, that species present in the past are the same as those recorded today, and that the marine habitat around Orrak has not undergone massive reorganisation, the latter of which could lead to mistaken impressions of people's ability to access specific marine habitats.

Analyst B: methods and results

Habitat designations for Palauan fish communities were completed using a hierarchical classification scheme that provides a systematic approach for classifying benthic habitats. This method has demonstrated utility for documenting the spatial distribution of marine habitats for conservation and monitoring (Kendall et al. 2012; Mumby & Harborne 1999a, b). Methods adopted for this analysis follow Harris and Weisler's (2016: 10-14) study of prehistoric forager decision-making on Ebon Atoll, where molluscs were assigned to a range of habitats according to a hierarchical classification scheme. Harris and Weisler (2016) used the relative abundance of identified taxa from each habitat to provide probabilistic determinations of the habitats that were exploited during prehistory. According to this scheme, a habitat is defined by: location in relation to the shoreline; major geomorphological structure (e.g. hardbottom or unconsolidated sediments); and benthic cover (Kendall et al. 2012). Here, a modified version of the hierarchical classification scheme developed by Battista et al. (2007) was used for characterising the benthic habitats of the Republic of Palau. The scheme has two hierarchical attributes: Zone (relationship to shoreline) and Geomorphological Structure. Geomorphological Structure is composed of two sub-attributes:

Major Geomorphological Structure (substrate type) and Detailed Geomorphological Structure (including associated biological cover).

All fish taxa were assigned a combination of Zone, Major Geomorphological Structure and Detailed Geomorphological Structure, based on known habitat proclivities obtained from FishBase (Froese & Pauly 2016) and Myers (1989), with the exception of Elasmobranchii, Rajiformes and Lamniformes, as these classifications were deemed too general to allow for habitat assignment, and as such referred to as "Unknown" (Supplement 2). Factors such as intra-family/genus variability, day/night cycles, growth stage, feeding behaviour and seasonality were all considered when assigning taxa to a range of habitats. When family-level or genus-level identifications were reported archaeologically, the range of species included for each family/genus was based on modern geographical ranges reported on FishBase (Froese & Pauly 2016; see also references within the checklist). Those species that do not currently occur in Palauan waters were not included in the analysis.

For each habitat designation, the total MNI of assigned taxa was summed and converted to a percentage of the total MNI of each cultural layer. This provides a probabilistic assessment of those habitats in which the majority of fishes could have been captured (Harris & Weisler 2016: 14). The strength of this method is that it recognises the complex range of habitats that fish exploit on daily, monthly and annual cycles throughout their life history, which is an alternative to more reductionist approaches to habitat reconstructions; that is, those that collapse habitats into broader categories.

The results of Analysis B are based on those habitats that accounted for ≥80% of total MNI for each Phase (Table 3; see also Supplement 3 for graphic quantification of all habitat combinations). A cut-off was established to allow for a more manageable assessment of the assemblages over

time; this is due to the majority of habitats being well represented, probably a result of the predominance of family-level identifications in the assemblage. This arbitrary ≥80% cut-off was deemed suitable to adequately represent variation across the three phases.

For Phase II, 11 habitats accounted for ≥80% of total MNI. The majority of individuals could have been captured from hardbottom environments – specifically, aggregate reef (~86–95% of total MNI) and rubble (~94% of total MNI). Unconsolidated sediments were also highly represented, as a large portion of the assemblage (~92% of total MNI) could have been captured from sand habitats. Fishes with high relative abundance associated with these habitats include balistids, labrids, lethrinids, scarids1 and serranids. There is evidence for all zones from the reef flat to the bank/shelf being exploited, as well as reef holes and channels.

For Phase III, nine habitats accounted for ≥80% of total MNI. The majority of individuals could have been captured from hardbottom environments – specifically, aggregate reef (~82–92% of total MNI), rubble (~81% of total MNI) and individual patch reef (~92% of total MNI). Individual patch reefs are isolated areas of dense coral growth, forming a similar habitat to aggregate reefs, and hosting a similar suite of fish. Taxa with high relative abundance associated with these habitats include balistids, labrids, lethrinids, scarids and serranids. There is evidence for the exploitation of all zones from the reef flat to the bank/shelf, including reef holes and channels.

Finally, for Phase IV, seven habitats accounted for ≥80% of total MNI. Similar to Phase III, the majority of individuals could have been captured from hardbottom environments – specifically, aggregate reef (~80–88% of total MNI) and individual patch reef (~90% of total MNI). Fishes with high relative abundance associated with these habitats include labrids, lethrinids and scarids. Comparable to Phases II and III, there is evidence for all zones from the reef flat to the bank/shelf being exploited, as well as reef holes.

Temporally, there is a decrease in the number of individuals represented by sand and rubble habitats over time. In Phase II, ~94% of the assemblage MNI could have been captured from sand habitats, but by Phase IV this had declined to 80%. Similar trends were noted for rubble habitats, with a reduction from ~76% to 94% MNI (Figure 4). *Chlorurus* sp. increases in abundance from Phase II (3.0% of total MNI) to Phase III (13.1% of total MNI). This genus feeds predominantly on algae and is associated with hardbottom environments, such as aggregate reef, individual patch reef, pavement and rubble, which is consistent with the corresponding decrease over time in the number of individuals that could have been captured from sand habitats (from ~94% to 80%). This reduction in the number of taxa exploited from sandy habitats probably relates to the decline over time in the relative abundance of acanthurids (5.0% to 3.5%), balistids (8.7% to 2.4%) and scarids (29.5% to 11.8%). Interestingly, based on modern assessment of the benthic habitats in Palau, unconsolidated sediments of sand and mud as well as pavements are prominent around the site (Battista et al. 2007).

Overall, Analysis B indicates that a diverse range of habitats were potentially exploited across the three phases of site occupation. For all phases, fishes caught in areas of coral growth were highly represented. There is also evidence for the exploitation of all reef zones from the inshore reef flat to the deeper, oceanward portion of the reef at the bank/shelf. Across all phases, 80% of total MNI could have been captured from each of the documented zones (reef flat, back reef, reef crest, etc.), with the exception of the shoreline intertidal (~40–50% of total MNI). Confident determination of specific habitats is hindered by the predominance of family-level identifications, no quantification of juvenile individuals in the assemblage, and a lack of proxy data relating to the configuration of the reef throughout prehistory. At this stage, it is not possible to determine whether the potential decline in the number of individuals associated with sand and rubble habitats is related

to changes in the exploitation of those fishes, a result of alternations in the configuration of the marine environment over time or a combination of these factors. Based on the current configuration of the marine environment, all taxa could have been recovered from within the immediate vicinity (~800 m) of the site (Battista et al. 2007).

Discussion: comparison of analyses A and B

While there are some overarching similarities in the results of Analyses A and B – for example, evidence for shifts in fishing areas and an emphasis on habitats easily accessible within 1 km of the Chelechol ra Orrak site – there are a number of disparities that suggest that analytical protocols do influence resulting interpretations of environmental exploitation. Methodologically, the two approaches produce different types of data, hindering quantitative comparisons between the two approaches. Qualitative contrasts are, however, still informative. Analysis B employs a fine-grained partitioning of zone and geomorphological structure to produce what amounts to a probabilistic statement about the environmental areas in which fish in the assemblage occur and are therefore likely to be caught. This approach treats all combinations of zones and geomorphologies equally, however, without reference to the actual incidence of occurrence or population abundance of fishes assigned to these areas. For example, in the reef flat, populations of a given fish might naturally spend 90% of their time over aggregate reef and 10% of their time over seagrass, yet the binary approach used in Analysis B only marks the presence/absence of this fish over the two substrates, so that both are weighted the same. By comparison, the method employed in Analysis A is reductionist, aggregating all habitats where a given taxon can be found into broad environmental categories. The disparity in habitat weighting disappears because the distinction between these habitats has been eliminated. For Analysis A, this tradeoff comes with a loss of precision. The effect is similar to collapsing ratio data into ordinal categories. Environments

vary continuously across space, but in Analyst A's approach, the need to define discrete categories that can be manipulated for analytical purposes requires that this variation be divided and consolidated.

At the larger scale, both environmental reconstructions indicate a primary emphasis on reef-associated habitats (reef flat and back to fore/outer reef) (Figure 2), but trends through time are differentially reconstructed. In Analysis A, there is a decrease through time in the use of the lagoon to outer reef environment, with concomitant expansion into shore to reef flat and offshore pelagic areas. Change is detected and defined on the basis of space as it relates to distance from the Orrak shoreline. In Analysis B, by contrast, the trend for decreased capture of fish over sand and rubble reflects change measured on the basis of substrate type, irrespective of spatial proximity to the shore. We speculate that changes in fishing areas detected on the basis of (horizontal) space versus substrate could influence interpretation of the cause of these changes, especially as these relate to foraging impacts and technological developments. For example, an increase in offshore pelagic fishing is probably more likely to be attributed to overfishing of inshore stocks than is a decline in the fishing of sand and rubble bottoms. In any case, for both analyses, downward trends are partly driven by the large decline in taxa such as scarids and acanthurids. In neither instance, however, is the ultimate cause for these shifts clear (for discussions of declining fish abundance and its possible relation to resource depression, see Fitzpatrick & Kataoka 2005; Fitzpatrick et al. 2011; Giovas et al. 2010, 2016). Notably, Analysis B did not record the abrupt appearance of pelagic fishing after 500 calBP in Phase IV. Pelagic/oceanic taxa are not explicitly captured by this hierarchical classification scheme, as its method is based on intertidal and nearshore benthic habitats. However, additional categories can be included by the analyst employing this approach when those fishes are present in an assemblage.

Methodologically, the inability to extract high-resolution habitat information from fish attributions was a reoccurring theme identified by both analysts. The two approaches recognise the complex range of habitats that fish exploit on daily, monthly and annual cycles throughout their life history, but the analytical utility of both analyses was hindered by higher-level taxonomic identifications (family-level and above) and by absence of age data for the fish in the assemblage (i.e. abundance of adults versus juvenile specimens). The environmental complexity of the region, the diversity of the assemblage and the potential species richness involved meant that both analysts spent considerable time reconstructing fishing zones and habitats. In the end, however, no significant new insights came of this investment. Both Analyst A and Analyst B expressed the opinion that, because of the prevalence of family-level identifications, their final conclusions did not differ much from those that might be reached by simply scanning the list of identified taxa and their relative abundances. Effectively, low-data quality has reduced the power of the more systematic methods employed here to that of more impressionistic approaches, yielding what amounts to the same, broad understanding of fishing at the site: people at Orrak probably used a range of technologies to fish the reef and nearby areas, targeting a variety of specific habitats and substrates. Despite evidence for change over time, reef-associated habitat remains consistently important through 1400 years of occupation.

Conclusion

In this study, we compared two blind reconstructions of fish habitat to evaluate the effect of variable decision protocols on resulting environmental exploitation profiles. Not surprisingly, our results suggest that the level of taxonomic identification, the relative detail of habitat information (which will vary by source), and methods for creating, quantifying and weighting environmental variables do impact reconstructions of fishing environments. The results also demonstrate that

differences between approaches become less meaningful as taxonomic specificity declines. The two methods illustrate how unspoken assumptions about the significance of certain factors for understanding fishing behaviour – in this case, foraging distance from shore and benthic substrate occupied by fish – can influence the reconstruction of those activities.

In the end, both analyses were restricted to fairly general and similar conclusions, due to the very low resolution of habitat information provided by fish assigned to the family level or above. Where species-specific habitat information was employed, however, it proved useful, allowing for the detection of offshore pelagic fishing that would otherwise be invisible at higher taxonomic levels. Because fish habitat data can ultimately influence interpretations about seafaring ability and the sophistication of fishing and boating technologies available to people in the past – including instances where the antiquity of these adaptations may be at issue (e.g. Béarez et al. 2016; O'Connor et al. 2011; Pickard & Bonsall 2004) – we suggest that researchers interested in past marine habitat use would benefit from pursuing lower-level taxonomic identifications (potentially facilitated by aDNA analysis; e.g., Cannon and Yang 2006; Grier et al. 2013; Grealy et al. 2016) paired with analyses of fish size that discriminate between juvenile and adult fish (see discussions in Lambrides and Weisler 2015; Weisler and Green 2013). Adoption of analytical guidelines that incorporate reliable data on fish ecology and behaviour would also streamline reconstructions and foster appropriate comparison of results between sites. While the ability to follow these recommendations will depend on a number of variables, including the level of specimen fragmentation and availability of comprehensive comparative collections, finer-grained habitat reconstructions are almost certainly not possible without these steps, at least not in highly biodiverse, spatially heterogeneous environments such as those of the Western Pacific.

Acknowledgements

Note

Recent molecular and morphological analyses (e.g. Westneat & Alfaro 2005; Westneat et al. 2005; see also Page et al. 2013) place parrotfish (formerly family Scaridae) as a subfamily (Scarinae) of the wrasses (Labridae). In this study, we retain the family-level designation of the originally published dataset (Fitzpatrick and Kataoka 2005) to facilitate correspondence and comparison of this study's results with those of the original analysis. Parrotfish skeletal elements can be readily distinguished from those of other labrids, allowing them to be treated as a discrete analytical category. Thus, taxonomic revision does not impact the results of our study. For clarity, Tables 1 and 2 and the online supplements make use of both the family (Scaridae) and subfamily (Scarinae) names.

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Table 1. Fish identifications and abundance across three occupation phases at Chelechol ra Orrak, Palau. See endnote 1 for an explanation of the Scaridae /Labridae, Scarinae designation.

Taxon	Common name	No. Recorded Palauan Spp.	Phase II (Layer 7) NISP	%NISP	MNI	%MNI	Phase III (Layers 4–6) NISP	%NISP	MNI	%MNI	Phase IV (Layers 1–3) NISP	%NISP	MNI	%MNI	Site Total NISP	%NISP	MNI	%MNI
Chondrichthyes (cartilagenous fishes)																		
Elasmobranchii	sharks, skates, rays		11	0.5	3	1.0	22	5.6	4	3.7	–		–		33	1.3	7	1.4
Rajiformes	skates, guitarfish	1[*]	63	3.1	3	1.0	19	4.9	4	3.7	3	1.7	3	3.5	85	3.3	10	2.0
Lamniformes	mackerel sharks	2	–		–		–		–		6	3.4	5	5.9	6	0.2	5	1.0
Actinopterygii (bony ray-finned fishes)																		
Acanthuridae	surgeonfishes	41	371	18.2	15	5.0	47	12.0	5	4.7	13	7.4	3	3.5	431	16.6	23	4.7
Balistidae	leatherjackets	18	113	5.5	26	8.7	27	6.9	9	8.4	5	2.9	2	2.4	145	5.6	37	7.6
Belonidae	needlefishes	9	–		–		1	0.3	1	0.9	1	0.6	1	1.2	2	0.1	2	0.4
Carangidae	jacks	39	12	0.6	4	1.3	3	0.8	3	2.8	–		–		15	0.6	7	1.4
Diodontidae	porcupinefishes	4	111	5.4	3	1.0	22	5.6	4	3.7	7	4.0	5	5.9	140	5.4	12	2.4
Haemulidae	grunts	13	–		–		1	0.3	1	0.9	–		–		1	0.0	1	0.2
Plectorhinchus sp.	sweetlips grunts	10	1	0.0	1	0.3	–		–		–		–		1	0.0	1	0.2
Holocentridae	squirrelfishes	29	31	1.5	8	2.7	10	2.6	6	5.6	5	2.9	5	5.9	46	1.8	19	3.9
Kyphosidae	sea chubs	2	–		–		–		–		–		–		–		–	
Kyphosus sp.	sea chubs	2	1	0.0	1	0.3	–		–		–		–		1	0.0	1	0.2
Labridae	wrasses	112	182	8.9	39	13.1	34	8.7	10	9.3	29	16.6	13	15.3	245	9.4	62	12.7
Lethrinidae	emperor breams	24	142	7.0	25	8.4	20	5.1	9	8.4	20	11.4	9	10.6	182	7.0	43	8.8
Monotaxis grandoculis	bigeye seabream	1	26	1.3	10	3.4	1	0.3	1	0.9	–		–		27	1.0	11	2.2
Lutjanidae	snappers	34	16	0.8	7	2.3	7	1.8	3	2.8	5	2.9	3	3.5	28	1.1	13	2.7
Mugilidae	mullets	7	–		–		–		–		1	0.6	1	1.2	1	0.0	1	0.2
Mullidae	goatfishes	13	42	2.1	13	4.4	8	2.0	3	2.8	8	4.6	4	4.7	58	2.2	20	4.1
Muraenidae	moray eels	52	15	0.7	8	2.7	10	2.6	3	2.8	4	2.3	3	3.5	29	1.1	14	2.9
Ostraciidae	boxfishes	7	79	3.9	3	1.0	9	2.3	4	3.7	6	3.4	4	4.7	94	3.6	11	2.2
Scaridae/Laridae, Scarinae	parrotfishes	36	609	29.9	88	29.5	88	22.5	8	7.5	43	24.6	10	11.8	740	28.4	106	21.6
Bolbometopon muricatum	green humphead	1	7	0.3	2	0.7	–		–		1	0.6	1	1.2	8	0.3	3	0.6
Chlorurus sp.	parrotfishes	7	9	0.4	9	3.0	14	3.6	14	13.1	6	3.4	6	7.1	29	1.1	29	5.9
Calotomus sp.	parrotfishes	2	14	0.7	4	1.3	1	0.3	1	0.9	–		–		15	0.6	5	1.0
Leptoscarus sp.	parrotfishes	1	–		–		–		–		1	0.6	1	1.2	1	0.0	1	0.2
Scorpaenidae	scorpionfishes	25	68	3.3	2	0.7	–		–		–		–		68	2.6	2	0.4
Serranidae	sea basses	88	109	5.3	21	7.0	46	11.8	13	12.1	8	4.6	5	5.9	163	6.3	39	8.0
Siganidae	rabbitfishes	13	6	0.3	3	1.0	1	0.3	1	0.9	3	1.7	1	1.2	10	0.4	5	1.0
Total identified			2038		298		391		107		175		85		2604		490	

[*]Froese & Pauly (2016) list a single Rajiform for Palau, *Rhynchobatus djiddensis*, as a questionable occurrence, but Myers (1999) lists this species as present.

Table 2 Environmental designations made by Analyst A. See endnote 1 for an explanation of the Scaridae /Labridae, Scarinae designation.

Enviro Zone Taxon	Common name	Phase II (Layer 7)				Phase III (Layers 4–6)				Phase IV (Layers 1–3)				Site total				Remarks
		NISP	% NISP	MNI	% MNI	NISP	% NISP	MNI	% MNI	NISP	% NISP	MNI	% MNI	NISP	% NISP	MNI	% MNI	
Shore to reef flat																		
Mugilidae	mullets	–		–		–		–		1	0.6	1	1.2	1	0.0	1	0.2	
Rajiformes (*Rhynchobatus djiddensis*)	skates, guitarfish	63	3.1	3	1.0	19	4.9	4	3.7	3	1.7	3	3.5	85	3.3	10	2.0	Froese and Pauly (2016) list a single Rajiform for Palau, *Rhynchobatus djiddensis*, as a questionable occurrence, but Myers (1999) lists this species as present
		63	3.1	3	1.0	19	4.9	4	3.7	4	2.3	4	4.7	86	3.3	11	2.2	
Seagrass beds to reef																		
Calotomus sp.	parrotfishes	14	0.7	4	1.3	1	0.3	1	0.9	–		–		15	0.6	5	1.0	Froese and Pauly (2016) and Myers (1999) list just two species: *Calotomus spinidens* and *C. carolinus*
Leptoscarus sp. (*Leptoscarus vaigiensis*)	parrotfishes	–		–		–		–		1	0.6	1	1.2	1	0.0	1	0.2	Froese and Pauly (2016) and Myers (1999) list a single species for Palau, *Leptoscarus vaigiensis*
		14	0.7	4	1.3	1	0.3	1	0.9	1	0.6	1	1.2	16	0.6	6	1.2	
Lagoon to outer reef (includes reef flat for some taxa)																		
Acanthuridae	surgeonfishes	371	18.2	15	5.0	47	12.0	5	4.7	13	7.4	3	3.5	431	16.6	23	4.7	Froese and Pauly (2016) list two *Kyphosus* species for Palau, *K. cinerascens* and *K. vaigiensis*
Balistidae	leatherjackets	113	5.5	26	8.7	27	6.9	9	8.4	5	2.9	2	2.4	145	5.6	37	7.6	
Holocentridae	squirrelfishes	31	1.5	8	2.7	10	2.6	6	5.6	5	2.9	5	5.9	46	1.8	19	3.9	
Kyphosus sp. (*K. cinerascens* or *K. vaigiensis*)	sea chubs	1	0.0	1	0.3	–		–		–		–		1	0.0	1	0.2	
Labridae	wrasses	182	8.9	39	13.1	34	8.7	10	9.3	29	16.6	13	15.3	245	9.4	62	12.7	
Monotaxis grandoculis	bigeye seabream	26	1.3	10	3.4	1	0.3	1	0.9	–		–		27	1.0	11	2.2	
Mullidae	goatfishes	42	2.1	13	4.4	8	2.0	3	2.8	8	4.6	4	4.7	58	2.2	20	4.1	
Muraenidae	moray eels	15	0.7	8	2.7	10	2.6	3	2.8	4	2.3	3	3.5	29	1.1	14	2.9	
Ostraciidae	Boxfishes	79	3.9	3	1.0	9	2.3	4	3.7	6	3.4	4	4.7	94	3.6	11	2.2	
Scaridae/Labridae, Scarinae	Parrotfishes	609	29.9	88	29.5	88	22.5	8	7.5	43	24.6	10	11.8	740	28.4	106	21.6	
Bolbometopon muricatum	Green humphead	7	0.3	2	0.7	–		–		1	0.6	1	1.2	8	0.3	3	0.6	
Chlorurus sp.	Parrotfishes	9	0.4	9	3.0	14	3.6	14	13.1	6	3.4	6	7.1	29	1.1	29	5.9	
Scorpaenidae	Scorpionfishes	68	3.3	2	0.7	–		–		–		–		68	2.6	2	0.4	
Serranidae	Sea basses	109	5.3	21	7.0	46	11.8	13	12.1	8	4.6	5	5.9	163	6.3	39	8.0	
		1662	81.6	245	82.2	294	75.2	76	71.0	128	73.1	56	65.9	2084	80.0	377	76.9	

Shore to outer seaward reef

Family	Common name																	Notes
Haemulidae	grunts	–		–		1	0.3	1	0.9	–		–		1	0.0	1	0.2	
Plectorhinchus sp.	sweetlips grunts	1	0.0	1	0.3	–		–		–		–		1	0.0	1	0.2	
Lethrinidae	emperor breams	142	7.0	25	8.4	20	5.1	9	8.4	20	11.4	9	10.6	182	7.0	43	8.8	
Siganidae (*Siganus*)	rabbitfishes	6	0.3	3	1.0	1	0.3	1	0.9	3	1.7	1	1.2	10	0.4	5	1.0	All species reported by Froese and Pauly (2016) and Myers (1999) belong to the genus *Siganus*
		149	7.3	29	9.7	22	5.6	11	10.3	23	13.1	10	11.8	194	7.5	50	10.2	

Offshore pelagic

Family	Common name																	Notes
Lamniformes (*Isurus oxyrinchus* or *Alopias pelagicus*)	mackerel sharks	–		–		–		–		6	3.4	5	5.9	6	0.2	5	1.0	Froese and Pauly (2016) list two Lamniformes for Palau, *Isurus oxyrinchus* and *Alopias pelagicus*
		–		–		–		–		6	3.4	5	5.9	6	0.2	5	1.0	

Spatially extensive range of habitats

Family	Common name																
Belonidae	needlefishes	–		–		1	0.3	1	0.9	1	0.6	1	1.2	2	0.1	2	0.4
Carangidae	jacks	12	0.6	4	1.3	3	0.8	3	2.8	–		–		15	0.6	7	1.4
Diodontidae	porcupinefishes	111	5.4	3	1.0	22	5.6	4	3.7	7	4.0	5	5.9	140	5.4	12	2.4
Elasmobranchii	sharks and rays	11	0.5	3	1.0	22	5.6	4	3.7	–		–		33	1.3	7	1.4
Lutjanidae	snappers	16	0.8	7	2.3	7	1.8	3	2.8	5	2.9	3	3.5	28	1.1	13	2.7
		150	7.4	17	5.7	55	14.1	15	14.0	13	7.4	9	10.6	218	8.4	41	8.4

Table 3. Environmental designations made by Analyst B. Habitat MNI is the total MNI of all taxa associated with each habitat classification (Zone, Major Geomorphological Structure, and Detailed Geomorphological Structure). Because taxa can be assigned to multiple habitats, total percentages exceed 100%. MNI and %MNI values in parentheses represent totals for a given zone as a whole.

Zone	Major Geomorphological Structure	Detailed Geomorphological Structure	Phase II (Layer 7)		Phase III (Layers 4–6)		Phase IV (Layers 1–3)	
			Habitat MNI	% MNI	Habitat MNI	% MNI	Habitat MNI	% MNI
Shoreline Intertidal			(114)	(38.3)	(54)	(50.5)	(38)	(44.7)
	Unconsolidated Sediments	Mud	114	38.3	54	50.5	38	44.7
Reef Flat			(285)	(95.6)	(99)	(92.5)	(78)	(91.8)
	Coral Reef and Hardbottom	Aggregate Reef	257	86.2	89	83.2	68	80.0
		Pavement	234	78.5	77	72.0	57	67.1
		Rubble	194	65.1	61	57.0	40	47.1
	Unconsolidated Sediments	Mud	114	38.3	54	50.5	38	44.7
		Sand	231	77.5	73	68.2	55	64.7
		Seagrass	201	67.5	51	47.7	45	52.9
Back Reef			(282)	(94.6)	(98)	(91.6)	(75)	(88.2)
	Coral Reef and Hardbottom	Aggregate reef	282	94.6	98	91.6	75	88.2
		Individual Patch Reef	15	5.0	5	4.7	3	3.5
Reef Crest			(283)	(95.0)	(92)	(86.0)	(70)	(82.4)
	Coral Reef and Hardbottom	Aggregate Reef	283	95.0	92	86.0	70	82.4
		Pavement	41	13.8	14	13.1	5	5.9
Fore Reef			(282)	(94.6)	(97)	(90.7)	(74)	(87.1)
	Coral Reef and Hardbottom	Aggregate Reef	282	94.6	97	90.7	74	87.1
		Pavement	15	5.0	5	4.7	3	3.5
		Rock/Boulder	223	74.8	61	57.0	52	61.2
		Spur and Groove	127	42.6	51	47.7	32	37.7
Bank/Shelf			(279)	(93.6)	(92)	(86.0)	(68)	(80.0)
	Coral Reef and Hardbottom	Aggregate Reef	279	93.6	92	86.0	68	80.0
		Rubble	232	77.9	69	64.5	53	62.4

Lagoon			(292)		(98.0)	(99)		(92.5)	(77)	(90.6)
	Coral Reef and Hardbottom	Aggregate Reef	88		29.5	8		7.5	10	11.8
		Individual Patch Reef	282		94.6	98		91.6	77	90.6
		Rubble	279		93.6	87		81.3	65	76.5
	Unconsolidated Sediments	Sand	273		91.6	81		75.7	65	76.5
		Seagrass	25		8.4	9		8.4	9	10.6
Reef Hole			(292)		(98.0)	(99)		(92.5)	(77)	(90.6)
	Coral Reef and Hardbottom	Aggregate Reef	266		89.3	91		85.1	68	80.0
		Pavement	81		27.2	24		22.4	18	21.2
	Unconsolidated Sediments	Sand	273		91.6	81		75.7	65	76.5
Channel			(279)		(93.6)	(89)		(83.2)	(65)	(76.5)
	Coral Reef and Hardbottom	Aggregate Reef	267		89.6	88		82.2	64	75.3
	Unconsolidated Sediments	Sand	176		59.1	51		47.7	46	54.1
Unknown			6		2.0	8		7.5	8	9.4

Figure 1. Map of Western Pacific Islands showing locations of Palau and the Chelechol ra Orrak site, with satellite imagery depicting contemporary marine habitat surrounding Orrak Island (figure modified from Google Earth).
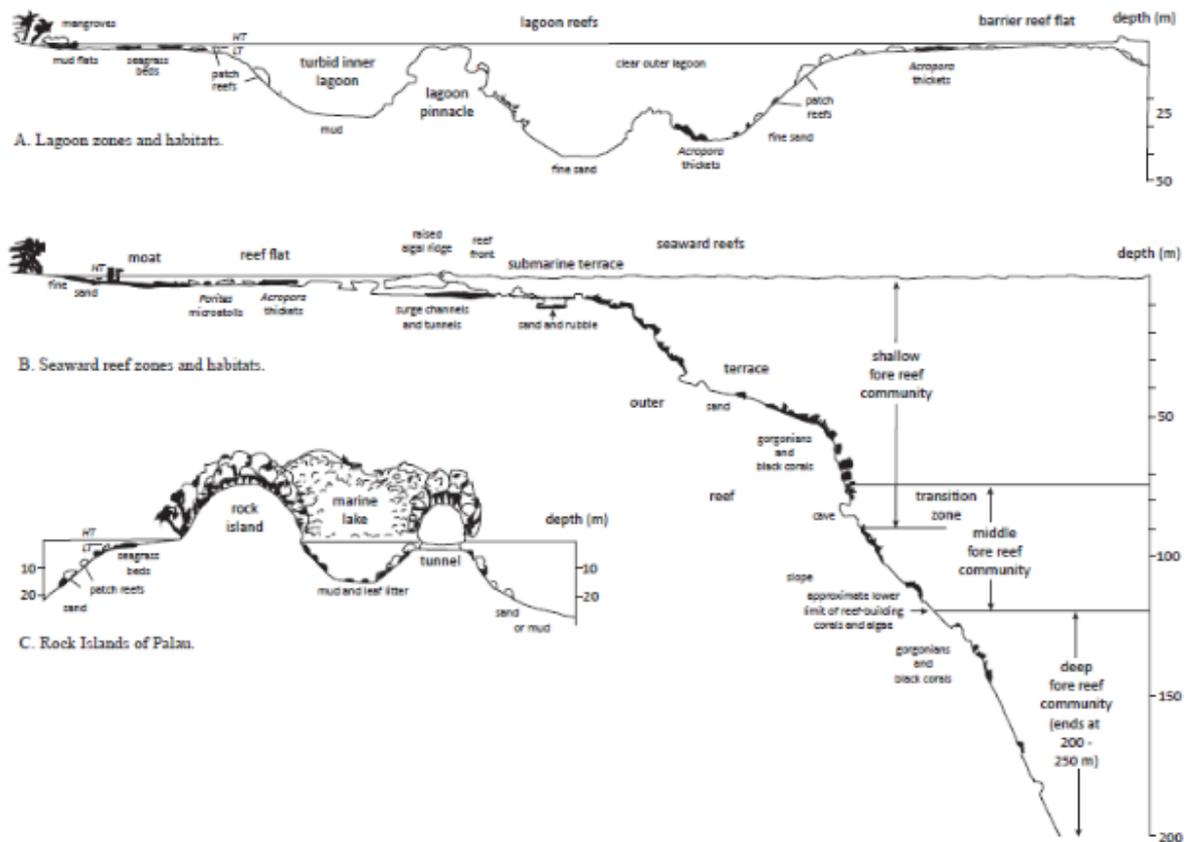
Figure 2. Typical Micronesian marine zones and habitats: (a) Lagoon zones and habitats. (b) Seaward reef zones and habitats: depth zonation of the inshore fish communities is indicated on the far right. (c) The rock islands of Palau. HT, High tide; LT, low tide (modified from Myers 1999, fig. 4).
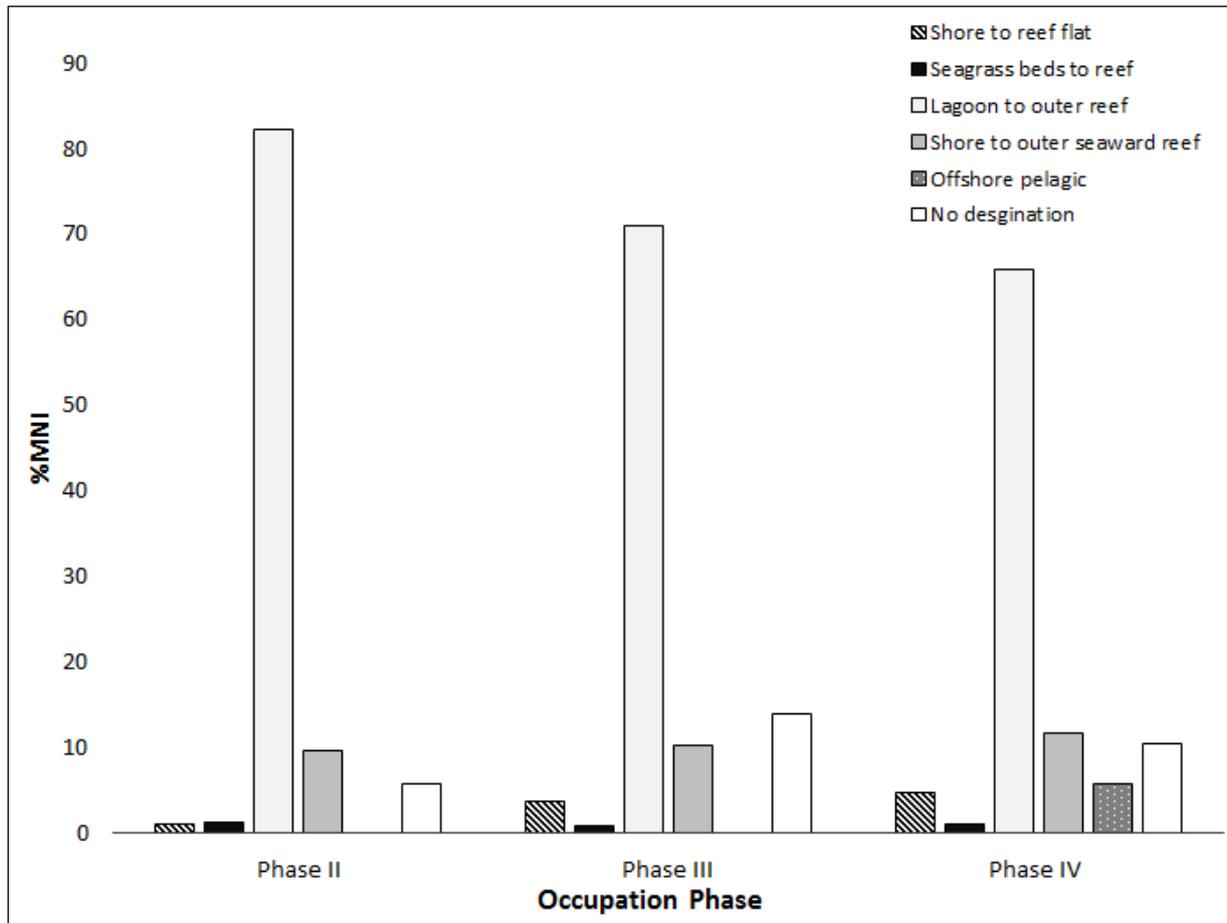
Figure 3. Analyst A reconstructed environmental zone representation and change through time based on MNI.
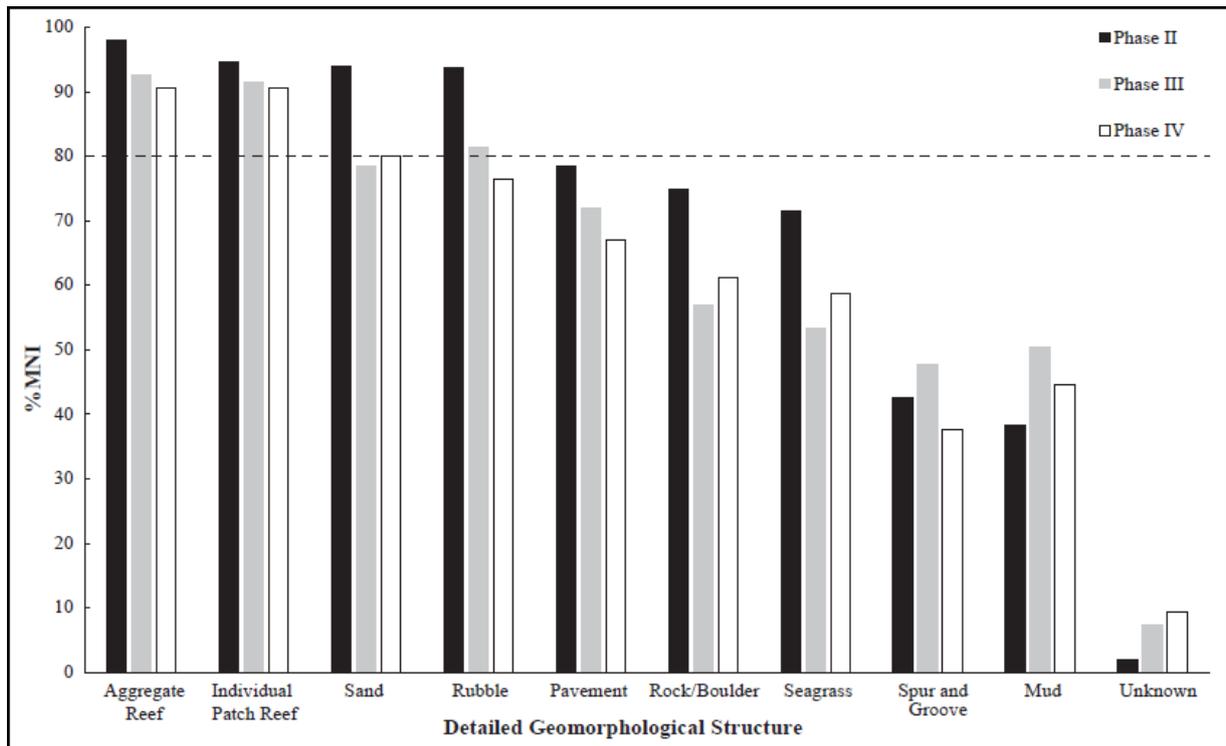
Figure 4. Analyst B reconstructed habitat representation and change through time based on MNI (Detailed Geomorphological Structure only).