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Late Holocene Marshall Islands archaeological tuna records provide proxy evidence for ENSO variability in the western and central Pacific Ocean

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Abstract: Tuna will have increased importance to Pacific Island nations in coming decades for food security and economic needs; consequently, sustainable fisheries management policies are imperative. The frequency and temporal distribution of tuna bones from tropical Pacific archaeological sites is essential for documenting millennial scale records that detail the responses of tuna stocks to anthropogenic fishing pressure and climatic variability. We highlight the potential impacts of El Niño-Southern Oscillation (ENSO) variability on the western and central Pacific Ocean skipjack (*Katsuwonus pelamis*) fishery over the last 2000 years. Ebon Atoll (4°38′24.67″N, 168°42′23.56″E), Republic of the Marshall Islands (RMI) archaeological data and regional western and central Pacific Islands archaeological tuna fishery data are evaluated. These datasets are compared to palaeoclimate records, which track hydroclimate variability during the last 2000 years, and recent historic capture records, which document associations between ENSO and skipjack abundance and range throughout the tropical Pacific Ocean. Results suggest that regional and temporal trends in archaeological scombrid/skipjack abundance provide proxy evidence for western and central Pacific Ocean ENSO variability, while prehistoric human impacts to the tuna fishery appear to be negligible. Future research should include species-level identification of all archaeological tuna bones and establish fine-grained local climate data across the region that is tied to well-dated archaeological sequences, thus enhancing our understanding of how regional climate influences the geographic distribution and relative abundance of tuna species over millennia.

Keywords: El Niño-Southern Oscillation, historical ecology, *Katsuwonus pelamis*, Pacific Islands, zooarchaeology

Introduction

Zooarchaeological datasets have enabled the global investigation of alterations in resource availability in response to both anthropogenic factors and climate variability, indicated by changes in relative abundance of taxa across centuries to millennial time scales (e.g. Andrus et al. 2002; Aswani and Allen 2009; Barrett et al. 2011; Broughton 1997; Butler and Campbell 2004; Erlandson et al. 2009; Faith 2014; Fitzpatrick and Donaldson 2007; Giovas et al. 2016; Grayson 2001; Lyman 2016; Moss 2012; Nagaoka 2002; Reitz 2004; West 2009). We highlight the potential impact of ENSO variability on the western and central Pacific Ocean skipjack (*Katsuwonus pelamis*) fishery over the last 2000 years. Focusing on Ebon Atoll at the southern extent of the Republic of the Marshall Islands (RMI), the frequency and distribution of archaeological tuna bones are evaluated in conjunction with regional trends in the western and central Pacific Islands archaeological tuna fishery data. These datasets are then compared to palaeoclimate records, which track hydroclimate variability over the last 2000 years, and recent historic capture records, which document the impact of ENSO on skipjack abundance and range throughout the tropical Pacific Ocean.

Tuna will have increased importance to Pacific Island nations over the next several decades, given tuna must supply ~25% of fish required for food security by 2035 (Bell et al. 2015). The RMI has an industrial purse-seine tuna fishery that exceeds 47,000 tons per year (2004-2008), worth > USD 56.7 million. Fishery efforts predominately target the southern RMI, with skipjack accounting for 74% of the total catch in 2012 (Bell et al. 2011; Western and Central Pacific Fisheries Commission 2014). Under low and high emissions scenarios for the RMI, predictions suggest there will be increases in average sea surface temperature (SST), sea levels, and ocean acidification and reductions in primary production and zooplankton biomass (Bell et al. 2011). Catches of skipjack and yellowfin (*Thunnus albacares*) are expected to initially increase with these conditions (>20%), but big eye tuna (*Thunnus obesus*) will decrease under both scenarios (~30% by 2100 under the A2 scenario); skipjack biomass is predicted to stabilize by 2050, then begin decreasing from 2060, which is associated with less favorable spawning conditions (Bell et al. 2011; Lehodey et al. 2013: 95).

Given the contemporary importance of tuna fisheries in the RMI, archaeological data from this region is essential for establishing tuna fisheries responses to both anthropogenic fishing pressure and climatic variability throughout the entire 2000 year-long culture-historical sequence of the archipelago. Nicol et al. (2013: 132) have argued 'fisheries management policies that are resilient and can be adapted to climate change' are needed. Migratory fish, such as tuna, are valuable for investigating human responses to climate variability both locally (e.g. Ebon Atoll) and for providing proxy evidence for regional climatic variability (e.g. western and central Pacific Ocean). These analyses have only recently become possible in the Pacific given more specific taxonomic identifications of archaeological tuna bones and the implementation of more rigorous methods and analytical frameworks such as historical ecology used to frame this study (Lambrides and Weisler 2016; Rick and Lockwood 2013).

Background

Ethnography of Pacific skipjack fishing

Schools of skipjack were commonly located by tracking seabird flocks (e.g. Buck 1957; Burrows 1936; Johannes 1981), and were viewed as a sacred fish in many regions (e.g. Akimichi 1986; Huntsman and Hooper 1996; Ivens 1927; Ono and Addison 2009). Trolling for tuna was common (Buck 1950; Dye 1983; Kirch and Dye 1979), but no longer practiced in some areas by the early 20th century (Burrows 1936, 1937). Tuna fishing carried a great deal of social and cultural significance (e.g. Davenport 1971; Kennedy 1931; Nordhoff 1930a, b), as in the southeast Solomon Islands where skipjack were considered the 'king of fish' (Iven 1926: 130) and its capture was 'imbued with ritual and mystical significance' (Walter and Green 2011: 10).While tuna fishing was often described as the least economically important mode of fishing (e.g. Lieber 1994), 'when the tuna are there, the pace of island life quickens' (Johannes 1981: 91). On Ifaluk Atoll, Caroline Islands, skipjack trolling was the most celebrated, with five of the 16 known fishing songs associated with this activity; significantly, no other kind of fishing had more than two songs (Burrows and Spiro 1957:105). In Samoa, Buck (1930: 124) reports the ceremonial division of skipjack, where the chiefs were given the most important portions or in Tokelau the catch was distributed if communally obtained, known as *inati* (Hooper and Huntsman 1991; Ono and Addison 2009). Seine net, purse net, or coconut frond sweeps—depending on the region—were considered the most successful techniques for capturing schools of skipjack. On Ifaluk Atoll, multiple seines were stretched end to end, often up to ~800 m long, to surround the school once it entered the lagoon; the whole community would participate and get a portion of the catch (Burrows and Spiro 1957). Similar strategies have been reported elsewhere in the Pacific, including the RMI (e.g. Akimichi 1986; Erdland 1914; Krämer and Nevermann 1938; Lieber 1994; Severance 1986; Tinker 1950).

Archaeology of Pacific tuna fishing

Most Pacific archaeologists do not analyze tuna fisheries in detail due to identification protocol bias (but see Fraser 1998; Fraser 2001; Lambrides and Weisler 2015a; Ono and Intoh 2011); consequently, family level identifications are most often reported in the literature, the shortcoming of which have been critiqued by Anderson (2013). Our review focuses on those sites where scombrids contributed ~20% of minimum number of individuals (MNI) at an archaeological site although we acknowledge that MNI protocols may not have been consistently reported in the early Pacific fishing literature and this may impact intersite comparisons. Throughout this paper all radiocarbon age determinations from the published literature have been converted to cal BP for comparability.

Within Polynesia, sites from the Marquesas Islands, including Hane, Ua Huka (Davidson et al. 1999; Fraser 1998: 81-92), Te Anapua, Ua Pou (Fraser 1998: 92-101; Leach et al. 1997), and Hanamiai, Tahuata (Rolett 1998), and the Vaito‘otia/Fa‘ahia complex, Huahine in the Society Islands (Fraser 1998: 102-114; Leach et al. 1984) provide the most detailed records of tuna fishing in the eastern Pacific Ocean (Figure 1). These assemblages were initially dominated by scombrids and other mostly piscivorous taxa (feeding on fish), which were associated with offshore environments, and then at some sites, inshore taxa (e.g. acanthurids and scarids) increased during late prehistory. A lack of high resolution dating at these sites makes it difficult to correlate site chronologies and changing scombrid abundance to regional climatic trends.

The archaeological record of the western and central Pacific Ocean is especially relevant for documenting long-term trends in the exploitation of the tuna fishery as displacement of the equatorial Pacific warm pool, due to ENSO events, influences tuna recruitment and range (Lehodey et al. 1997). Sites from Palau and the Caroline Islands provide the western Pacific records and Tokelau, American Samoa, and Samoa (formerly, Western Samoa) are the most detailed for the central Pacific Ocean.

Masse et al. (2006) reported a decline in skipjack between 750 and 350 cal BP at the Rock Islands, Palau, attributed to a shift from angling to the use of nets and basket traps, argued to be more reliable due to the climatic variability associated with the Medieval Warm Period (MWP)/Little Ice Age (LIA) transition. On Fais Island, Caroline Islands, Ono and Intoh (2011) provide a well dated sequence, which tracks variability in the prehistoric tuna fishery over ~1800 years. The initial increase in scombrid abundance in Phase IIA occurs at ~1550-1350 cal BP, abundance counts peak in Phase IIB (~1350-1150 cal BP), with scombrids reported as the highest ranked taxon by MNI. Abundance then declines from ~750-550 cal BP (Phases III and IV). Overall, scombrids account for 11.1% of total site MNI. Cultural and climatic factors were suggested as driving these changes including dietary preference, social control, and the ‘AD 1300 Event’ discussed by Nunn (2000a).

For the central Pacific Ocean, Ono and Addison (2013) report increased abundances of pelagic taxa, such as scombrids, at ~600 cal BP on Atafu Atoll, Tokelau. Across the eight excavated 1m^2 units, scombrids were ranked third after scarids and acanthurids, accounting for 12.1% of total MNI. The most recent deposits were dated to ~200 cal BP, and had higher abundances of inshore taxa. Some skipjack were identified at this site, but abundance was not reported. Weisler et al. (2016), documented three cultural phases on Ofu Island, American Samoa, with first occupation at 2700-1500 cal BP. Skipjack were only identified in the post-800 cal BP deposits and while this taxon was low ranking overall, the timing of tuna in the sequence closely aligns with the Atafu Atoll data. Lastly, at Siʻutu, Savaiʻi Island, Samoa, a late prehistoric site, occupied post ~650 cal BP, Ishimura and Inoue (2006) reported scombrid remains (number of identified specimens [NISP]=19) although the abundance and distribution of skipjack, while identified to taxon, was unclear. The data available for the central Pacific Ocean is not as comprehensive, but scombrids and in some cases *K. pelamis*—where specific identifications have been reported—are more prevalent in assemblages that post-date ~850-650 BP while, at a similar time, this taxon is decreasing at western Pacific sites (Ishimura and Inoue 2006; Masse et al. 2006; Ono and Addison 2013; Ono and Intoh 2011; Weisler et al. 2016). More archaeological data are needed to explore these regional trends, particularly from central Pacific locations.

Tuna biology, fisheries and climate variability

Approximately 70% of the world's annual tuna catch is from the Pacific Ocean (Lehodey et al. 1997). Continued capture of skipjack and yellowfin through intensive commercial fishing have had substantial consequences given their prominent role in the food web (Evans et al. 2015). Primary productivity in the tropical Pacific is strongly influenced by ENSO events, which influence vertical and horizontal habitat conditions (Lehodey et al. 1997; Nicol et al. 2014), and while these climatic effects are global reaching, the strongest signatures have been measured between 10ºN and 10ºS in the tropical Pacific Ocean (Nicol et al. 2014). Tropical tuna species such as skipjack and yellowfin have higher recruitment during El Niño, compared to subtropical albacore species (*Thunnus alalunga*), which have higher recruitment during La Niña (Lehodey et al. 2003). Preferences in habitat between tuna species results in differential responses to climate variability and ocean conditions (Nicol et al. 2014).

Skipjack is the primary focus, given its prominence in the Ebon Atoll archaeological assemblages. Spawning occurs throughout the year, with no obvious seasonal trends; minimum size at maturity is around 35-40 cm fork length (FL) and ~1-3 kg, and maximum FL is ~108 cm with weights of 32.5 to 34.5 kg; this is relatively small compared to *Thunnus* spp. (e.g., bigeye and yellowfin) with maximum recorded FLs of 200+ cm and weights of ~180-200 kg (Ashida et al. 2010; Collette and Nauen 1983; Hoyle et al. 2011). They are a schooling species, foraging during the day for fish, squid and crustaceans, which are usually a few millimeters to several centimeters (Lehodey 2001). Skipjack swim constantly as a means of counterbalancing their negative buoyancy, and therefore travel significant distances, resulting in high foraging demands. Temperature and dissolved oxygen concentration are highly correlated with tuna behavior, given the specialized morphological and physiological adaptations that enable thermoregulation and high efficiency oxygen extraction (Ganachaud et al. 2013). Skipjack occur in waters ranging between 20 and 30ºC, with a lower limit of 15ºC, and as optimal spawning conditions peak between 26 and 30ºC, there are higher larval abundances in the western and central Pacific Ocean, which increase tuna recruitment (Ganachaud et al. 2013; Hoyle et al. 2011; Lehodey 2001; Schaefer 2001). Seasonal factors can extend skipjack range, for instance the development of a seasonal fishery off the coast of Japan around summer (May to August) due to sub-tropical warming of surface waters (Lehodey 2001). However, highest catch per unit effort (CPUE) comes from the surface mix layer of the western equatorial and subtropical Pacific Ocean where SST is more consistently ~28-29ºC. Maximum skipjack biomass is situated in the Pacific warm pool, a region that features low primary productivity rates, with the exception of coastal waters, in contrast to the central equatorial Pacific cold tongue, a strong divergent upwelling that produces high levels of primary productivity (Lehodey et al. 1997; Nicol et al. 2014). Tuna abundance throughout the Pacific Ocean is counterintuitive due to the relationship between primary productivity and tuna biomass. The warm pool provides skipjack with the most suitable environmental conditions (i.e. temperature, oxygen and water clarity), but lower secondary production than the eastern Pacific, which has less optimal habitats (Lehodey 2001).

Historically, during La Niña phases, the Pacific warm pool contracts and sits around the Philippines to 160ºE in a low primary productivity state, which corresponds to a westward displacement of the cold tongue (extending as far west as 160ºE). In contrast, during El Niño phases, the cold tongue is displaced east to around ~180º, which extends the warm pool into the central Pacific thus increasing primary production between the Philippines and 160ºE-180º (Lehodey 2001; Lehodey et al. 1997). The location of the warm pool shifts according to these ENSO phases, and influences the distribution and abundance of skipjack, but seasonal factors also have an impact on the position of the warm pool (Lehodey et al. 1997; Nicol et al. 2014). During the La Niña periods of 1988-1989, late 1990 to early 1991, and 1995, the purse seine fleets remained west of 160ºE, west of the RMI, but during El Niño (1992-1994), fishing efforts were extended east to 160ºW, the approximate location of the Cook Islands (Lehodey et al. 1997: 715-716). Following the 2009-2010 El Niño event, higher skipjack recruitment occurred in 2010, but as a result of the high intensity La Niña event that developed in 2010-2011, lower skipjack recruitment was reported in early 2011 (Lehodey et al. 2011). Long-term, time series data has the potential to refine our understanding of the complicated relationship between tuna fisheries and these climatic variables.

Pacific Ocean late Holocene palaeoclimate records

Relevant palaeoclimate records are reviewed for the last ~2000 years, including a discussion of the MWP or Medieval Climate Anomaly (MCA), LIA, frequency of El Niño and La Niña events, changes in SSTs, and shifts in the Intertropical Convergence Zone (ITCZ). These hydroclimate records are still widely contested, especially marine palaeo-ENSO indicators, however, more recent research has started to address these inconsistences (e.g. Griffiths et al. 2016; Rustic et al. 2015; Yan et al. 2015).

There is significant variability in the reported date ranges of the MWP or MCA (~1050-500 cal BP) and LIA (~500-100 cal BP); we report the upper and lower limits to capture this variability (e.g. Griffiths et al. 2016; Jones et al. 2001; Nunn 2012; Rustic et al. 2015). Nunn (2000a, b) argues the transition between the two periods brought rapid cooling, sea-level fall, and increased precipitation in certain areas of the Pacific basin. This has been supported by Oppo et al. (2009), who reported warmer SSTs between ~950 and 700 BP—during the MCA—and 0.5 to 1ºC colder than modern averages in the warm pool during the LIA, a decrease in SST that began ~650 cal BP and peaked in the middle of the LIA. In contrast, Allen (2006) considered late Holocene climate variability in the central Pacific by reviewing palaeoclimate records and suggests that while the rest of the world was experiencing the MCA, conditions in the tropical Pacific were cool and possibly dry, and during the LIA the central (equatorial) Pacific was comparatively warm and wet, with stormy conditions more common.

Most recently, Griffiths et al. (2016) reconstructed the western Pacific hydroclimate using speleothem records and suggested that a poleward expansion of the ITCZ and weakening of the Pacific Walker circulation (PWC) occurred between ~950 and 450 cal BP, in contrast to an equatorial contraction of the ITCZ and strengthening of the PWC from ~450 – 50 cal BP. Shifts in the ITCZ, which occur in a north-south direction, broadly impact precipitation and the records from Flores—in the western Pacific—suggest a drier climate at the following periods: ~1950-1550 cal BP; ~950-550 cal BP, which roughly corresponds with the MCA, and ~50 cal BP-present and a wetter climate at ~1550-950 cal BP and ~550-50 cal BP (Griffiths et al. 2016). Records from Washington Island (or Teraina Island, northern Line Islands) in the central Pacific Ocean indicate wet conditions during the MCA (Sachs et al. 2009). This supports the model proposed by Yan et al. (2015) for an ITCZ expansion during the LIA and contraction during the MCA. The PWC, an east-west pressure gradient, alters trade winds, deep convection, extends the reach of ENSO events, and can impact global temperatures (Griffiths et al. 2016). Records suggest the western Pacific was generally drier during the MCA, whereas the central and eastern Pacific experienced wetter conditions, which can be equated to a weakening PWC producing a more ‘El Niño-like’ mean state. Conversely, the western Pacific was generally wetter during the LIA and the central and eastern Pacific experienced drier conditions, similar to modern La Niña events, indicating strengthening of the PWC (Griffiths et al. 2016; Thompson et al. 2013; Yan et al. 2011). These trends described by Griffiths et al. (2016) are in opposition to some earlier published ENSO reconstructions that suggest the MCA was associated with ‘La Niña-like’ conditions, which produced wetter conditions in the central Pacific (e.g. Cobb et al. 2003; Oppo et al. 2009).

While marine palaeo-ENSO signals are still widely contested, a recent reconstruction of eastern Pacific SSTs by Rustic et al. (2015) suggests that the MCA was associated with warm SSTs, consistent with Griffiths et al. (2016) western Pacific hydroclimate records. Critically, ‘modern observations do not yet distinguish between the PWC’s response to global warming’, which can confound interpretation of the palaeoclimate records (Griffiths et al. 2016: 5-6), and additionally, inconsistencies in the palaeoclimate records themselves, further complicate our understanding of long-term tropical Pacific Ocean climate variability and its associated effects on tuna fisheries (Yan et al. 2015).

Sites and Samples

Beginning just north of the equator and 3850 km southwest of Hawai‘i, the RMI is comprised of 29 atolls and five limestone islands without a lagoon (total land area of 181 km^2), dispersed over 2,000,000 km^2 of ocean (Figure 1). There is a pronounced north-south rainfall gradient across the RMI, with annual precipitation at ~1500 mm in the dry north, and ~4000 mm in the wet south, where Ebon Atoll is situated at the southernmost end of the archipelago. Ebon Atoll is comprised of 22 islets (total land area of 5.75 km^2), encircling a 104 km^2 lagoon, and a 22 km^2 reef platform. The reef to terrestrial land area is high (4:1), and hosts 800 fish taxa within 60 m ocean depth (Myers 1999).

Weisler initiated a research program in 1993 to assess regional variation in the RMI archaeology as it relates to the north-south rainfall gradient, with broad project aims addressing chronology, sea level change and islet development, material culture, marine subsistence, terrestrial production, human impacts, and anthropogenic landscape change (Christensen and Weisler 2013; Pregill and Weisler 2007; Weisler 1999a, b, 2001a, b, c, 2002; Weisler and Swindler 2002; Weisler et al. 2012). Similar to the general chronology of atoll emergence for the RMI (Dickinson 2003; Kayanne et al. 2011; Weisler et al. 2012), 2000 BP appears to be the earliest date Marshall Islands atolls were inhabitable—although some reef islands are appreciably older (Kench et al. 2014)—and this matches closely with the earliest human colonization dates for Utrōk Atoll (Weisler 2001b), Majuro Atoll (Kayanne et al. 2011), Maloelap Atoll (Weisler 1999a: 640; Weisler et al. 2012: 117), and Ebon Atoll (Weisler et al. in prep).

Two field seasons (1995-1996, 2011-2012) of survey and excavation were directed by Weisler (2002) on Ebon Atoll. Ebon Islet as the largest islet, with the most developed Ghyben-Herzberg fresh water lens, hosts the most extensive village and horticultural systems and the oldest habitation sites (Weisler 2001a; Weisler et al. 2012). With 11 documented archaeological sites on Ebon Islet, we focus on

MLEb-1 and MLEb-5 (Figure 2), as these sites provide well-preserved early, middle, and late period prehistoric faunal assemblages. Only four AMS radiocarbon dates from the sites discussed here were included, but the comprehensive Ebon Atoll chronology developed from 59 radiocarbon and U-series dates (Weisler et al. in prep) supports a model of continuous occupation over two millennia. The dates, reported here, are all on coconut husk or shell and calibrated to two standard deviations (with median reported) using IntCal09 curve and the OxCal program (Reimer et al. 2009). All excavated sediments were wet-screened through 6.4 mm mesh, and only TP 6 and TP 17 (MLEb-1) and TP 13 (MLEb-5) were sieved using 3.2 mm mesh. As very few scombrid bones were reported in the 3.2 mm screens, these sampling protocols did not influence the observed trends. However, variability between assemblages screened with 6.4 mm and 3.2 mm mesh and those screened with only 6.4 mm mesh are discussed in the results section.

MLEb-1

Site MLEb-1 covers 30 m^2 between 25 m from the lagoon beach to 200 m inland and, along with other habitation sites, including MLEb-5, forms a near-continuous prehistoric village that runs parallel to the lagoon shore of Ebon Islet for nearly 2 km. Excavated 40 m inland of the lagoon shore and 20 m northwest of the current primary school, a 2 x 2 m unit (TP 17, 18, 19 and 20, each 1 m^2) was excavated over a low artificial mound developed by successive living floors or coral pavements. Cultural deposits were encountered to a depth of 1.75 m. Three main prehistoric layers, capped by a ~4 cm thick layer containing historic artefacts and sparse midden, were encountered. Layer I, ~60 cm thick, consists of black (Munsell 5Y2.5/1, taken moist in shade) gravelly sand with dense prehistoric midden and gravel transported for village pavements. This layer, divided into an upper layer IA, was darker and more compact than IB. Layer II, also divided into an upper IIA and lower IIB due to increasing sand and mottled pockets with depth, was ~118 cm thick and a very dark grey (5Y3/1) sandy gravel midden. Layer IIIA is grey (5Y5/1) sand that is almost completely sterile. Radiocarbon age determinations from Layer IIIA of TP 17 and 19 were 925-790 cal BP (median = 855 cal BP, OZP-927) and TP19/12; IIIA 920-775 cal BP (median = 850 cal BP, OZP928), respectively. These layers overlie palaeo-beach deposits of coarse sand and coral gravel, encountered to ~ 190 cm below surface.

TP 6 is located ~150 m inland of the lagoon shore and cultural material was encountered to a depth of ~1 m. Three layers were each divided into sub-layers based on differences in sediment texture, color and compaction. Layer IA was a black (5Y2.5/1), gravelly sand matrix with dense water-rounded coral gravel and abundant shellfish midden, bone and artefacts. Layer IB had similar cultural content, but with less gravel and lighter sediment color (5Y3/1, very dark grey). Layer IIA was a dark grey sand (2.5Y4/1) with combustion features with less shellfish midden, bone and artefacts, grading to Layer IIB which was light grey (2.5Y7/1) with dispersed charcoal and a combustion feature, otherwise relatively sterile. Layer III was divided into an upper Layer IIIA (5Y7/1, light grey) that was nearly sterile, but with dispersed charcoal and few oven stones. Layer IIIB (2.5Y7/1, light grey) was completely sterile sand differentiated from Layer IIIC (7.5YR8/2, pinkish white) which was slightly cemented, but otherwise similar. A radiocarbon age determination towards the base of the cultural deposit, from within Layer IIIA, dated to 1895-1730 cal BP (median = 1840 cal BP, OZP925).

MLEb-5

Site MLEb-5 is ~670 m east of MLEb-1, along the main village path. The site is situated ~40 to 250 m from the lagoon beach. A 3 x 5 m unit (TP 1, 13 and 15-27, each 1 m^2) was excavated ~120 m from the lagoon shore. The main cultural deposit, Layer I, consisted of dense, water-rounded gravel in a sticky, gravelly black (5Y2.5/1), sandy matrix extending to ~0.5 m below surface in most TPs. Aside from the fish bone reported here, there was dense marine shellfish, plentiful shell artefacts (adzes, beads, worked pearlshell, arm rings, fishhook tabs), coral abraders, and combustion features. The sterile subsoil (Layer II), was a pinkish white (7.5YR8/2) sand. One radiocarbon age determination returned the oldest dated habitation remains for the atoll at 2295-1995 cal BP (median = 2085 cal BP, OZP932).

Methods

Identification and quantification protocols

Fish remains were identified to the lowest taxonomic level using the comparative collection curated at The University of Queensland archaeology laboratory (Lambrides and Weisler 2015b: 57; Weisler 2001b: appendix 3, for a description of the fish comparative collection). All cranial and post-cranial fish bone elements were attempted for identification (Lambrides and Weisler 2015a); genus- and species-level identifications were assigned cautiously to avoid over-identification given the richness of tropical western Pacific marine fish species (Driver 1992; Gobalet 2001; Lambrides and Weisler 2016; Wolverton 2013). Species-level identifications of *Katsuwonus pelamis* were achieved using few cranial elements (i.e., basypterygia, dentaries, scapulae, and quadrates), but caudal vertebrae were found to be the most useful, particularly C21-C25. Taxonomic abundance was quantified by NISP and MNI, with MNI values quantified using established zooarchaeological protocols for vertebrate fauna (Grayson 1984; Reitz and Wing 2008). For each reported cultural layer, MNI was calculated using the most frequent non repetitive element (NRE) for each side (left or right) for cranial elements and for post cranial elements, type and number along the vertebral column was used. For the units sampled with 6.4 and 3.2 mm mesh screens, the assemblages for each cultural layer were pooled prior to MNI calculation. Fish bone size was considered in all MNI calculations. Contiguous TPs were consolidated as single deposits to minimize aggregation issues.

Statistical analyses and measurement protocols

Relative taxonomic abundance was utilized to evaluate variation in composition of fish bone assemblages that extend from the initial human colonisation of Ebon Atoll to the historic period; specifically, to determine the contributing factors driving the variation over time in the relative taxonomic abundance of scombrids, particularly *Katsuwonus pelamis*. All TPs from MLEb-5, represent the early prehistoric period (~2085 cal BP, median date), MLEb-1, TP 6, the middle prehistoric period (~1840 cal BP, median date), and MLEb-1, TPs 17-20, the late prehistoric and historic periods of atoll occupation (~850 cal BP, median date – historic). All statistical analyses were conducted using MNI and NISP values. As similar trends were revealed, MNI values were used for comparability with other Pacific Island assemblages. All statistical analyses were completed using Past, version 3.11 (Hammer et al. 2001) and IBM SPSS Statistics, version 20.0.

For all richness and evenness calculations taxa were aggregated based on mutually exclusive categories. NTAXA (number of taxa) was calculated to assess taxonomic richness for each cultural layer. Shannon-Weiner index of diversity (*H′*) and Shannon's evenness (E) are measures of evenness, the proportional representation of taxa in an archaeological assemblage *H*' values can range between 0 and a theoretical maximum of 5, but commonly values are between 1.5 and 3.5, with greater species diversity and richness indicated by higher *H*' values. E values range between 0 and 1, assemblages dominated by single taxa are indicated by 0 and those that are rich and even are closer to 1 (Lyman 2008; Reitz and Wing 2008). Simpson's index of diversity (1-*D*) allowed an assessment of dominance, as values ranging between 0 and 1, low values indicate assemblages dominated by a single taxon (Magurran 2004). As NTAXA and Shannon's indices can be influenced by sample size (Faith 2013), Fisher's α was calculated to examine diversity as it is considered to be independent of sample size effects (Hayek and Buzas 2010). By tracking the occurrence of taxa represented by single individuals, Fisher's α provides a measure of overall diversity (Karlson et al. 2004). After Harris et al. (2016), chord distance analysis was employed using relative abundance data grouped by NTAXA and CA using non-aggregated (i.e. not aggregated by NTAXA) relative abundance data. Chord distance analysis is a measure of taxonomic dissimilarity and is useful for examining the degree of taxonomic change between successive cultural layers (Faith et al. 1987; Legendre and Gallagher 2001). Values range from 0 for assemblages with similar relative taxonomic abundances to $\sqrt{2}$ for assemblages with no taxa in common. Chord distance was calculated across sequential pairs of cultural layers, which were ordered chronologically within and between sites (e.g. between MLEb-5

I and MLEb-1 TP 6 IIIA, MLEb-1 TP 6 IIIA and IIA, etc.). CA allowed the associations between taxonomic composition and site/cultural layers to be examined. These statistics have been successfully implemented to examine variations in taxonomic composition of archaeological faunal and archaeobotanical assemblages (Faith 2013; Harris et al. 2016; Wright et al. 2015).

Mean trophic level (*MTL*) for each cultural layer was estimated using MNI following the formula adapted by Reitz (2004: 70) after Pauly and Christensen (1995) (see also Wing and Wing 2001). Trophic levels were assigned using data obtained from FishBase (Froese and Pauly 2016). Assessments of mean trophic level have been utilized to assess the productivity and overall sustainability of marine fisheries (e.g. Pauly et al. 1998; Pauly et al. 2000). The limitations of trophic level analysis have been discussed in both modern fisheries literature (e.g. Branch et al. 2010) and archaeological contexts (e.g. Carder and Crock 2012), given the importance of tracking true ecosystem abundance rather than using proxy catch-based trends. Archaeologically, it is important to demonstrate whether declines in trophic level actually reflect human overexploitation of the fishery and to be aware of the configuration of the marine environments as alterations through time can influence trophic interactions (Keegan 2009). Here, we do not use the *MTL* data to directly assess fishery productivity or food web stability as this would require additional ecological and zooarchaeological datasets, rather, this data is used to examine whether there is variation in the feeding guilds targeted through time. The relationship between any given taxon and trophic level is complex, for instance, fish size is not always an accurate indicator of trophic level (e.g., Jennings et al. 2001; Layman et al. 2005; Yasuno et al. 2016). Therefore, results of the *MTL* analysis should be treated as indicative of broad assemblage trends rather than a complete representation of trophic level through time.

In addition to *MTL*, we provide a preliminary assessment of trophic interactions through time by testing Houk and Musburger's (2013) model of modern coral reef stability in response to anthropogenic presence in the RMI. They report a higher biomass of large-bodied piscivores in the absence of major human populations, and under significant human exploitation a doubling in the density and biomass of small-bodied surgeonfish/unicornfish and a halving of large-bodied parrotfish (Houk and Musburger 2013: 23). In testing this model, several restrictions were dictated by sample size. Because there were insufficient samples from MLEb-1, TP 6 (6.4 mm) and from the 3.2 mm assemblages (all sites), trends between successive cultural layers for each site (MLEb-1 and MLEb-5) could not be tested, and given the limited number of measurable acanthurid bones, alterations in abundance rather than size had to be assessed. Given these parameters, the most suitable approach for testing Houk and Musburger's (2013) model was a comparison of early (MLEb-5, all TPs) and late (MLEb-1, TPs 17-20) assemblages. Alterations in fish bone size have been assessed according to methods described by Lambrides and Weisler (2015a). Scombrids identified to species, in this case, *Katsuwonus pelamis*, and scarids aggregated at the family-level, were used for this analysis. There was insufficient sample size to consider the specimens identified to genera (*Calotomus* spp*.,* *Chlorurus* spp., *Hipposcarus longiceps*, and *Scarus* spp.) individually, and while there is a similar distribution of these reported genera in the early and late assemblages, the aggregation of scarids at the family-level is problematic so the results for this taxonomic group are considered preliminary. Vertebrae were the most highly represented element for the scombrids and scarids and measurement protocols follow Lambrides and Weisler (2015a: 58). Three measurements were recorded for each vertebrae M1, M2, and M3 (Lambrides and Weisler 2015b: Figure 3). Changes in fish bone size were assessed using both Kruskal-Wallis one way analysis of variance and effect size (η^2) (Lambrides and Weisler 2015b) and bootstrapping around the median (Giovas et al. 2016) to determine whether there are statistical differences between the early (MLEb-5, all TPs) and late (MLEb-1, TP 17-20) assemblages.

Results

Tables 1 and 2 provide the quantification of fish remains from sites MLEb-1 and MLEb-5, all TPs, and 6.4 and 3.2 mm screened samples. The MNI and NISP values have been aggregated by site or, in the case of MLEb-1, spatially distinct areas of the site (TP 6 and TPs 17-20) for brevity in the text (Appendix C, provides taxonomic assignments and relative abundance grouped by site and cultural layer). Across all sites (6.4 mm only), 5959 (NISP) specimens were identified to taxon, comprising 817 (MNI) individuals; for the 6.4 mm units that also had 3.2 mm sampled assemblages, 3995 (NISP) specimens were identified to taxon, comprising 657 (MNI) individuals. Identification rates were high, with 43.1% of recovered fish specimens identified from the 6.4 mm only assemblages, and 13.2% of the 6.4 mm and 3.2 mm sampled assemblages. High identification rates were likely facilitated by the comprehensiveness of the comparative collection and consideration of all cranial and postcranial elements for identification. For example, 95% of *K. pelamis* identifications were on vertebrae. All statistical analyses reported below were completed using MNI values for comparability with other Pacific Island assemblages, but statistical analyses utilizing NISP values were tested and revealed similar trends.

Across all cultural layers of the MLEb-1 assemblages (6.4 mm samples only), the middle and late prehistoric assemblages are rich and even, with no evidence of taxonomic dominance (Table 3). However, trends for TP 6 (MLEb-1) are likely influenced by sample size effects. This is compared to MLEb-5, which dates to the earliest occupation phase, with lower values of 1-*D*, *H'*, E, and Fisher's α reported. These higher dominance values may be indicative of the increased relative abundance of tuna compared to other taxa at the site. The 6.4 and 3.2 mm sampled assemblages (all sites), were rich and even, with no evidence of taxonomic dominance, similar to the MLEb-1 6.4 mm sampled assemblages. These outcomes are influenced by the occurrence of taxa represented by a single individual, particularly the increased identification of rare taxa for the 3.2 mm samples.

Chord distance analysis (Figure 3) provided a means of assessing the dissimilarity between cultural layers at each site (MLEb-5) or area of the site (MLEb-1 TP 6 and TPs 17-20). For the 6.4 mm sampled assemblages, limited change in faunal community composition across cultural layers for each site was documented. However, the greatest changes are reported across the transition from MLEb-1, layers IIB and IIIA (TPs 17-20) and layers IIA and IIIA (TP 6), a trend that can be attributed to the significant decline in NTAXA in the basal layers (Table 3). The deposits were also ordered temporally based on radiocarbon dates to determine any further patterning in the data. Inter-site comparisons were hindered by the low number of individuals represented in the basal layers, resulting in high accounts of dissimilarity between temporally ordered site transitions. Generally, there was less dissimilarity between sequential pairs of cultural layers that were associated with the historic and late prehistoric periods. When comparing the assemblages sampled by 6.4 mm only and those sampled by 6.4 and 3.2 mm screens, less dissimilarity between successive pairs of cultural layers is apparent, which likely relates to the higher identification of rare taxa for the 3.2 mm samples.

To further elucidate the outcomes of the diversity indices and chord distance analysis, temporal variation in taxonomic composition at MLEb-1 and MLEb-5 were considered using CA. We investigated whether variation in the abundance of tuna at the sites may be contributing to these documented trends. For 6.4 mm only assemblages, Figure 4a illustrates the CA on fish bone abundances, with axis 1 accounting for 35.5% of variance and axis 2 accounting for 12.7% of variance (Appendix D, provides the CA raw data). Assemblages with positive axis 1 scores are associated with a higher number of taxonomic categories and are generally late prehistoric and historic. In contrast, assemblages with negative axis 1 scores are most associated with Scombridae and *K. pelamis* and generally early prehistoric. *Seriola* sp. is represented by one individual from MLEb-5. Figure 4b illustrates the broad changes in axis 1 scores through time; however, scores for layer IIIA (MLEb-1: TP 6 and TPs 17-20) are likely driven by low analytical samples, as a wide range of taxa, each represented mostly by a single individual, are reported for these cultural layers. Middle and late prehistoric assemblages are generally characterized by negative axis 1 scores that increase through time until they peak in the historic period. For the 6.4 mm and 3.2 mm assemblages, axis 1 accounts for 18.0% of variance and axis 2 accounts for 16.0% of variance (Appendix D, provides the CA raw data). While less pronounced than trends noted for the 6.4 mm only sampled assemblages, due to the low relative absence of tuna remains in TP 17 (MLEb-1), Scombridae, *K. pelamis*, and *Thunnus* spp.

are more associated with earlier prehistoric assemblages as are sharks (Selachii, *Carcharhinus* spp., *Nebrius ferrugineus*), however, the MNI is low for these taxa.

MTL tends to be highest for the earlier prehistoric assemblages, with a broad decline in *MTL* over time noted across the sites (Table 4). The highest *MTL* was reported from the MLEb-5 (6.4 mm only) assemblage, which likely relates to the high abundance of *K. pelamis*. We also report a corresponding decline in the relative abundance of this taxon over time (MLEb-1 TP 6 and TPs 17-20) compared to scarids, serranids, acanthurids, balistids, and holocentrids (Appendix C). *MTL* was not correlated with sample size, with the exception of TP 17 (6.4 mm and 3.2 mm); however, when layer IIIA—due to small sample size—was excluded from the Spearman's rho calculations, a non-significant result was reported ($r_s = 0.60$, $p = 0.23$) (Table 4).

Preliminary assessments of trophic interactions through time in response to anthropogenic factors were tested using Houk and Musburger's (2013) model of modern RMI coral reef stability. Changes in fish bone size were assessed using both Kruskal-Wallis one way analysis of variance and effect size (η^2) and bootstrapping around the median (Appendix E). Due to insufficient sample size, changes in acanthurid bone size could not be tested, but acanthurids are more associated with historic and late prehistoric assemblages (Table 5). For the scarids, median caudal measurements (M1, M2, and M3) for C1 and C2, were compared between the early (MLEb-5, all TPs) and late (MLEb-1, TPs 17-20) deposits, with overlap at the 95% and 99% levels reported, suggesting no statistical difference between the assemblages, which is further supported by non-significant Kruskal-Wallis test results. These outcomes are also influenced by the aggregation of genera identifications at the family-level. *K.* pelamis, median caudal measurements (M1, M2, and M3) for C21-C25 produced variable outcomes, but at this stage there is no evidence to support size change between the early and late assemblages.

Discussion

Alterations in the Ebon Atoll prehistoric tuna fishery

Analyses of two sites—MLEB-1 and MLEb-5—on Ebon Islet, have provided a continuous ~2000 year occupation sequence that tracks alterations in fish exploitation from initial colonisation of the atoll. Skipjack are more associated with the earliest prehistoric assemblages, and the highest *MTL* was also reported from the earliest habitation context at MLEb-5 where skipjack was ranked highest. A broad decline in *MTL* is noted over time, and likely relates to the declines in the relative abundance of skipjack and specimens only identified to Scombridae, when compared to scarids, serranids, acanthurids, balistids, and holocentrids. Based on the Pacific Islands archaeological studies reviewed previously, the MLEb-5 Ebon Islet site, provides the highest contribution to total MNI by scombrids for any recorded site in the region, but we acknowledge that this is likely influenced by the large area excavated, comprehensive nature of the comparative collection, range of cranial and postcranial elements used for taxonomic identification, screen sizes used with either wet and/or dry sieving, taphonomic condition of the bone, and experience of the analyst. Comparatively, fish bone assemblages from the other excavated islets on Ebon, such as the temporarily-occupied campsite on Moniak Islet and the small village site on Enekoion Islet, reported a low contribution of scombrids to the total fish catch (Harris et al. 2016). The distinctions in the spatial distribution of this resource are potentially a reflection of both site function and the assigned importance or value of scombrids. Ebon Islet has the largest village on the atoll (prehistorically and today) and it is where the *Irooj* (chief) currently lives, so it is possible, as Buck (1930) described for Samoa, that skipjack was also a high status food in the Marshall Islands. Both social and/or environmental factors were considered possibilities for driving these observed trends in archaeological scombrid abundance, but with a particular focus on skipjack fishing.

As a means of assessing coral reef stability in response to human occupation on Ebon Atoll, we tested Houk and Musburger's (2013) model that was developed using modern observations in the RMI. A higher biomass of large-bodied piscivores in the absence of major human populations was reported, and under significant human exploitation a doubling in the density and biomass of small-bodied acanthurids and a halving of large-bodied scarids. For these reasons, we assessed alterations in skipjack size over time (as a large-bodied piscivorous taxon), and using scarid and acanthurid remains, explored the potential for trophic cascades or other markers of human impacts to coral reefs driving this archaeological trend in skipjack abundance. Based on the available data, Houk and Musburger's (2013) model was not supported, and while we broadly see a decline in the relative abundance of scombrids, specifically skipjack, there is no evidence to support a change in fish size between the early and late assemblages. Houk and Musburger (2013: 30-32) reported reductions in the biomass of sharks and large-bodied piscivores due to human predation, with associated prey release of acanthurids, and while acanthurids were more prominent in the historic/late prehistoric archaeological assemblages, there was no evidence for a decline in scarid body size. While scarids are extremely susceptible to overfishing, given their high visibility day and night and preference for shallower inshore reef habitats, these life-history traits do not directly predict the probability of overexploitation for all scarid species. For instance, slow growing and large-bodied species are the most susceptible to stock depletion, but resilient life history strategies, as displayed by the tan-faced parrotfish (*Chlorurus frontalis*), can mitigate these threats and decrease the likelihood of overexploitation (Taylor et al. 2014). For these trends to be comprehensively assessed on Ebon Atoll and broadly across the Pacific Islands, more specific taxonomic identifications are required.

Based on the available samples and given the limitations discussed previously regarding the scarid and acanthurid size analysis data, at this stage there are no obvious indications of significant human impact to the inshore reef taxa Houk and Musburger (2013) identified as being susceptible, nor is there evidence for alterations in food web stability influencing skipjack abundance through time. As skipjack are a migratory species that congregate in large schools, it is unlikely that localized human predation pressure could produce the reported outcomes; that is, there was no indication that skipjack body size varied between the early and late assemblages and the frequency of these remains archaeologically does not suggest intensive exploitation of the skipjack fishery through prehistory. Thomas (2014) has stated that there is little evidence that prehistoric atoll dwellers needed to implement conservation strategies to ensure marine resource availability, due to the size and productivity of reef habitats available for resource extraction (see also Weisler 2001b). Expanding on these principles, Giovas (2016) suggested that sustainability is not merely a function of the abundance of marine resources available for exploitation, but flexible foraging practices that target a broad range of taxa, as well as the resilience and structure of exploited marine environments are all key to long-term sustainability on small islands (see also Campbell and Butler 2010; Reitz 2014). Trends documented by Houk and Musburger (2013), may actually reflect a decline in reef resilience that has developed from a combination of millennial-long human-environment interactions (e.g. Erlandson and Fitzpatrick 2006; Rick et al. 2013) and the effects of modern climate change (e.g. Graham et al. 2013; Hughes et al. 2007; van Oppen et al. 2015). However, McKechnie et al. (2014: E807) described a 10,000 year archaeological sequence of Pacific herring exploitation as ‘an example of long-term sustainability and resilience in a fishery known for its modern variability’ that, today, is associated with industrial harvesting and influenced by climatic factors, disease, and alterations in predator-prey interactions.

The changes in relative abundance of skipjack tuna could potentially be explained by a shift in capture strategies through time. For instance, a decrease in the relative importance of offshore trolling relative to other inshore strategies, such as netting, spearing, and fish traps. Historic records describe large schools of skipjack entering the lagoon that were surrounded by coconut frond sweeps, then driven to shore (Erdland 1914; Krämer and Nevermann 1938; Tinker 1950); this capture method is practiced today on Ebon. For the Ebon archaeological assemblages, there is limited evidence to support changes in capture strategy or shifts from targeting offshore to inshore resources through time, given taxonomic composition remains relatively consistent both temporally and spatially, with the exception of scombrid relative abundance, and there are no indications of relative declines in associated ‘offshore’ taxa. Fishing gear included one trolling lure fragment, two whole rotating pearlshell fishhooks and several fragments, so it is not possible to meaningfully discuss chronological trends in these artefacts. As outlined previously, ethnographic and historic accounts of tuna fishing in the Pacific, and specifically the RMI, indicate the economic, cultural, and social importance of this resource and we are not aware of any instance of avoiding tuna for cultural reasons. Given tuna are migratory fish, archaeological trends may indicate changes in the *availability* of this particular resource through time

The western and central Pacific tuna fishery and ENSO variability over the last 2000 years

Historical ecology is considered to be ‘the use of historic and prehistoric data to understand ancient and modern ecosystems, often with the goal of providing context for contemporary conservation’ (Rick and Lockwood 2013: 46-47). Using a historical ecological approach, we evaluated the Ebon Atoll archaeological data, provided links to regional trends in the western and central Pacific Islands archaeological tuna fishery data, and assessed these within the context of palaeoclimate records, which track hydroclimate variability over the last 2000 years, and recent historic capture records, which document the impact of ENSO on skipjack abundance and range throughout the tropical Pacific Ocean. This approach tested the applicability of utilizing archaeological records that document the exploitation of migratory fish to assess human responses to climate variability, both locally and to establish proxy evidence for regional models. Archaeological data from Fais Island (western Pacific) and Atafu Atoll, Ofu Island, and Savai‘i Island (central Pacific) was considered in addition to the Ebon Atoll data (Figure 1). With the exception of the Ofu Island assemblage, only family level identifications were reported by analysts, and as discussed previously, responses to ENSO variability differ depending on the species of tuna, and while problematic for considering regional trends, this does not detract from highlighting the utility of this approach.

Given the predominance of skipjack in the Ebon Atoll archaeological deposits, broad trends in historic skipjack abundance and range as they relate to ENSO variability as well as relevant palaeoclimate data is summarized briefly prior to evaluating the regional archaeological context (Griffiths et al. 2016; Lehodey 2001; Lehodey et al. 1997; Lehodey et al. 2011; Nicol et al. 2014; Thompson et al. 2013; Yan et al. 2011). The following trends relate to the western Pacific, but inverse relationships were noted for the central and eastern Pacific (Griffiths et al. 2016: Figure 4). Drier climate was recorded at ~1950-1550 cal BP and ~950-550 cal BP, with the latter period roughly corresponding to the MCA; these periods were associated with El Niño-like conditions. Based on historic records, these conditions bring an eastward displacement of the warm pool to around ~180º, corresponding to a high productivity state that expands modern commercial fisheries efforts east near 160ºW (Figure 1). Wetter climate was recorded at ~1550-950 cal BP and ~550-50 cal BP, with the latter period roughly corresponding to the LIA, similar to La Niña-like conditions, which historically see contraction of the warm pool to west of 160ºE; given its low productivity state, modern commercial fisheries commonly remain west of 160ºE. There was variability within these hydroclimate records and this needs to be considered when correlating this data with time averaged archaeological data (Figure 1).

On Ebon Atoll, skipjack are mostly associated with the earliest prehistoric assemblages, particularly MLEb-5 (~2085 cal BP), and this roughly corresponds to the dry climatic conditions and potential El Niño-like mean state that occurred between ~1950 and 1550 cal BP. While negative impacts on catchability have been reported in the west Pacific Ocean during El Niño phases, at the warm pool-cold tongue convergence zone, which is associated with an eastward displacement of the warm pool, there are increases in catchability (Lehodey 2001). Ebon Atoll is located closer to this convergence than Fais Island. This could have contributed to the comparatively delayed increase in scombrids on Fais Island between ~1550 and 1150 BP (Ono and Intoh 2011), as eventually El Niño events have a favorable impact on recruitment in the west (Lehodey 2001). However, these alterations in tuna recruitment usually operate on much smaller time scales (monthly/annually), and depend on ENSO intensity (Lehodey et al. 2011), making archaeological detection challenging. Nonetheless, given the location of Fais Island, even during La Niña events when the warm pool is at a low productivity state, historically, modern fisheries target this zone west of 160ºE, in response to the shifts in ENSO. Accordingly, the increase in scombrids represented archaeologically between ~1550 and 1150 BP, would be consistent with modern commercial fishing practices, given it is within a region that historically would contain the highest biomass of skipjack during these climatic conditions.

The Ebon Atoll results demonstrate a decline in relative abundance of scombrids/skipjack between ~850 cal BP and the historic period; specifically, scombrids are still present at the site, but do not remain the top ranked taxon. This decline is consistent with the MCA/LIA transition, with El Niño-like conditions associated with the period from ~850 to ~550 cal BP, similar conditions associated with the earliest prehistoric Ebon assemblages. Following the transition to the LIA, associated with La Niña-like conditions, the warm pool potentially contracted west, resulting in a low productivity state that would have reduced biomass in the region and had associated effects on skipjack catchability—relative to other taxa—through to the historic period. Declining abundance of scombrids between ~750 and 550 cal BP on Fais Island (Ono and Intoh 2011), was also potentially consistent with the timing of the MCA, a dry period associated with an El Niño-like mean state, suggesting the warm pool was highly productive, associated with less favorable habitats (see also Masse et al. 2006). Based on historical trends, these conditions result in an extension of commercial fisheries as far east as 160ºW, and counterintuitively these conditions negatively impact skipjack catchability in the west (Lehodey 2001), but to what extent this can be detected archaeologically requires further exploration. The sample size of archaeological tuna bones for the central Pacific is even smaller than for the western Pacific, but based on available data from Atafu Atoll, Ofu Island

and Savai‘i Island, scombrids are more prevalent in assemblages that post-date ~850-650 cal BP (Ishimura and Inoue 2006; Ono and Addison 2013; Weisler et al. 2016), a period associated with the MCA/LIA transition. This is consistent with El Niño-like conditions, increasing the catchability of scombrids/skipjack around the warm pool/cold tongue convergence zone.

Conclusion

The likelihood that ENSO variability is driving the observed trends in skipjack relative abundance on Ebon Atoll is enhanced by the corresponding regional similarities identified. The archaeological and palaeoclimate records were difficult to correlate, given that regional climate data and local/site specific archaeological fishing trends were compared. There is a need for high-resolution local palaeoclimate data, since only then can specific ecological factors be assessed (e.g. seasonality, rainfall variability, island accretion rates, reef calcification rates, etc.), prior to establishing links to regional models of climate change and resource abundance. Additional radiocarbon dating of the sites, and especially direct dating of tuna bones, could also refine the chronology and allow assessment of fine-scale temporal changes in tuna abundance.

Cultural factors undoubtedly influenced these archaeological trends in tuna fishing, as the occurrence of scombrids at these sites is a direct reflection of human subsistence practices, decision making, and social dictates. However, in this region of the Pacific we have highlighted the potential influence of ENSO variability on the skipjack fishery over the last 2000 years and the relevance of utilizing archaeological abundance data to contribute to our understanding of long term patterning in tuna biogeography. Moving forwards there is a need to complete species-level identifications of archaeological tuna remains, coupled with new high-resolution, local climatic data throughout the late Holocene for assessing long term trends in the western and central Pacific Ocean tuna fishery. By utilizing archaeological data, past trends in tuna abundance and distribution in relation to climate models may provide useful insights for managing sustainable fisheries into the future.

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Table 1. Quantification of fish remains from MLEb-1 and MLEb-5 (6.4 mm only).

	MLEb-1				**MLEb-5**	
	Late (TP 17-20)		**Middle (TP 6)**		**Early (All TPs)**	
Taxon	**NISP (%)**	**MNI (%)**	**NISP (%)**	**MNI (%)**	**NISP (%)**	**MNI (%)**
Actinopterygii (unid. to element)	129		3		31	
Selachii (sharks)	8 (0.2)	2 (0.4)	17 (20.0)	2 (5.3)	9 (0.6)	1 (0.4)
Carcharhinidae (requiem sharks)						
Carcharhinus cf. *longimanus*	1 (<0.1)	1 (0.2)	1 (1.2)	1 (2.6)		
Carcharhinus cf. *melanopterus*	1 (<0.1)	1 (0.2)				
Muraenidae (moray eels)	16 (0.4)	7 (1.4)				
Acanthuridae (surgeonfishes)	103 (2.5)	26 (5.1)			9 (0.6)	5 (1.9)
Acanthurus spp.	43 (1.0)	7 (1.4)			5 (0.3)	1 (0.4)
Ctenochaetus spp.	11 (0.3)	4 (0.8)			1 (0.1)	1 (0.4)
Naso spp.	9 (0.2)	3 (0.6)			5 (0.3)	4 (1.5)
Balistidae (triggerfishes)	587 (14.0)	23 (4.5)	1 (1.2)	1 (2.6)	29 (1.8)	9 (3.3)
Belonidae (needlefishes)	13 (0.3)	6 (1.2)			4 (0.3)	2 (0.7)
Bothidae (lefteye flounders)	18 (0.4)	5 (1.0)	1 (1.2)	1 (2.6)	3 (0.2)	1 (0.4)
Carangidae (jacks)	83 (2.0)	15 (2.9)	1 (1.2)	1 (2.6)	9 (0.6)	1 (0.4)
Carangoides spp.	8 (0.2)	3 (0.6)			2 (0.1)	1 (0.4)
Caranx spp.	45 (1.1)	8 (1.6)	1 (1.2)	1 (2.6)	18 (1.1)	3 (1.1)
Decapterus spp.	32 (0.8)	6 (1.2)	1 (1.2)	1 (2.6)	8 (0.5)	4 (1.5)
Elagatis bipinnulatus	27 (0.6)	3 (0.6)			1 (0.1)	1 (0.4)
Selar spp.	87 (2.1)	7 (1.4)			2 (0.1)	1 (0.4)
Seriola spp.					1 (0.1)	1 (0.4)
Chaetodontidae (butterflyfishes)	9 (0.2)	1 (0.2)				
Cirrhitidae (hawkfishes)	43 (1.0)	8 (1.6)			7 (0.4)	3 (1.1)
Diodontidae (porcupinefishes)						
Diodon spp.	192 (4.6)	6 (1.2)			5 (0.3)	1 (0.4)
Exocoetidae (flying fishes)	54 (1.3)	6 (1.2)			2 (0.1)	2 (0.7)
Fistulariidae (cornetfishes)						
Fistularia commersonii	24 (0.6)	5 (1.0)			11 (0.7)	2 (0.7)
Holocentridae (squirrelfishes)	88 (2.1)	26 (5.1)	1 (1.2)	1 (2.6)	8 (0.5)	5 (1.9)
Myripristis spp.	22 (0.5)	3 (0.6)			6 (0.4)	2 (0.7)
Neoniphon spp.	11 (0.3)	3 (0.6)				
Sargocentron spp.	78 (1.9)	12 (2.4)	1 (1.2)	1 (2.6)	13 (0.8)	2 (0.7)
Kuhliidae (flagtails)						
Kuhlia spp.	8 (0.2)	3 (0.6)			1 (0.1)	1 (0.4)
Kyphosidae (sea chubs)						
Kyphosus spp.	72 (1.7)	5 (1.0)			5 (0.3)	1 (0.4)
Labridae (wrasses)	75 (1.8)	13 (2.6)			16 (1)	6 (2.2)
Lethrinidae (emperors)	37 (0.9)	6 (1.2)	3 (3.5)	2 (5.3)	9 (0.6)	1 (0.4)
Gnathodentex aureolineatus	2 (<0.1)	2 (0.4)			1 (0.1)	1 (0.4)
Lethrinus spp.	110 (2.6)	15 (2.9)			41 (2.6)	4 (1.5)
Monotaxis grandoculis	35 (0.8)	9 (1.8)			23 (1.5)	7 (2.6)
Lutjanidae (snappers)	145 (3.5)	14 (2.8)	1 (1.2)	1 (2.6)	9 (0.6)	2 (0.7)
Lutjanus spp.	137 (3.3)	16 (3.1)			46 (2.9)	4 (1.5)
Lutjanus cf. *kasmira*	42 (1.0)	13 (2.6)	2 (2.4)	2 (5.3)	13 (0.8)	4 (1.5)
Mugilidae (mullets)	16 (0.4)	5 (1.0)			2 (0.1)	1 (0.4)
Mullidae (goatfishes)	25 (0.6)	4 (0.8)				
Mulloidichthys spp.	55 (1.3)	7 (1.4)			4 (0.3)	1 (0.4)
Parupeneus spp.	24 (0.6)	5 (1.0)			8 (0.5)	1 (0.4)
Ostraciidae (boxfishes)	58 (1.4)	1 (0.2)				
Pomacentridae (damselfishes)	11 (0.3)	1 (0.2)			1 (0.1)	1 (0.4)
Scaridae (parrotfishes)	233 (5.6)	37 (7.3)	12 (14.1)	5 (13.2)	216 (13.6)	16 (5.9)
Calotomus spp.	9 (0.2)	4 (0.8)				
Chlorurus spp.	47 (1.1)	12 (2.4)			39 (2.5)	7 (2.6)
Hipposcarus longiceps	103 (2.5)	14 (2.8)	4 (4.7)	2 (5.3)	103 (6.5)	9 (3.3)
Scarus spp.	104 (2.5)	10 (2.0)			35 (2.2)	5 (1.9)
Scombridae (mackerels and tunas)	75 (1.8)	15 (2.9)	19 (22.4)	5 (13.2)	161 (10.2)	42 (15.6)
Katsuwonus pelamis	387 (9.2)	27 (5.3)	11 (12.9)	5 (13.2)	567 (35.8)	83 (30.7)
Thunnus spp.	13 (0.3)	5 (1.0)			3 (0.2)	1 (0.4)

Serranidae (groupers)	550 (13.1)	33 (6.5)	6 (7.1)	4 (10.5)	100 (6.3)	7 (2.6)
Anyperodon leucogrammicus	10 (0.2)	2 (0.4)			1 (0.1)	1 (0.4)
Cephalopholis spp.	9 (0.2)	4 (0.8)			1 (0.1)	1 (0.4)
Epinephelus spp.	19 (0.5)	7 (1.4)			10 (0.6)	3 (1.1)
Plectropomus spp.	7 (0.2)	2 (0.4)			2 (0.1)	2 (0.7)
Variola louti	18 (0.4)	5 (1.0)	1 (1.2)	1 (2.6)	7 (0.4)	3 (1.1)
Siganidae (rabbitfishes)						
Siganus spp.	118 (2.8)	11 (2.2)	1 (1.2)	1 (2.6)	2 (0.1)	1 (0.4)
Sphyraenidae (barracudas)						
Sphyraena spp.	21 (0.5)	5 (1.0)			2 (0.1)	1 (0.4)
Total identified	4188	509	85	38	1586	270
Total bones	10666		154		2761	
Total weight (g)	1590.8		56.1		850.0	
% identified	39.26		55.2		57.4	

Table 2. Quantification of fish remains from MLEb-1 and MLEb-5 (6.4 mm and 3.2 mm).

	MLEb-1				**MLEb-5**	
	Late (TP 17)		**Middle (TP 6)**		**Early (TP 13)**	
Taxon	**NISP (%)**	**MNI (%)**	**NISP (%)**	**MNI (%)**	**NISP (%)**	**MNI (%)**
Actinopterygii (unid. to element)	310		66		31	
Selachii (sharks)	2 (0.1)	1 (0.3)	28 (2.7)	2 (0.9)		
Carcharhinidae (requiem sharks)						
Carcharhinus cf. *amblyrhynchos*	1 (<0.1)	1 (0.3)				
Carcharhinus cf. *melanopterus*	1 (<0.1)	1 (0.3)	39 (3.7)	4 (1.9)	6 (2.1)	1 (1.5)
Triaenodon obesus			1 (0.1)	1 (0.5)		
Ginglymostomatidae (carpet sharks)						
Nebrius ferrugineus			1 (0.1)	1 (0.5)		
Muraenidae (moray eels)	54 (2.0)	11 (2.9)	37 (3.5)	7 (3.3)	1 (0.3)	1 (1.5)
Acanthuridae (surgeonfishes)	78 (2.9)	16 (4.2)	18 (1.7)	5 (2.3)		
Acanthurus spp.	25 (0.9)	8 (2.1)	2 (0.2)	2 (0.9)	1 (0.3)	1 (1.5)
Ctenochaetus spp.	5 (0.2)	3 (0.8)	1 (0.1)	1 (0.5)		
Naso spp.	4 (0.2)	2 (0.5)	4 (0.4)	2 (0.9)	1 (0.3)	1 (1.5)
Balistidae (triggerfishes)	255 (9.6)	11 (2.9)	69 (6.6)	9 (4.2)	10 (3.4)	1 (1.5)
Belonidae (needlefishes)	50 (1.9)	5 (1.3)	60 (5.7)	8 (3.7)	21 (7.2)	1 (1.5)
Bothidae (lefteye flounders)	31 (1.2)	5 (1.3)	13 (1.2)	2 (0.9)	5 (1.7)	1 (1.5)
Caesionidae (fusiliers)	1 (<0.1)	1 (0.3)				
Carangidae (jacks)	84 (3.2)	8 (2.1)	46 (4.4)	6 (2.8)	12 (4.1)	2 (3.1)
Carangoides spp.	9 (0.3)	2 (0.5)			1 (0.3)	1 (1.5)
Caranx spp.	11 (0.4)	7 (1.9)	4 (0.4)	2 (0.9)	2 (0.7)	1 (1.5)
Decapterus spp.	49 (1.8)	11 (2.9)	23 (2.2)	8 (3.7)	7 (2.4)	2 (3.1)
Elagatis bipinnulatus	10 (0.4)	3 (0.8)				
Scomberoides Iysan			1 (0.1)	1 (0.5)		
Selar spp.	27 (1.0)	8 (2.1)	3 (0.3)	2 (0.9)		
Seriola spp.			1 (0.1)	1 (0.5)		
Chaetodontidae (butterflyfishes)	8 (0.3)	2 (0.5)	2 (0.2)	1 (0.5)	1 (0.3)	1 (1.5)
Cirrhitidae (hawkfishes)	67 (2.5)	9 (2.4)	21 (2.0)	8 (3.7)	10 (3.4)	3 (4.6)
Diodontidae (porcupinefishes)						
Diodon spp.	78 (2.9)	3 (0.8)	11 (1.0)	1 (0.5)	1 (0.3)	1 (1.5)
Exocoetidae (flying fishes)	267 (10.1)	12 (3.2)	78 (7.4)	7 (3.3)	20 (6.9)	1 (1.5)
Fistulariidae (cornetfishes)						
Fistularia commersonii	11 (0.4)	3 (0.8)	1 (0.1)	1 (0.5)	2 (0.7)	1 (1.5)
Gerreidae (mojarras)						
Gerres spp.	6 (0.2)	4 (1.1)				
Holocentridae (squirrelfishes)	76 (2.9)	19 (5.0)	35 (3.3)	7 (3.3)	8 (2.8)	3 (4.6)
Myripristis spp.	47 (1.8)	8 (2.1)	18 (1.7)	5 (2.3)	3 (1)	1 (1.5)
Neoniphon spp.	6 (0.2)	2 (0.5)	2 (0.2)	1 (0.5)		
Sargocentron spp.	103 (3.9)	12 (3.2)	35 (3.3)	9 (4.2)	16 (5.5)	2 (3.1)
Kuhliidae (flagtails)						
Kuhlia spp.	18 (0.7)	5 (1.3)	7 (0.7)	2 (0.9)		
Kyphosidae (sea chubs)						
Kyphosus spp.	36 (1.4)	7 (1.9)	5 (0.5)	2 (0.9)	2 (0.7)	1 (1.5)
Labridae (wrasses)	31 (1.2)	8 (2.1)	20 (1.9)	5 (2.3)	4 (1.4)	2 (3.1)
Lethrinidae (emperors)	60 (2.3)	8 (2.1)	45 (4.3)	5 (2.3)	8 (2.8)	1 (1.5)
Lethrinus spp.	84 (3.2)	12 (3.2)	19 (1.8)	8 (3.7)	3 (1.0)	1 (1.5)
Monotaxis grandoculis	43 (1.6)	7 (1.9)	22 (2.1)	2 (0.9)	17 (5.9)	4 (6.2)
Lutjanidae (snappers)	106 (4)	12 (3.2)	31 (3.0)	5 (2.3)	11 (3.8)	2 (3.1)
Aprion virescens	1 (<0.1)	1 (0.3)			1 (0.3)	1 (1.5)
Lutjanus spp.	66 (2.5)	11 (2.9)	3 (0.3)	2 (0.9)	10 (3.4)	2 (3.1)
Lutjanus cf. *kasmira*	9 (0.3)	4 (1.1)	2 (0.2)	2 (0.9)	3 (1.0)	2 (3.1)
Mugilidae (mullets)	8 (0.3)	2 (0.5)	5 (0.5)	2 (0.9)	4 (1.4)	1 (1.5)
Mullidae (goatfishes)	17 (0.6)	5 (1.3)	18 (1.7)	5 (2.3)	10 (3.4)	1 (1.5)
Mulloidichthys spp.	35 (1.3)	7 (1.9)	14 (1.3)	4 (1.9)	7 (2.4)	1 (1.5)
Parupeneus spp.	18 (0.7)	5 (1.3)	3 (0.3)	2 (0.9)	4 (1.4)	1 (1.5)
Ostraciidae (boxfishes)	50 (1.9)	4 (1.1)	12 (1.1)	2 (0.9)		
Pomacentridae (damselfishes)	24 (0.9)	5 (1.3)	2 (0.2)	1 (0.5)	4 (1.4)	1 (1.5)

Scaridae (parrotfishes)	99 (3.7)	11 (2.9)	87 (8.3)	9 (4.2)	10 (3.4)	2 (3.1)
Chlorurus spp.	9 (0.3)	4 (1.1)	13 (1.2)	3 (1.4)	3 (1.0)	1 (1.5)
Hipposcarus longiceps	25 (0.9)	9 (2.4)	12 (1.1)	5 (2.3)	1 (0.3)	1 (1.5)
Scarus spp.	16 (0.6)	6 (1.6)	7 (0.7)	4 (1.9)		
Scombridae (mackerels and tunas)	56 (2.1)	11 (2.9)	43 (4.1)	8 (3.7)	9 (3.1)	5 (7.7)
Katsuwonus pelamis	64 (2.4)	10 (2.6)	14 (1.3)	5 (2.3)	9 (3.1)	2 (3.1)
Thunnus spp.	6 (0.2)	3 (0.8)	3 (0.3)	3 (1.4)		
Serranidae (groupers)	336 (12.7)	22 (5.8)	81 (7.7)	12 (5.6)	34 (11.7)	3 (4.6)
Anyperodon leucogrammicus	2 (0.1)	2 (0.5)			1 (0.3)	1 (1.5)
Cephalopholis spp.	6 (0.2)	2 (0.5)	4 (0.4)	2 (0.9)		
Epinephelus spp.	13 (0.5)	5 (1.3)	4 (0.4)	3 (1.4)	2 (0.7)	1 (1.5)
Variola louti	2 (0.1)	2 (0.5)	4 (0.4)	3 (1.4)		
Siganidae (rabbitfishes)						
Siganus spp.	20 (0.8)	5 (1.3)	9 (0.9)	2 (0.9)	1 (0.3)	1 (1.5)
Sphyraenidae (barracudas)						
Sphyraena spp.	29 (1.1)	5 (1.3)	7 (0.7)	2 (0.9)	4 (1.4)	1 (1.5)
Total identified	2655	378	1050	214	290	65
Total bones	18480		9168		2727	
Total weight (g)	591.17		268.93		64.52	
% identified	14.4		11.5		10.6	

Table 3. Measures of taxonomic heterogeneity: NTAXA, Shannon-Weiner index of diversity (*H'*) and Shannon's evenness (E), Simpson's index of diversity (1-*D*) and Fisher's α: (a) 6.4 mm only, and (b) 6.4 mm and 3.2 mm. No fish bones were recovered from the TP 6 IIB (6.4 mm only) assemblage.

(a)

	MLEb-1											**MLEb-5**
	Late (TP 17-20)						**Middle (TP 6)**					**Early (All TPs)**
Index	**Historic**	**IA**	**IB**	**IIA**	**IIB**	**IIIA**	**IA**	**IB**	**IIA**	**IIB**	**IIIA**	**I**
NTAXA	13	27	23	19	22	7	10	4	4	-	4	24
1-*D*	0.891	0.909	0.925	0.922	0.888	0.857	0.880	0.694	0.667	-	0.720	0.749
H'	2.362	2.676	2.799	2.729	2.600	1.946	2.207	1.277	1.242	-	1.332	2.032
E	0.921	0.812	0.893	0.927	0.841	1	0.959	0.921	0.896	-	0.961	0.640
Fisher's α	7.490	7.351	10.710	13.750	12.350	0	7.959	3.878	5.245	-	9.284	6.364

(b)

	MLEb-1											**MLEb-5**
	Late (TP 17)						**Middle (TP 6)**					**Early (TP 13)**
Index	**Historic**	**IA**	**IB**	**IIA**	**IIB**	**IIIA**	**IA**	**IB**	**IIA**	**IIB**	**IIIA**	**I**
NTAXA	13	29	28	20	20	10	26	21	15	9	7	25
1-*D*	0.882	0.928	0.936	0.931	0.919	0.876	0.930	0.934	0.924	0.880	0.840	0.932
H'	2.340	2.897	2.968	2.823	2.752	2.205	2.887	2.850	2.636	2.164	1.889	2.906
E	0.912	0.860	0.891	0.942	0.919	0.958	0.886	0.936	0.974	0.985	0.971	0.903
Fisher's α	8.721	10.560	12.420	18.530	16.470	19.860	10.520	12.010	17.120	43.450	14.490	14.870

Table 4. *MTL* analysis of fish remains from MLEb-1 and MLEb-5 by cultural layers (6.4 mm and 3.2 mm) and Spearman's rho calculations to assess sample size effects. Non-significant Spearman's rho results ($\alpha = >0.05$) indicate there was no correlation between sample size and *MTL.* No fish bones were recovered from the TP 6 IIB (6.4 mm only) assemblage and no historic material was recovered from TP 6.

	6.4 mm only		**6.4 mm and 3.2 mm**	
	MLEb-1			
Layer	**Late (TP 17-20)**	**Middle (TP 6)**	**Late (TP 17)**	**Middle (TP 6)**
Historic	3.16	-	3.20	-
IA	3.31	3.78	3.44	3.56
IB	3.61	3.60	3.57	3.49
IIA	3.53	3.83	3.38	3.51
IIB	3.63	-	3.63	3.73
IIIA	3.53	2.78	3.63	3.44
$r_s =$	0.20, $p = 0.72$	0.70, $p = 0.23$	1.00, $p = 0.00$	0.30, $p = 0.52$
	MLEb-5			
	Early (All TPs)		**Early (TP 13)**	
I	3.75		3.62	

Table 5. Quantification of fish remains from MLEb-1 and MLEb-5 by cultural layers for Acanthuridae, Scaridae and Scombridae (6.4 mm and 3.2 mm), by NISP and MNI reported in brackets.

	MLEb-1											**MLEb-5**
Taxon	**Hist.**	**IA**	**IB**	**IIA**	**IIB**	**IIIA**	**IA**	**IB**	**IIA**	**IIB**	**IIIA**	**I**
(6.4 mm only)	**Late (TP 17-20)**						**Middle (TP 6)**					**Early (All TPs)**
Acanthuridae	9(2)	87(19)	3(1)	3(3)		1(1)						9(5)
Acanthurus spp.	17(3)	25(3)		1(1)								5(1)
Ctenochaetus spp.	4(1)	6(2)	1(1)									1(1)
Naso spp.		7(1)	1(1)		1(1)							5(4)
Scaridae	3(2)	205(28)	12(2)	3(1)	10(4)		5(2)	3(1)	3(1)		1(1)	216(16)
Calotomus spp.	1(1)	6(1)			1(1)	1(1)						
Chlorurus spp.	2(1)	40(8)	4(2)		1(1)							39(7)
Hipposcarus longiceps		85(9)	8(1)	3(2)	7(2)			3(1)			1(1)	103(9)
Scarus spp.	4(1)	89(5)	7(2)	2(1)	1(1)							35(5)
Scombridae		36(4)	9(3)	5(1)	25(7)		9(2)	8(2)	2(1)			161(42)
Katsuwonus pelamis		207(9)	46(6)	35(4)	95(7)	4(1)	6(2)	3(1)	2(2)			567(83)
Thunnus spp.		5(1)	5(2)	1(1)	2(1)							3(1)
(6.4 mm and 3.2 mm)	**Late (TP 17)**						**Middle (TP 6)**					**Early (TP 13)**
Acanthuridae	14(2)	38(7)	21(4)	2(1)	2(1)	1(1)	12(2)	5(2)		1(1)		
Acanthurus spp.	9(3)	12(3)	3(1)	1(1)				1(1)	1(1)			1(1)
Ctenochaetus spp.	2(1)	3(2)							1(1)			
Naso spp.	3(1)	1(1)					3(1)	1(1)				1(1)
Scaridae	3(1)	71(6)	15(2)	4(1)	6(1)		65(5)	15(2)	5(1)		2(1)	10(2)
Calotomus spp.												
Chlorurus spp.		6(2)	2(1)	1(1)			9(2)	4(1)				3(1)
Hipposcarus longiceps		16(5)	3(1)	5(2)	1(1)		1(1)	9(2)	1(1)		1(1)	1(1)
Scarus spp.	3(1)	6(2)	6(2)		1(1)		4(3)	3(1)				
Scombridae		32(4)	17(3)	3(1)	4(3)		29(5)	11(2)	3(1)			9(5)
Katsuwonus pelamis		33(3)	6(2)	8(2)	16(2)	1(1)	8(2)	3(1)	3(2)			9(2)
Thunnus spp.		3(1)	2(1)		1(1)		3(3)					

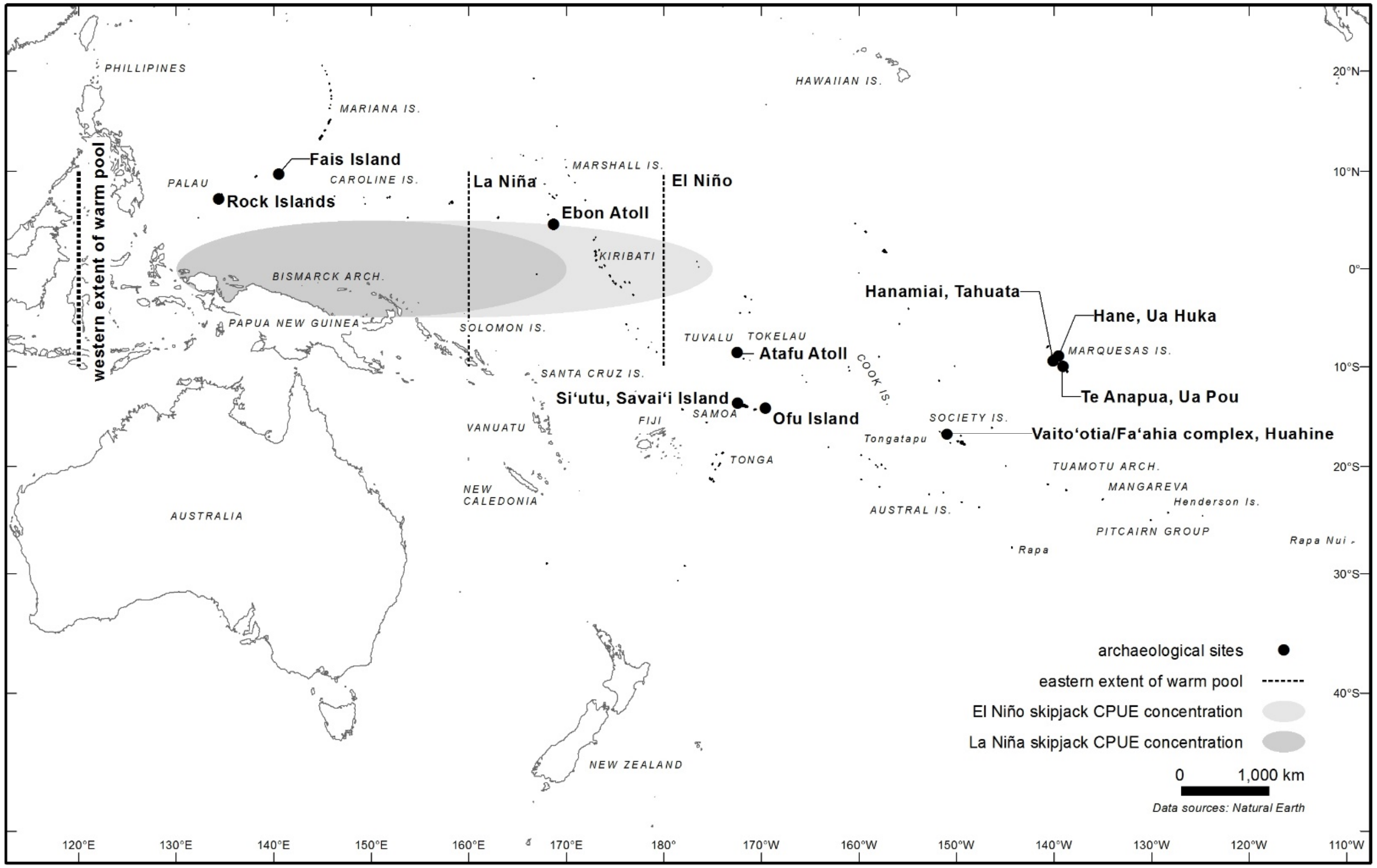

Figure 1. Map of the Pacific Islands with key archaeological sites mentioned in text (Davidson et al. 1999; Fraser 1998; Ishimura and Inoue 2006; Leach et al. 1997; Leach et al. 1984; Masse et al. 2006; Ono and Addison 2013; Ono and Intoh 2011; Rolett 1998; Weisler et al. 2016). The dotted lines provide the approximate extent of the warm pool under La Niña and El Niño conditions recorded historically (Lehodey 2001; Lehodey et al. 1997). The shaded areas indicate the location of the highest recorded skipjack CPUE concentration for the western and central Pacific Ocean under La Niña and El Niño conditions recorded in the late 20th century (after Lehodey et al. 1997:Figure 1).

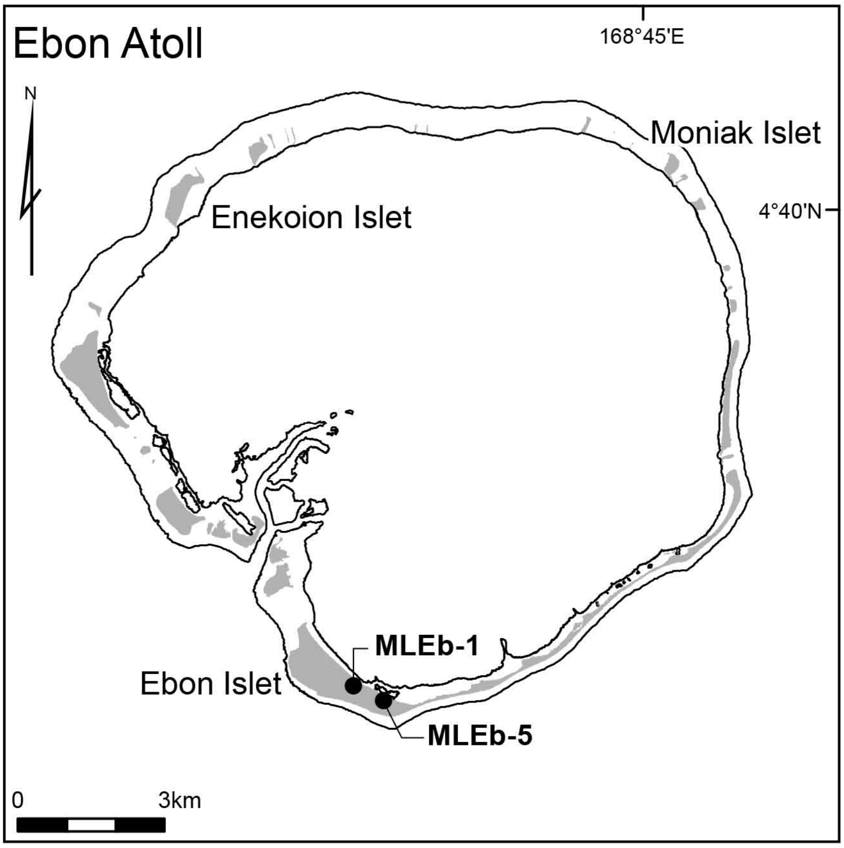

Figure 2. Map of Ebon Atoll with the location of archaeological sites mentioned in text labelled.

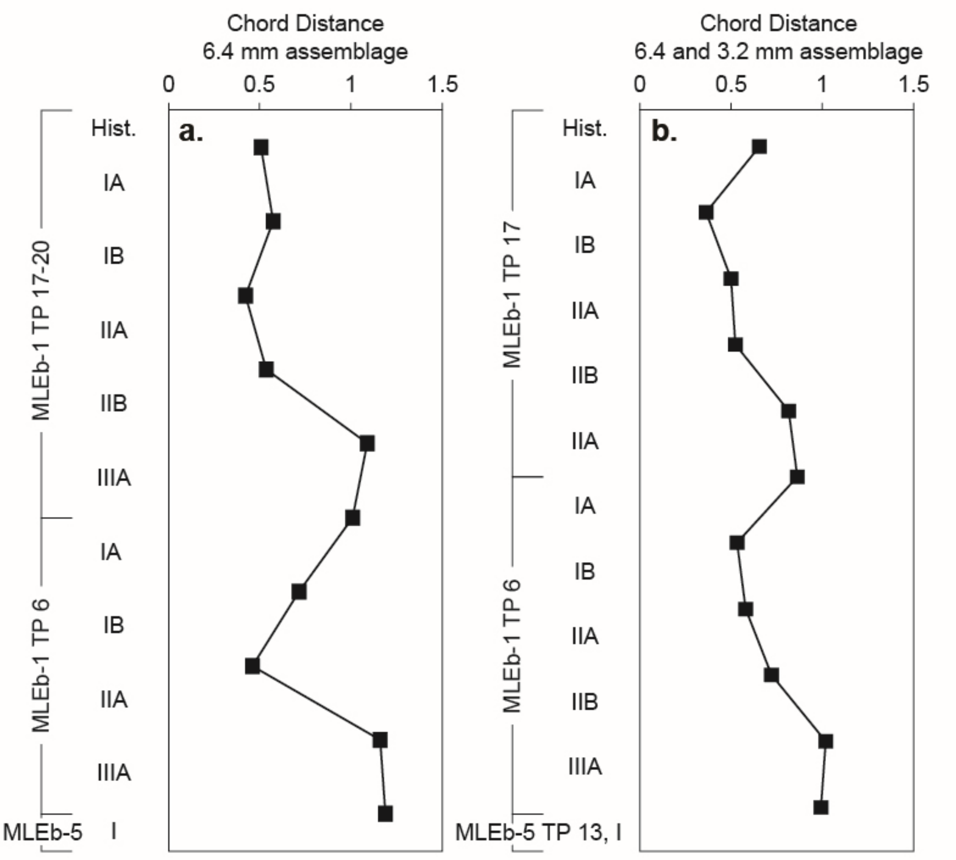

Figure 3. Chord distance analysis across sequential pairs of cultural layers, ordered chronologically within and between sites: (a) 6.4 mm only, and (b) 6.4 mm and 3.2 mm.

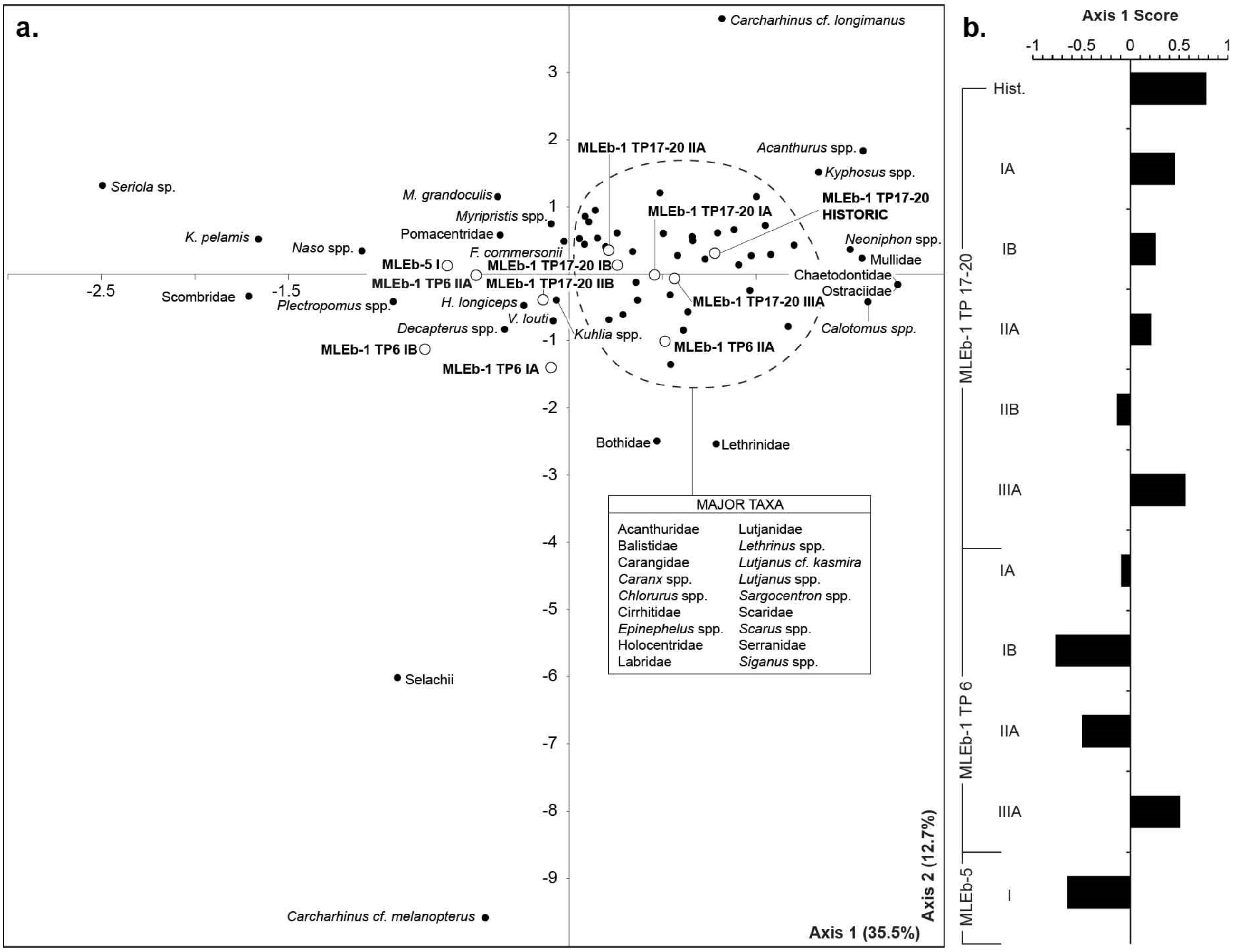

Figure 4. (a) Correspondence analysis of taxonomic composition across all cultural layers at MLEb-1 and MLEb-5, and for brevity, major taxa are defined as those represented by at least 10 individuals, and (b) axis 1 scores ordered from the oldest assemblage (MLEb-5) to the most recent historic assemblage.