

ORIGINAL ARTICLE OPEN ACCESS

Zooarchaeological Analysis of an Atoll Assemblage From Central Micronesia

Philippa Jorissen¹  | Gabriel Sanchez^{1,2} | Scott M. Fitzpatrick^{1,2} 

¹Department of Anthropology, University of Oregon, Eugene, Oregon, USA | ²Museum of Natural and Cultural History, University of Oregon, Eugene, Oregon, USA

Correspondence: Philippa Jorissen (pjorisse@uoregon.edu)

Received: 18 April 2025 | **Revised:** 28 January 2026 | **Accepted:** 29 January 2026

Keywords: Caroline Islands | faunal analysis | Mwoakilloa (Mokil) | Micronesia | Pacific | Remote Oceania

Mots-Clés: Mwoakilloa (Mokil) | analyse faunique | îles Carolines | Micronésie | Pacifique | Océanie éloignée

ABSTRACT

There has been a dearth of archaeological research on atolls in the central-eastern Caroline Islands of Micronesia. This has limited our understanding of pre-contact subsistence and settlement strategies in these more marginal and remote environments, particularly in regards to zooarchaeological data. Here, we present the first analysis of faunal material recovered from Mwoakilloa (Mokil) atoll with occupation dating between ca. 1700 calBP to the present. The sample comprises nearly 6000 specimens across 53 families, representing both vertebrates and invertebrates, and is dominated by molluscs. Overall results indicate that bivalves declined over time, while gastropods increased slightly. The most prominent families include mesodesmatids, cone snails, true conchs, and ceriths. Fish, particularly parrotfish, wrasses, and groupers, were intensively harvested between 1550 – 910 calBP. Rats also first appeared around the same time, while birds and dogs were found earlier, ca. 1700 – 1400 calBP. Neither rat nor dog are represented in the earliest layers, suggesting that these species, often considered part of the “transported landscape” were not initially introduced when the island was settled.

Résumé

Les recherches archéologiques sur les atolls du centre-est des îles Carolines en Micronésie sont rares. Ceci a limité notre compréhension des stratégies de subsistance et d'établissement précontact dans ces environnements plus marginaux et reculés, notamment en ce qui concerne les données zooarchéologiques. Nous présentons ici la première analyse de matériel faunique récupéré sur l'atoll de Mwoakilloa (Mokil), occupé entre environ 1700 calBP et aujourd'hui. L'échantillon comprend près de 6000 spécimens répartis en 53 familles, représentant à la fois des vertébrés et des invertébrés, et est dominé par les mollusques. Les résultats globaux indiquent que les bivalves ont décliné au fil du temps, tandis que les gastéropodes ont légèrement augmenté. Les familles les plus importantes comprennent les mésodesmatides, les escargots cônes, les conques et les cérithes. Les poissons, en particulier les poissons-perroquets, les labres et les mérous, ont été intensivement pêchés entre 1550 et 910 calBP. Les rats ont également fait leur apparition à la même époque, tandis que les oiseaux et les chiens ont été découverts plus tôt, vers 1700 – 1400 calBP. Ni le rat ni le chien ne sont représentés dans les couches les plus anciennes, ce qui suggère que ces espèces, souvent considérées comme faisant partie du “transported landscape”, n'ont pas été initialement introduites lors de la colonisation de l'île.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2026 The Author(s). *Archaeology in Oceania* published by John Wiley & Sons Australia, Ltd on behalf of University of Sydney.

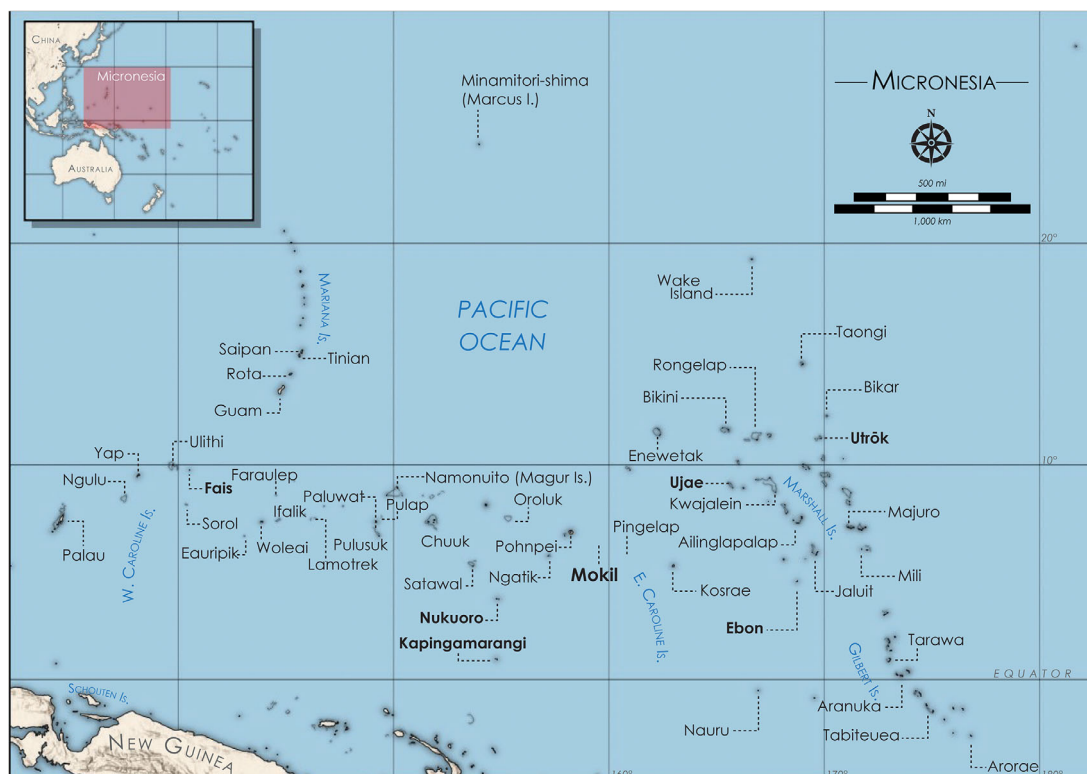


FIGURE 1 | Map of western-central Micronesia with the discussed atolls in bold.

1 | Introduction

Compared to other parts of Remote Oceania, Micronesia, and atolls in particular, have received less attention archaeologically. Micronesia, an expansive region in the northwest tropical Pacific, covers an area of around 7.4 million km² and comprises more than 2000, mostly low-lying islands (Fitzpatrick and Napolitano 2023; Gakuhari et al. 2013; Thomas 2019). This lack of research generally has limited our understanding of how this region was first settled, subsequent adaptations that took place—particularly in terms of subsistence—and how atolls compare to the larger, mostly high volcanic islands scattered unevenly across the region. Zooarchaeological research to examine these trends is thus also fairly limited as are sites with securely or well-dated contexts (Thomas 2019).

Our research focuses on understanding pre-European contact resource acquisition and subsistence strategies on Mwoakilloa (Mokil), a small atoll in the Central Caroline Islands of Micronesia (Figure 1). In particular, we were interested in comparing our observations with other atolls in the general region to gather a better understanding of: (1) the potential effects of human predation on marine resources over time, which is important for understanding past human-environmental interactions and the legacy of these processes on the present biodiversity of Mokil (see Braje et al. 2017; Pauly et al. 1998; Thomas 2019); and (2) the timing of the arrival of commensal animals on Mokil and in the region, as this can contribute to our understanding of not only early subsistence strategies but also timing and direction of human movement in the area.

Below, we first provide an environmental and archaeological background for Mokil and Micronesia. We then discuss the

methods used in our analysis on a sample of the larger zooarchaeological assemblage recovered from a 1 × 1 m unit that was excavated to a depth of 2.9 m. Next, we report on the analysis of both invertebrate and vertebrate remains. Our results indicate that a diverse array of invertebrate and vertebrate taxa native to the region were harvested during site occupation. We also found there to be similarities in subsistence strategies between Utrök (Weisler 2001a), Ujae (Weisler 2001b), Ebon (Marshall Island) (Harris et al. 2016), Fais (Ono and Intoh 2011), Kapingamarangi (Federated States of Micronesia) (Leach and Davidson 1988), and Mokil, which showed emphases on similar fish families and sometimes invertebrates. However, compared to previous studies (e.g. Weisler 2001a), we did not find any evidence of overexploitation (unsustainable harvesting or consumption of a resource) or extirpation (to completely destroy or remove something).

Additionally, we found that non-native taxa were introduced to the site either intentionally or unintentionally by some of the earliest human settlers as part of the well-established commensal model (Matisoo-Smith 2009). This is similar to Utrök (Marshall Islands) (Weisler 2001a), where dog and rat were recorded around the same time as on Mokil, but different from Ebon (Harris et al. 2016) and Fais (Ono and Intoh 2011), where pig was also encountered.

1.1 | Environmental Background and Geography

Micronesia covers an area of approximately 7,400,000 km², but of that vast area of ocean, only around 4,100 km² (0.0006%) is land. Nearly all of the thousands of islands in Micronesia are islets found within atolls, which are typically ≤3 m in elevation at mean sea level. These consist of low-lying carbonate substrates and are

primarily coral reef systems covered in loose coral rock, rubble, and sand, only becoming habitable over the last few thousand years when sea levels stabilized and a Ghyben Herzberg lens formed so that people could reliably access freshwater (Dickinson 2003; Irwin 1992; Nunn 1994; Weisler et al. 2012).

Archaeologists have argued that the absence of surface water, poor soil development, and low diversity of terrestrial flora and fauna required various adaptations to sustain human populations through time (Kirch 2017; Thomas 2009; Wickler 2004). As a result, atolls are sometimes characterised as ‘biodiverse coldspots’ (Thaman 2008, p. 34) and ‘marginal living spaces’ with impoverished resource bases, from a terrestrial perspective (Thomas 2015, p. 1; Weisler 2001a, p. 111; Wickler 2004, p. 30). Additionally, these islands would have been, and continue to be, particularly vulnerable to climatic and weather events such as rising sea levels and tropical storms (Kirch 2000; Thomas 2019; Weisler 2001a, 2001b).

Freshwater is the most critical resource on atolls and smaller limestone islands in general (Fitzpatrick et al. 2016; Schneider et al. 2024; Taborosi and Collazo Sanchez 2009). While catchment systems are integral to capturing and storing water as a short-term measure, they would have been insufficient for long-term survival (Fitzpatrick et al. 2016). As a result, humans both in the past and today dig wells to access the Ghyben-Herzberg lens of freshwater from rainfall that sits above denser salt water (Thomas 2019; Schneider et al. 2024). Knowing how to access and exploit these lenses was essential to survival on atolls, not only for drinking water but also for cultivating plants that are not salt tolerant. Even today, people on Mokil and most other atolls rely heavily on these freshwater lenses. However, this does not always ensure a consistent source. During droughts, drinking water must be supplemented from rainwater catchments and coconuts (Taborosi and Collazo Sanchez 2009).

The soil on atolls is typically sandy with a high salt content, making them unsuitable for growing many types of plants. In the past, the introduction and cultivation of root and tree crops such as breadfruit (*Artocarpus altilis*), pandanus (*Pandanus* sp.), and coconut (*Cocos nucifera*)—which not only provided food but raw materials—supplemented the endemic plant assemblage (Kirch 2017; Weisler 1999b; Yamaguchi, et al. 2006). Additionally, aroids such as Giant swamp taro (*Cyrtosperma merkusii*), Giant taro (*Alocasia macrorrhiza*), and taro (*Colocasia esculenta*), among others, were also widely introduced and cultivated in interior swamps and pits, although some researchers have suggested that taro may have been dispersed naturally prior to human contact or settlement (Athens and Stevenson 2012; Thomas 2019). Some breadfruit taxa (*Artocarpus mariannensis*-*A. altilis*) were crossbred, resulting in a salt-tolerant variety (Ragone 1997), which provided atoll dwellers with a significant and consistent source of food, so much so that this is often referred to as the “breadfruit revolution” (see Petersen 2006; Thomas 2019).

Since the preponderance of vegetation on atolls was introduced by humans, Kirch (2017) dubbed atolls ‘consummate man-made environments’. In addition to plants, animals such as chickens, pigs, dogs, and rats also played important roles in long-term survival on some, but not all, atolls. Sometimes, these species were never introduced pre-contact or were introduced but did

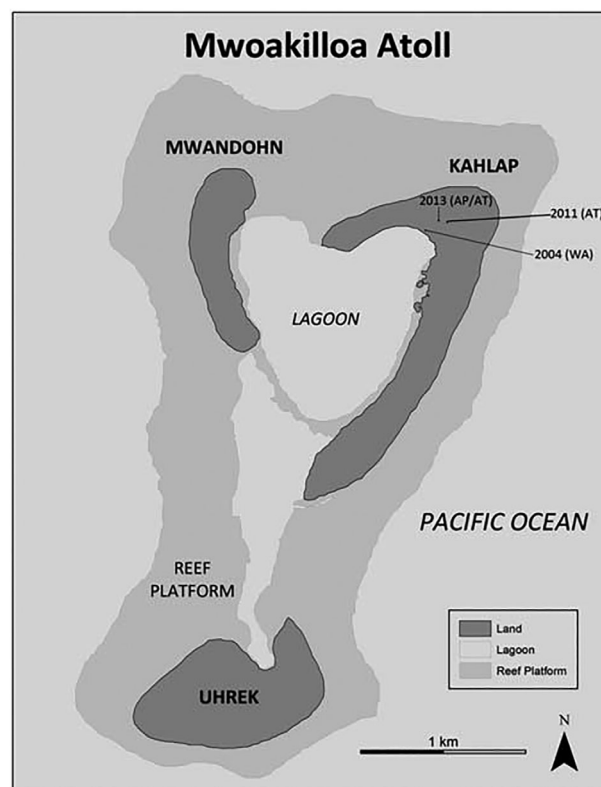


FIGURE 2 | Map of Mokil with locations of test units from the 2004, 2011, and 2013 field campaigns (Poteate et al. 2016).

not persist on the islands for more than short periods of time (Anderson 2009; Giovas 2006; Green and Weisler 2004; Intoh and Shigehara 2004; Poteate et al. 2016).

The surrounding reef environments and the lagoon provided abundant marine resources for atoll dwellers (Thomas 2019) that were critical for long-term habitation. Despite long-term settlement for many of these atolls over a millennia or more, most atolls show no signs of human overexploitation or extirpation of fish, molluscs, or other marine animals (Harris and Weisler 2018; Ono et al. 2013; Thomas 2002, 2019; for an exception, see Weisler 2001a). In contrast, terrestrial resources often show signs of impact, including the decline of tortoises, birds, and coconut crabs (Pregill and Steadman 2009; Weisler 1999a). Today, people living on atolls across the Pacific still rely on many of the same resources as their ancestors did thousands of years ago (Taborosi and Collazo Sanchez 2009).

Mokil exhibits the typical characteristics of atoll environments described above—such as water scarcity, nutrient-poor soils, and limited terrestrial resources, yet little research has been conducted on the environmental conditions in the past and subsequent human interventions. Mokil encompasses approximately 1.24 km² of habitable land, with a lagoon covering around 26 km². The atoll consists of several interconnected small islets: Mwandohn, Kahlap, and Uhrek (Figure 2). Most of the population currently lives on Kahlap, the largest and most elongated of the three islets, and the highest point of the atoll is ~2.2 m in elevation (Murphy 1950). Kahlap was also likely the main inhabited islet during the pre-contact era (Poteate et al.

2016). Mokil is one of only two atolls, including Pingelap, situated between the two high volcanic islands of Pohnpei and Kosrae. Pohnpei is around 160 km to the west-northwest of Mokil, while Pingelap is about 115 km to the southeast of Mokil (Figure 2). Daily average temperatures on Mokil range from 26–27°C with about 400 cm of annual rainfall (Taborosi and Collazo Sanchez 2009).

1.2 | Previous Research and Cultural Chronology

Over the past 70 years or so, there has been a gradual increase in archaeological research in Micronesia (Cochrane and Hunt 2018; Hunter-Anderson and Graves 1990; Liu et al. 2022), though this has been patchy, with a greater emphasis on sites in western Micronesia such as the Mariana Islands dating to ca. 3550 – 2950 calBP (Athens et al. 2004; Carson 2013), Palau around ca. 3000 calBP (Clark 2005; Clark et al. 2006; Fitzpatrick 2003; Masse, 1990), and Yap ca. 2200 – 2000 calBP (Descantes 1998; Napolitano et al. 2019), largely due to cultural resource management (CRM) projects. Research further east in central and eastern Micronesia has included the high islands of Pohnpei and Kosrae, which have both been inhabited since approximately 2000 calBP (at least 200–1300 years later than those islands in the west) (Athens 2018; Ayres 1990; Bryson 1989; Galipaud 2001; Haun 1984; McCoy et al. 2015; Rainbird 2004; Richards et al. 2015; Thompson 2016; Ward 1988; 2016), along with various atolls in the central/eastern Caroline Islands, Marshall Islands and Kiribati (e.g. see (Athens 1990, 1995; Davidson 1971; Descantes 1998; DiPiazza, 1999; Dye 1987; Galipaud 2001; Harris et al. 2016; Kayanne et al. 2011; Leach and Davidson 1988; Leach and Ward 1981; Masse 1990; Ono and Intoh 2011; Poteate et al. 2016; Shun and Athens 1990; Streck 1990; Weisler 1999a, 2001a, 2001b; Yamaguchi et al. 2009). Chuuk (Truk), despite the number and diversity of high and coral islands, its strategic position between Pohnpei and Guam, and its notable role in WWII as part of Operation Hailstone (in which a large part of the Imperial Japanese navy was sunk in the lagoon by the U.S. Navy), has received only cursory attention, mostly dating to the late 1970s and 1980s (Parker and King 1981; Takayama and Shutler 1978). In many of these archaeological investigations, however, zooarchaeological research has been relatively sparse.

Peoples who first migrated to Pohnpei, Kosrae, and Chuuk probably originated from the Southeast Solomon Islands (based on linguistics [Blust 2010]), or from the Papua New Guinea and the Admiralties area (based on genetics [Liu et al. 2022]), that is eastern Melanesia more generally. These island societies developed increasingly hierarchical political systems over time, reflected in the construction of monumental architecture and the establishment of prestige food economies based on mixed agroforestry (Haun 1984). Breadfruit (*A. altilis*), yam (*Dioscorea* sp.), bananas (*Musa* sp.), sakau/kava, coconut, and taro (*Araceae*), specifically *C. merkusii*, *C. esculenta*, *A. macrorrhiza*, and *Amorphophallus paeoniifolius* (Horrocks and Weisler 2006; S. Thompson 1982; Weisler 1999b), made up the most important cultivars managed in mixed agroforests (Balick 2009; Bascom 1965; Hunter-Anderson 1991).

Focusing on the atolls in the Easter Caroline Islands and the Marshall Islands, most of the investigations that have taken place have followed Leach's (1986) taxonomic identification and abundance quantification methods using the dentary, articular,

quadrate, maxilla, premaxilla and a handful of other special bones (Leach and Davidson 1988; Masse 1990; Weisler 1999a, 2001a, 2001b). Recently, criticisms have been raised regarding Leach's methodology and its application (Lambrides and Weisler 2015; Giovas 2018). Scholars have demonstrated that the selective sampling of specific anatomical specimens produces significantly different results than when all bones are used for taxonomic identification and abundance, and should thus be considered outdated (Giovas 2018; Lambrides and Weisler 2015). Additionally, this deviates from global zooarchaeological standard practice (e.g. Reitz and Wing 2008; Peres 2023; see also Moss et al. 2017; Butler et al. 2019, for examples in North American Archaeology; Prendergast and Lane 2010 for African Archaeology; Grouard 2001 for Caribbean Archaeology).

Currently, robust knowledge of human-animal interactions and subsistence within the central-eastern part of the Caroline Islands is generally sparse because there have been so few archaeological projects that have included comprehensive zooarchaeological analysis, following modern procedures (Giovas 2018; Thomas 2019). This gap in research is not unique as it reflects a broader regional issue, with Ebon (Harris et al. 2016) and Fais (Ono and Intoh 2011) being major exceptions. In the future, this list will include Pingelap, with research now in progress on excavated zooarchaeological assemblages (Levin et al. 2018). Thus far, studies on atolls indicate that there was a reliance on marine resources during initial settlement that would have been enough to sustain the population until plants such as bananas, pandanus, coconut, and breadfruit, were introduced or established and began yielding harvests that were sufficient enough to become a larger part of the diet (Weisler 2001b).

One of the earliest archaeological investigations on Mokil was by the Coordinated Investigation of Micronesian Anthropology (CIMA) in 1947 (Murphy 1950). Janet Davidson later visited the atoll in 1965 as part of a broader research programme to survey several high islands and atolls, including Pohnpei, Nukuoro, Mokil, Pingelap, Ngatik, Pakihn, Kapingamarangi, and Kusaie (Kosrae) (Davidson 1967). During this survey, Davidson (1967) noted that while Mokil's archaeological deposits were less dense than those on the nearby high island of Pohnpei, there was what appeared to be an artificially constructed mound formation higher in elevation than typically seen on most atolls. The mound contained a dense midden accumulation and coral blocks used in constructing platforms and facings, findings that were later corroborated by Rosendahl (1977).

The first excavation on Mokil consisted of a 1x1 m test unit, located near the main village on Khalap, on the lagoon side, conducted by William Ayers in 2004 (Figure 1). This test unit extended to a depth of 1.9 m and revealed both pre-contact and historic layers. The archaeological plan¹ extended 90 cm, with other related deposits reaching up to 120 cm in depth. Thompson (2011) later excavated a second 1x1 m unit adjacent to a taro patch behind the main village (Figure 2), aiming to assess the development and chronology of local agricultural practices. During the excavation, Thompson (2011) encountered findings similar to those in Ayres' 2004 research, including shell tools, commensal land snails, and other faunal remains, as well as volcanic stone artifacts and burned coconut endocarp. In 2013, Aaron Poteate and Adam Thompson returned and excavated

Test Unit 3 (East Wall) 2013

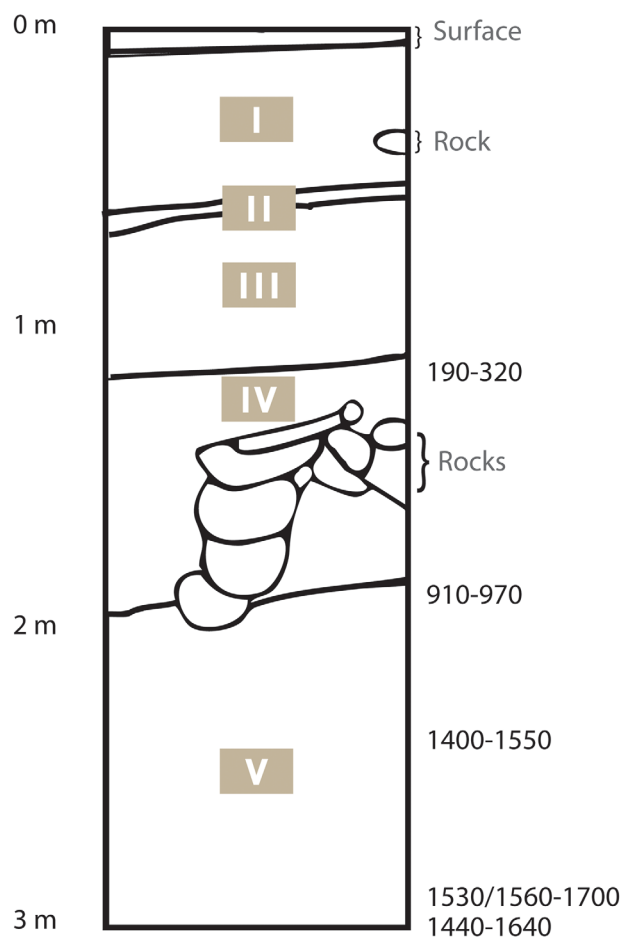


FIGURE 3 | Profile of test unit 3 with associated radiocarbon dates (calBP) (after Poteate et al. 2016).

another 1 × 1 m unit, also located on Kahlap and near the village's highest point (Figure 3) (Poteate et al. 2016). Stone artefacts, shell tools, faunal remains, potsherds, and burned coconut endocarp were recovered.

Radiocarbon dates produced by the most recent study indicate that Mokil was settled as early as 1700–1500 calBP (Poteate et al. 2016), about the same time as the nearby atoll of Pingelap and not long after what is thought to be the initial settlement of Kosrae and Pohnpei ca. 2000 calBP (Athens 1990, 1995; Ayres 1990). Results also suggested that Mokil was continuously inhabited after initial settlement (Poteate et al. 2016).

2 | Materials and Methods

The zooarchaeological material analysed in this study originates from Test Unit 3, which was excavated by Poteate and Thompson in 2013 (Poteate et al. 2016; Figures 1 and 3). The 1 × 1 m unit was placed away from taro patches since they are prone to post-depositional processes related to agricultural activities. Excavation was conducted using arbitrary 10 cm plana (levels) with stratigraphic layers ($n = 5$) also recorded (Figure 3). Layer

1 is around 50 cm thick, is made up of five plana (1 through 5), and consist of dark loose sand, roots, some coral, and shell. Layer 2 is around 10 cm thick, is made up of one planum (planum 6), and is a sandy layer, which is thought to be the aftermath of the 1775 typhoon (Poteate et al. 2016). Layer 3 is around 50 cm thick and is made up of five plana (7 through 11) comprising mostly mottled dark grey sand and abundant coral that becomes increasingly sandy with larger pieces of coral as the layer gets deeper. Layer 4 is 70 cm thick and made up of seven plana (12 through 18), which is sandy but dominated by larger chunks of coral rock that appear to be part of a residential feature. Lastly, Layer 5 is 110 cm thick with eleven plana (19 through 29) and consists primarily of loose sand (excavation notes Poteate 2013; Figure 3). All soil was wet sieved through at least ¼ inch (6.4 mm) mesh with a 0.5 × 0.5 m column sample sieved through nested ¼ inch and 1/8 inch mesh (3.18 mm). Five different plana throughout the stratigraphy were radiocarbon dated to provide a sequence of occupation (see Poteate et al. 2016; Table 1). It should be noted that all samples were originally calibrated and reported in Poteate et al. (2016) using OxCal v 4.2 (Ramsey 2009) with a global average marine reservoir effect (Marine13) used for marine shell as there were no ΔR currently available for the region (Reimer et al. 2013). There is still currently no local marine reservoir effect calculated for Mokil. However, as a comparison, we provide updated calibrations using CALIB 8.2 that factor in the new IntCal20 and Marine20 datasets (Table 1). Though there are negligible differences in the age ranges for some of the samples, in this paper we have continued to use the original calibrations presented in Poteate et al. (2016) for consistency.

For this study, we sampled the faunal constituents from the unit, not the column, that were excavated from plana 3, 8, 12, 15, 19, 20, 23, 24, 26, and 29. Both plana 3 and 8 were sieved through ⅛ inch (3.17 mm), while all other plana were sieved through ¼ inch (Table 2). These different mesh sizes should be taken into consideration when interpreting the results, as the smaller mesh size can increase the number of specimens and representation of smaller taxa and fragmented specimens. Even though recovery methods for plana 3 and 8 were different, they were included to approximate a more complete image of occupation through the unit's sequence but are discussed separately in the results section.

All plana for which radiocarbon dates were available are included except for 28, where planum 29 was analysed instead (Table 2). This decision was made because we thought it important to include the earliest occupation layer in the assemblage, and relative age can be inferred (e.g. planum 29 is older than planum 28). Further sampling was based on selecting plana that were generally separated throughout the unit depth and ensuring that equal numbers of plana were represented from each stratigraphic layer. Sampling began at planum 3 since the two earlier plana included topsoil and had been affected by post-depositional disturbances such as root growth (Poteate et al. 2016).

Detailed information was recorded for each specimen in the assemblage, including its taxonomic identification, skeletal element, portion, percentage of the element, side, weight, and any evidence of intentional or unintentional modifications and pathologies. We report the number of individual specimens (NISP), minimum number of individuals (MNI), and weight (g) to avoid using a single method for calculating the abundance

TABLE 1 | Radiocarbon samples from unit 3 with original C14 dates calibrated using OxCal v 4.2 (Bronk Ramsey 2009), with a global average marine reservoir effect (Marine13) (after Poteate et al. 2016), and revised calibrations using CALIB 8.2 with the IntCal20 and Marine20 datasets.

Lab No.	Sample ID	Material	Species	Test			Layer	Planum	14C date	12C/13C	2σ calibration		RAUPD	2σ calibration		RAUPD
				Unit	Depth						(BP)*	(BP)**				
D-AMS 006290	01MOK13	Marine shell	Trochus sp. (T. incrassatus?)	3	120		3/4	12	618 ± 25	2.7	190–320	0–224	0.97	0–224	1	1
D-AMS 006292	02MOK13	Charcoal	Coconut endocarp	3	185		4	19	1014 ± 24	–23.3	910–970	904–958	0.986	904–958	0.911	0.911
D-AMS 006799	04MOK13	Marine shell	Tridacna sp.	3	240		5	24	1936 ± 22	1.6	1400–1550	1208–1471	1	1208–1471	1	1
D-AMS 006291	03MOK13	Marine shell	Tonna sp.	3	280		5	28	2052 ± 29	–3.3	1530–1700	1308–1585	1	1308–1585	1	1
D-AMS 006802	05MOK13	Charcoal	Coconut endocarp	3	280		5	28	1722 ± 25	–21.4	1560–1700	1542–1699	1	1542–1699	1	1
D-AMS 006800	06MOK13	Marine shell	Strombidae sp.	3	290		5	29	1977 ± 25	0.4	1440–1620	1261–1511	1	1261–1511	1	1

of faunal remains (Klein and Cruz-Urbe 1984; Peres 2010; Reitz and Wing 2008), since quantification methods, and those that are more accurate or valid for specific outcomes, are highly debated (Grayson 2014; Lyman 2008, 2019; Lyman and Wolverson 2023).

Frequency was assessed across classes and time (plana). The most frequently occurring classes, discussed below, were also assessed at the family level per class. The MNI calculations for the Mokil assemblage followed the procedures outlined by White (1953), which assumed symmetry for bivalves, crustaceans, and vertebrates, allowing the MNI to be determined by counting the most abundant element per left or right side. Additionally, size was taken into account within the same provenience (Klein and Cruz-Urbe 1984; Lyman 1994a, 1994b, 2008) and completeness of each specimen per plana was also considered. Whenever MNI values were calculated, taxonomic identification with the highest MNI was used. To enhance readability of figures, only the most frequently occurring taxa are included in figures for gastropods and fish; for gastropods, any family that occurs in higher frequency than 1% NISP is included, while for fish any family that occurs in higher frequency than 0.5% NISP is included. For fish we have also included Kyphosidae and Cirrhitidae (which occur in lower frequency than 0.05%) since these are the only taxa that occur in planum 3. NISP, MNI at Wt (g) of all taxa is included in the Supplementary Information.

Richness, diversity, and evenness were calculated for each plana using the Shannon-Wiener index. Richness represents the number of different taxa within a sample (Reitz and Wing 2008, p. 11). Diversity is a statistical measure of the heterogeneity of a sample that considers both the abundance of each taxon (evenness) and the total number of different taxa (richness) within the sample (Rindos 1989, p. 14). As such, diversity is an indicator of which animals occurred in what proportions in an assemblage. Diversity indices, comparing assemblage composition between or within sites, can inform us about differences or changes in subsistence strategies and environmental or ecological settings, or help assess exploitation intensity (Leonard and Jones 1989; Reitz and Wing 2008).

We used previously outlined MNI counts to assess richness. Diversity was calculated by using the Shannon index $H' = -\sum (\pi_i \ln \pi_i)$ (H' : calculated diversity; π_i : relative abundance of taxon within the sample; $\ln \pi_i$: natural logarithm of π_i ; S : the number of taxonomic categories). The higher the diversity, the richer a sample is where each taxon is equally well represented. A lower diversity is indicative of a lower richness in combination with an uneven representation of taxa (Reitz and Wing 2008, p. 111). Evenness was calculated using the Shannon index $E = H'/\ln(S)$ (E : Evenness; H' : calculated diversity; $\ln S$: natural logarithm of the number of taxonomic categories). Evenness represents the similarity of abundances between different taxa within a sample, with 0 indicating a very uneven distribution and 1 indicating a completely even distribution.

Identification of fish specimens was facilitated with the help of a reference collection, including 35 families, 78 genera, and 128 species compiled by the lead author (PJ) that was used to identify the majority of specimens from the assemblage (see Supplementary Information 1 for the list of specimens). This was supplemented with information reported in well-known sources

TABLE 2 | Investigated plana and associated radiocarbon dates from unit 3 (Poteate et al. 2016). Samples were calibrated using OxCal v 4.2 (Bronk Ramsey 2009), with a global average marine reservoir effect (Marine13) used for marine shell as there is currently no ΔR currently available for the region (Reimer et al. 2013).

Planum	Stratigraphic Layer	Radiocarbon calBP (2 σ)	Cal calendrical years	Materials/species	Screen size (inch)
3	1				1/8
8	3				1/8
12	3/4	224 - 0	1630 - 1760 calAD	Marine shell/ <i>Trochus</i> sp.	1/4
15	4				1/4
19	4	958 - 904	980 - 1040 calAD	Charcoal/ Coconut endocarp	1/4
20	4				1/4
23	5				1/4
24	5	1471 - 1208	400 - 550 calAD	Marine shell/ <i>Tridacna</i> sp.	1/4
26	5				1/4
29	5	1511 - 1261	330 - 510 calAD	Marine shell/ <i>Strombidae</i> sp.	1/4

(Bergbauer and Kirschner 2020; Lieske and Myers 2001; Wheeler and Jones 1989) and archival websites (<http://osteobase.mnhn.fr/>; www.fishbase.org; WoRMS [World Register of Marine Species] <http://www.marinespecies.org/>; accessed on 11/7/23) where possible. Invertebrates were identified using a reference collection in the Island and Coastal Archaeology laboratory at the University of Oregon (see Supplementary Information 2 for a list of specimens) and various reference books (Dance 1976; Morris 1966; Sabelli 1980; Tinker and Tinker 1989) and websites. No reference collection was available for birds (aves) or sea urchins (Echinoidea), of which the remains occurred in very low frequencies and were fragmented beyond the identification of class.

The archaeological specimens were compared to those in the reference collections to identify each specimen to the most precise taxonomic level possible. Positive identifications were made only when distinct morphological characteristics were present and only after excluding all other potential taxa based on morphology or their general absence in Micronesia (e.g. Froese and Pauly 2021; Giovias 2013).

Given that preservation of organic remains can be variable in tropical regions, and the high biodiversity in the Micronesian region (e.g. 38 known species in the Acanthuridae family; 34 known species in the Chaetodontidae family) many of the archaeological specimens could only be identified to the level of genus or family. Despite recent molecular evidence suggesting that the family-level designation of Scaridae (parrotfish) should be revised to a subfamily (Scarinae) of Labridae (wrasses), the study continued to use the traditional family-level designation. This decision was based on the potential influence of behavioural differences between these two taxa on fishing practices (see Giovias 2013). Similarly, while Tridacninae (giant clams) belong to the Cardiidae family (true cockles), they were treated as a distinct category in this analysis because of their substantial cultural significance as both a dietary resource and a material for tool and artifact production. Additionally, Conidae (cone snails) and Strombidae were grouped together in the analysis (Strombidae/Conidae) as many were too fragmented to be iden-

tified as one or the other. The family Muridae (rats, mice, and relatives), recovered in the earliest plana, can only be *Rattus exulans* (Polynesian rat) or *Rattus tanezumi* (Temminck 1844), also sometimes referred to as *Rattus rattus mansorius* (Davidson 1971) (Asian house rat), since these were the only rodents that occurred in this region at that time (Wickler 2004) and an introduction of a completely unknown species is highly unlikely. We were unable to distinguish between these two species as we lacked specific reference specimens; therefore, all identifications were made at the genus level.

Toward our goal of better understanding regional and potentially overarching subsistence strategies and atoll settlement strategies, we have juxtaposed our results with data from the limited research available, albeit from the western and easternmost parts of Micronesia. Data from six other atolls are incorporated here, which include Utrök, Ebon, and Ujae in the Marshall Islands (between 700-1200 km east of Mokil), Nukuoro and Kapingamarangi (between 650 and 880 km southwest of Mokil) in the southern Caroline Islands, and Fais², located in the Western Caroline Islands approximately 2100 km to the west. Given that different researchers conducted these analyses, it is noteworthy that not all animal classes were incorporated in the investigations for each of these atolls; as such, comparisons were made only when possible. Moreover, for Utrök, when discussing the category of fish, this also includes Elasmobranchii and Muraenidae or Anguillidae (Weisler 2001a). Below, we discuss our results and contextualise them with comparisons for each of the other four islands.

3 | Results

A total of 53 families were identified within the Mokil zooarchaeological assemblage (Supplementary Information 3 and 6). Across these families, 5,995 NISP are present, weighing a total of 2999.48 g and representing 1055 MNI (Supplementary Information 3, 4, 5, 6, 7, and 8). Identified invertebrate taxa comprise 3135 NISP and 2569.45 g of the total weight and represent 885 MNI, followed by vertebrate taxa with 2860 NISP and 430.03 g, representing 178 MNI. Results per class and by plana are reported below.

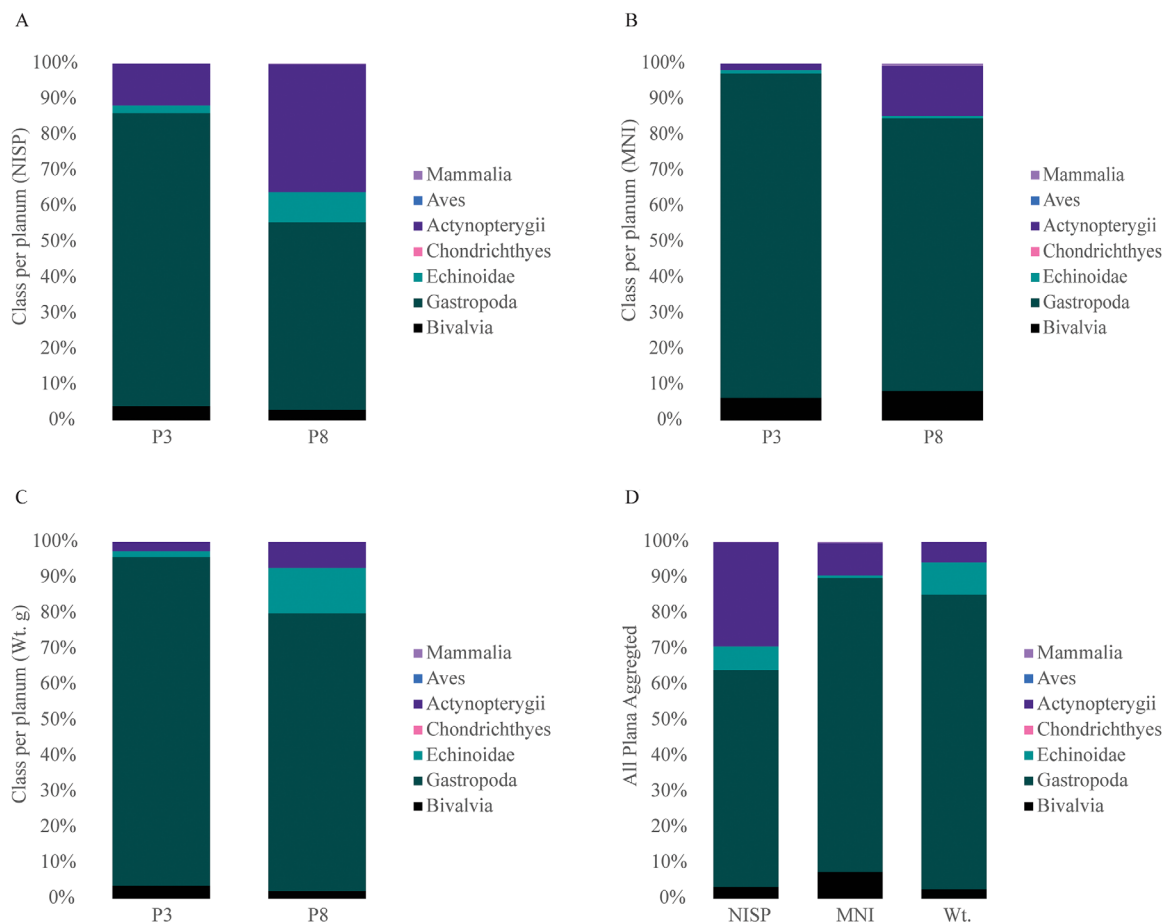


FIGURE 4 | Frequency per class for plana 3 and 8 in (a) NISP, (b) MNI, (c) Weight (g), and (d) all plana aggregated.

4 | Classes

4.1 | Plana 3 and 8 (1/8 Inch Fraction) (Post 320 calBP)

A total of 1006 NISP were identified for plana 3 and 8, representing 434.65 g and 267 MNI. Overall, the assemblage was dominated by Gastropoda and Actinopterygii (ray-finned fish) coupled with lower numbers of Bivalvia (bivalves) and Echinoidea (sea urchins). Mammalia only make up a fraction of these plana while Aves (birds) were absent (Figure 4). Gastropoda increased through time for these plana, which is most apparently countered by a decrease in both Actinopterygii and Echinoidea. Other classes remained approximately the same between these time periods (Figure 4; Supplementary Information 3, 4, and 5).

4.2 | Plana 12 Through 29 (1/4 Inch Fraction) (1620–190 calBP)

A total of 4,989 NISP were identified for plana 12 through 29, representing 2564.77 g and 786 MNI (Supplementary Information 6, 7, and 8). Overall, the assemblage was dominated by Gastropoda, Bivalvia, and Actinopterygii. As expected, Mammalia were present at much lower frequencies. All other classes, including Echinoidea and Aves, were minimally represented (Figure 5d).

From the earliest planum 29, Gastropoda decreased until planum 23. Planum 20 until 15 saw a return in the frequency of gastropods, though it did not reach the higher Gastropoda frequency found previously in planum 29. Gastropoda then declined again in planum 12.

This fluctuation in Gastropoda frequency is mostly juxtaposed by fluctuation in Actinopterygii frequency for which there appears to be an inverse relationship between Actinopterygii and Gastropoda, where one decreases as the other increases. From planum 29 until planum 23, Actinopterygii increased through time. Beginning in planum 20, and lasting until about planum 15, there is a decrease in Actinopterygii, with a resurgence in planum 12 (Figure 5).

There is no clear pattern of change across the Bivalvia frequency. Between plana 29 and 19, Bivalvia NISP are similar, MNI increases from plana 29 and to 23, and MNI decreases from 23 to 19, while weight decreases from planum 29 through planum 15. Beginning in planum 15 and lasting through planum 12, MNI decreases. NISP for plana 15 and 12 also shows a decrease from the previous plana. Conversely, weight in planum 12 increases significantly compared to planum 15 (Figure 5). This trend is discussed below when examining Bivalvia (Figure 5d).

Mammalia occur in low frequencies from planum 29 to 12 (<5% by NISP relative abundance), except for plana 15, 19, and 20, where

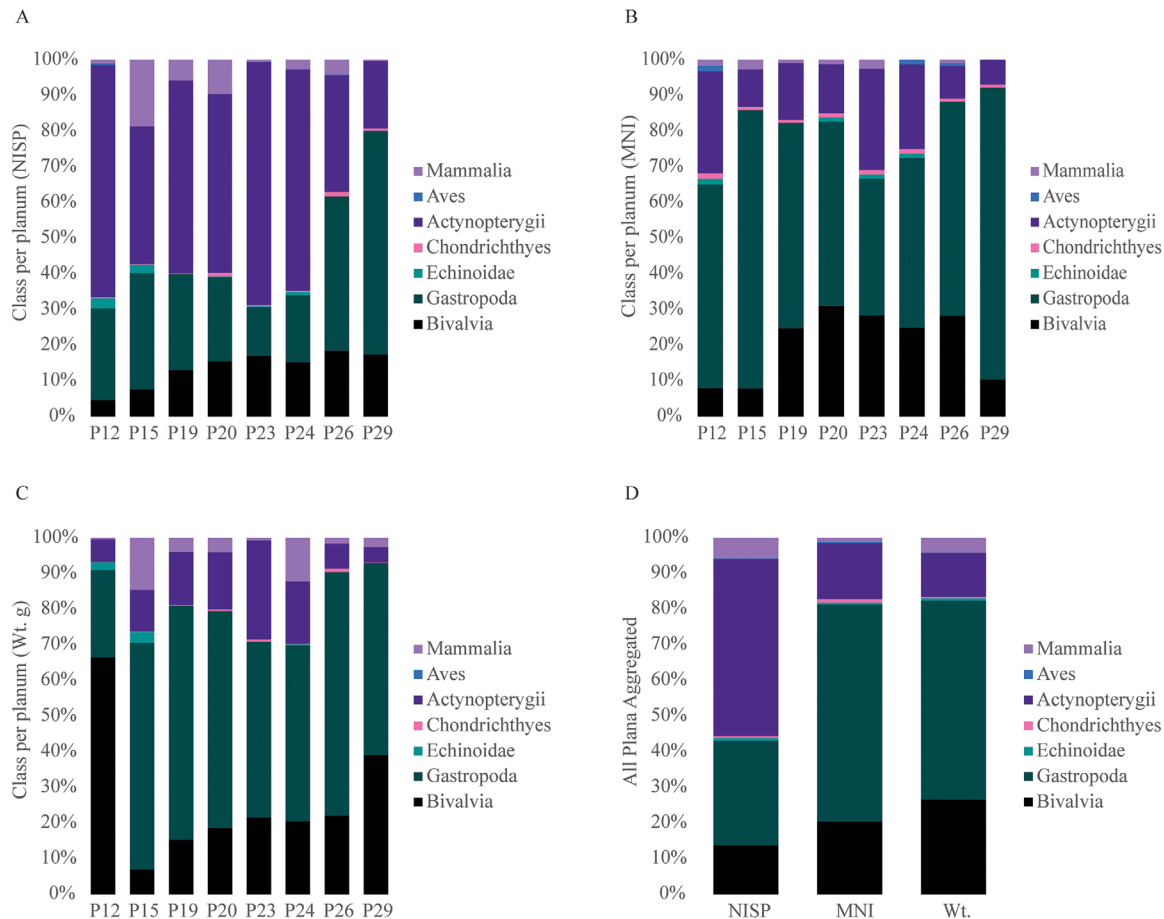


FIGURE 5 | Frequency per class for plana 12-29 in (a) NISP, (b) MNI, (c) Weight (g) and (d) all plana aggregated.

they occur in higher NISP frequencies (Figure 5). Plana 15 and 20 have the highest MNI for mammals of all plana, though these represent a much lower frequency when compared to the rest of the assemblage. The weight of mammals, as might be expected, is higher in plana 15 and 24 (Figure 5d).

5 | Bivalves

5.1 | Plana 3 and 8 (post 320 calBP)

For Bivalvia in plana 3 and 8 (33 NISP; 20 MNI; 10.37 g), no clear pattern can be discerned given that only four taxa were identified for this class. Overall, the most important taxon is Arcidae (ark shells) (10 NISP; 8 MNI; 3.35 g) (Figure 6; Supplementary Information 3, 4, and 5). Changes over time are most evident in the decline of Cardiidae and the increase in Tridacninae. Tellinidae (tellins) and Arcidae remain approximately constant between these two plana (Figure 6). Mesodesmatidae (Mesodesmatids) and Lucinidae (hatchet shells) are absent in plana 3 and 8.

5.2 | Plana 12 Through 29 (1620 – 190 calBP)

For plana 12 through 29 (629 NISP; 342 MNI; 636.93 g), a total of only six taxa were identified for this class. Overall, the three most important taxa are Mesodesmatidae (199 NISP; 207 MNI; 50.94 g), Tellinidae (296 NISP; 31 MNI; 148.40 g), and Tridacninae (28 NISP;

14 MNI; 378.47 g) in no particular order (Figure 7; Supplementary Information 6, 7, and 8). Mesodesmatidae and Tellinidae appear in each plana, while Tridacninae are absent in plana 15 and plana 20. In plana 24, Tellinidae appear to increase compared to lesser frequencies in plana 12 through 29. P. Meanwhile, in both plana 12 and 24 there is a decrease in Mesodesmatidae. Cardiidae appear in low numbers in plana 19 and plana 29 while Arcidae appear in both, and in plana 12 as well. Lucinidae do not appear anywhere, except in plana 12.

6 | Gastropoda

6.1 | Plana 3 and 8 (post 320 calBP)

For Gastropoda, 15 taxa were identified (602 NISP; 220 MNI; 342.88 g) (Supplementary Information 3, 4, and 5). Within this class, Conidae/Strombidae (104 NISP; 64 MNI; 39.26 g), Turbinidae (turban snail) (77 NISP; 8 MNI; 80.20 g), Trochidae (top snail) (82 NISP; 12 MNI; 58.33 g), Neritidae (nerites) (14 NISP; 11 MNI; 3.68 g), Cypraeidae (cowries) (28 NISP; 18 MNI; 23.08 g), and Cerithiidae (134 NISP; 66 MNI; 30.95 g) are the most prevalent. Between plana 8 and plana 3, Conidae/Strombidae, Turbinidae, Cypraeidae, and Neritidae generally increased, while Trochidae, Muricidae, and Cerithiidae decreased overall (Figure 8). Turbinellidae are absent here in both plana 3 and 8, while Marginellidae (margin shells) appear in plana 3.

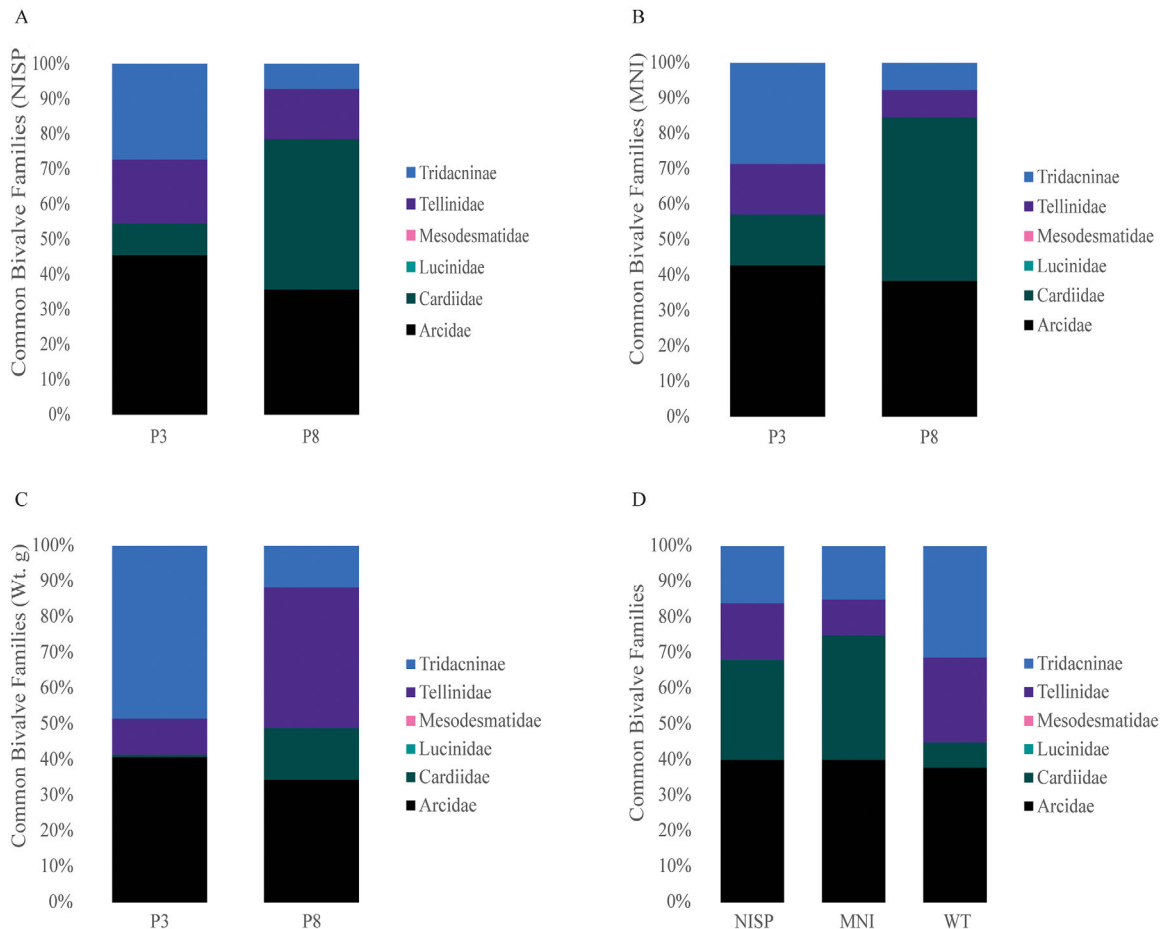


FIGURE 6 | Bivalvia family frequency for plana 3 and 8 in (a) NISP, (b) MNI, (c) weight (g), and (d) all plana aggregated.

6.2 | Plana 12 Through 29 (1620 – 190 calBP)

Eighteen taxa were identified in Gastropoda (1349 NISP; 478 MNI; 1339.17 g). Within this class, Conidae/Strombidae (149 NISP; 65 MNI; 76.71 g), Turbinidae (196 NISP; 37 MNI; 347.82 g), Trochidae (97 NISP; 25 MNI; 69.81 g), and Muricidae (19 NISP; 18 MNI; 10.50 g) are the most common and occur in all plana (Figure 9; Supplementary Information 6, 7, and 8). Conidae/Strombidae are prevalent through time; however, in planum 20 they become the dominant taxon by far. Other common taxa were Cerithiidae, which occur in all plana except planum 20, and Neritidae, which is found in all plana except for planum 12. Additional notable results include the disappearance of Turbinellidae after planum 20 and the presence of Marginellidae in only the oldest planum (29) (Figure 9).

7 | Fish

7.1 | Plana 3 and 8 (post 320 calBP)

There were only 13 taxa of fish recovered from plana 3 and 8, and only two were found in planum 3 (Supplementary Information 3, 4, and 5). The total fish recovered from these two plana was low (289 NISP; 24 MNI; 22.50 g). Cirrhitidae (hawkfish) and Kyphosidae (sea chubs) were the only two families found in planum 3 and each was represented by only one element (Figure 10). The most common taxa found in planum 8 were Ser-

ranidae followed by Mugilidae (mullets), Labridae/wrasse, Labridae/parrot, Diodontidae, Beloniformes (needlefish/halfbeaks), and Balsitidae (triggerfish) (Figure 10).

7.2 | Plana 12 Through 29 (1620 – 190 calBP)

A total of 23 taxa were identified for this class (2276 NISP; 123 MNI; 297.47 g). Diodontidae, Elasmobranchii, Labridae/parrot, Labridae/wrasse, Scombridae, and Serranidae appear in every planum (Supplementary Information 6, 7, and 8). Other frequently occurring taxa include Beloniformes and Lutjanidae (red snapper), which are all represented above 2% in NISP, MNI, and weight, and found in plana 29, 24, 19, 12, and 8, and plana 26, 24, 23, 19, 12, 8, respectively. Beloniformes display higher frequencies in the oldest plana, including 29 and 24, mostly in NISP and Wt. values, which we discuss below (Figure 11).

7.3 | Fish Diversity

Fish diversity is highly variable through time, ranging from lowest ($H' = 0.08$) in planum 3 and highest ($H' = 1.09$) in planum 12 (Figure 12). There is significant fluctuation over time in diversity, with higher values in plana 12 ($H' = 1.09$), 19 ($H' = 0.77$), 23 ($H' = 0.97$), and 24 ($H' = 1.01$) (Figure 12). Between these plana, evenness is also higher in plana 12 ($E = 0.42$) and 24 ($E = 0.37$), which could indicate a more generalist approach to

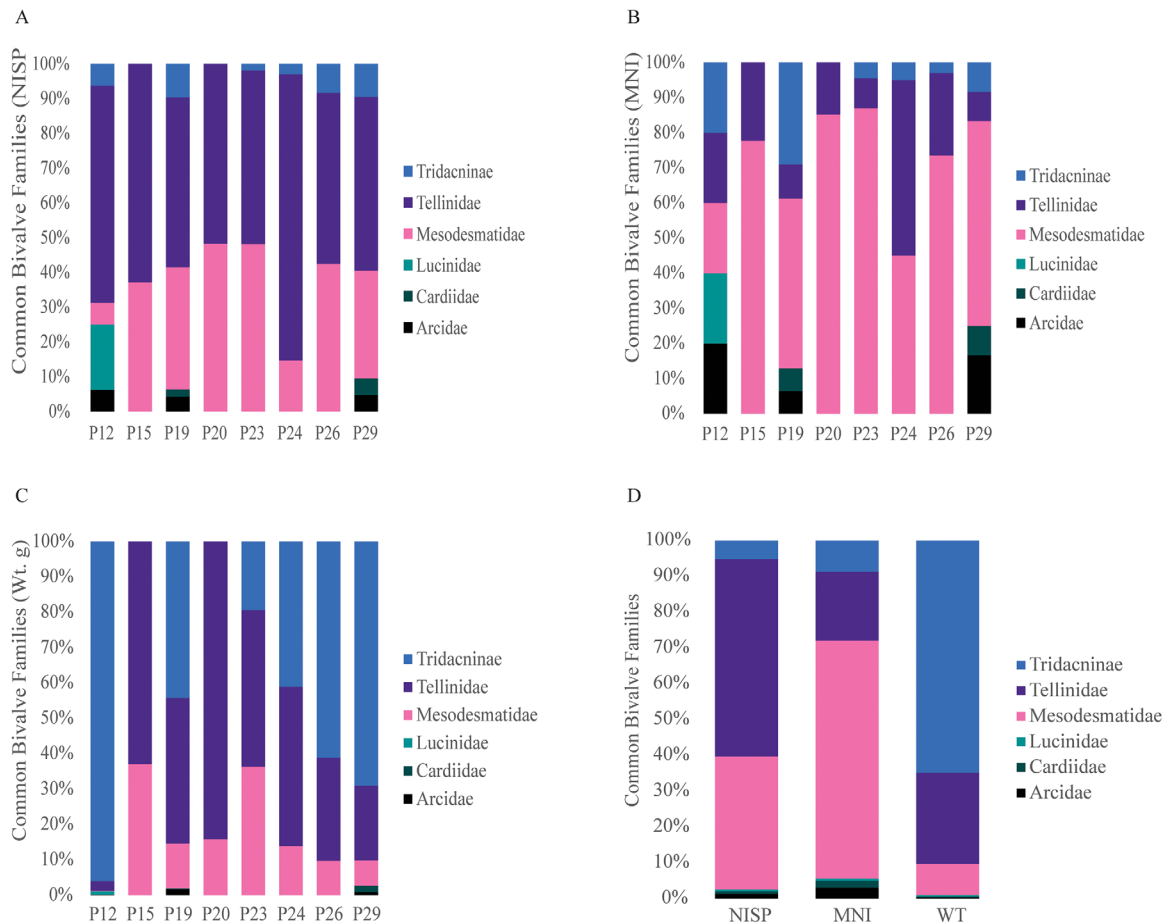


FIGURE 7 | Bivalvia family frequency for plana 12-29 in (a) NISP, (b) MNI, (c) weight (g), and (d) all plana aggregated.

TABLE 3 | NISP of birds, rats, and dogs.

Taxon	P3	P8	P12	P15	P19	P20	P23	P24	P26	P29	Total
Birds	—	—	2	—	—	—	—	1	2	—	5
Rats	—	1	—	19	—	—	2	—	—	—	22
Dogs	—	—	2	22	5	2	1	—	2	—	34
Total	0	1	4	41	5	2	3	1	4	0	61

fishing. Evenness is weak across the board as it is closer to 0 than to 1. The plana where diversity leans towards the low end also have low evenness, which could indicate more specialist or targeted fishing practices; these include plana 3, 15, 20, 26, and 29 (Figure 12). The lack of fish diversity or evenness in planum 3 can be attributed to the low MNI for fish overall in that planum (MNI = 2). The low R^2 values for both diversity ($H' = 0.019$) and evenness ($E = 0.002$) indicate that there is no correlation between time and either of these variables.

8 | Dogs, Rats and Birds

Canis familiaris (dogs) occur in all except two plana, the oldest planum 29, along with planum 24 (Tables 3 and Table 4). The earliest occurrence of *Rattus* is in planum 23, with the only other

occurrence in planum 15 (Tables 3 and Table 4). *Aves* occurs in just three layers: plana 26, 24, and 12, but in very low numbers (<2 NISP; <1 MNI) (Tables 3 and Table 4). Specimens were extremely fragmented and could not be identified to a lower taxon.

9 | Overall Diversity

Planum 20, in particular, shows low diversity ($H' = 2.10$), while there are two plana, 23 ($H' = 2.77$) and 24 ($H' = 3$), which have a high diversity (average $H' = 2.52$) compared to the rest of the assemblage (Figure 13). Evenness varies between 0.69 and 0.87 at its lowest in planum 20 and its highest in planum 24. Evenness numbers closer to 1, indicate that there are no dominating taxa in any plana (Figure 13). The low evenness and diversity in planum 20 could indicate a more specialist harvesting approach. Overall,

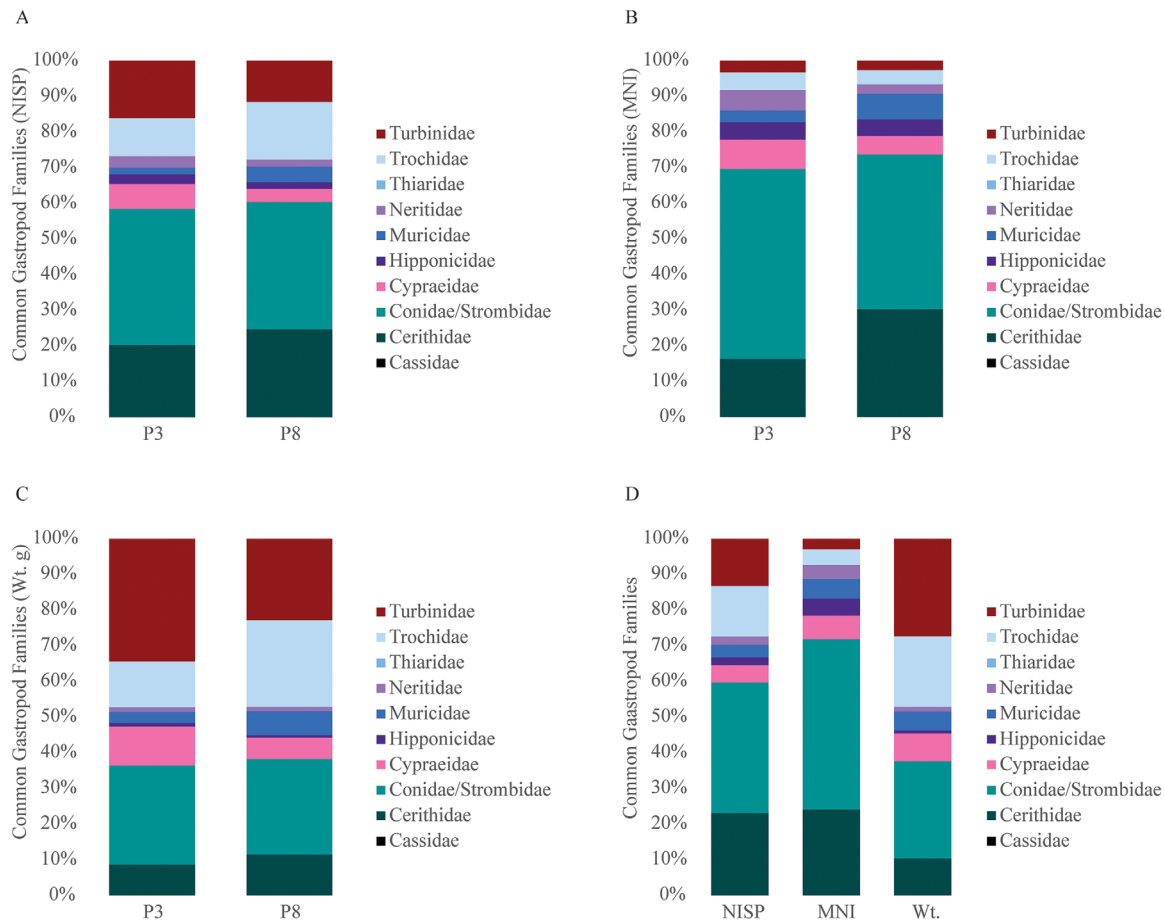


FIGURE 8 | Gastropoda family frequency for plana 3 and 8 in (a) NISP, (b) MNI, (c) weight (g), and (d) all plana aggregated. *Only families that occur in higher frequencies than 1% NISP were included in this figure.

TABLE 4 | MNI of birds, rats, and dogs.

Taxon	P3	P8	P12	P15	P19	P20	P23	P24	P26	P29	Total
Birds	—	—	1	—	—	—	—	1	1	—	3
Rats	—	1	—	2	—	—	1	—	—	—	4
Dogs	—	—	1	1	1	1	1	—	1	—	6
Total	0	1	2	3	1	1	2	1	2	0	13

the diversity R^2 score (0.065) and the evenness R^2 score (0.119) suggest a weak correlation between diversity and time, as well as between evenness and time.

10 | Discussion

There has been a paucity of analytically inclusive and taxonomically in-depth zooarchaeological analysis from atolls in Micronesia (Gakuhari et al. 2013), particularly in the central Caroline Islands (Thomas 2019). This has limited our understanding of animal harvest practices, island settlement strategies, and how these might compare to other islands in the region. Despite this, there have been some robust studies of faunal material recovered from a host of archaeological sites across the region. As such, we

have included data from several other similar islands to the west and east of Mokil for comparison.

Overall, the Mokil assemblage shows a high prevalence of Gastropoda, Bivalvia, and, to a lesser extent, Actinopterygii, with Mammalia, Aves, and Echinoidea minimally represented. Due to a lack of sufficient comparative materials, we are unable to identify Aves to a more specific taxonomic category. Consequently, it is unclear if our sample includes seabirds, migratory shorebirds, land birds, or possibly an early introduction of chicken (*Gallus gallus*). It must be taken into account that this pattern could be the result of a larger screen size; using a finer mesh (e.g., 1/8 inch/ 3 mm) consistently would be preferable to improve recovery of smaller bird bones and echinoderm remains.

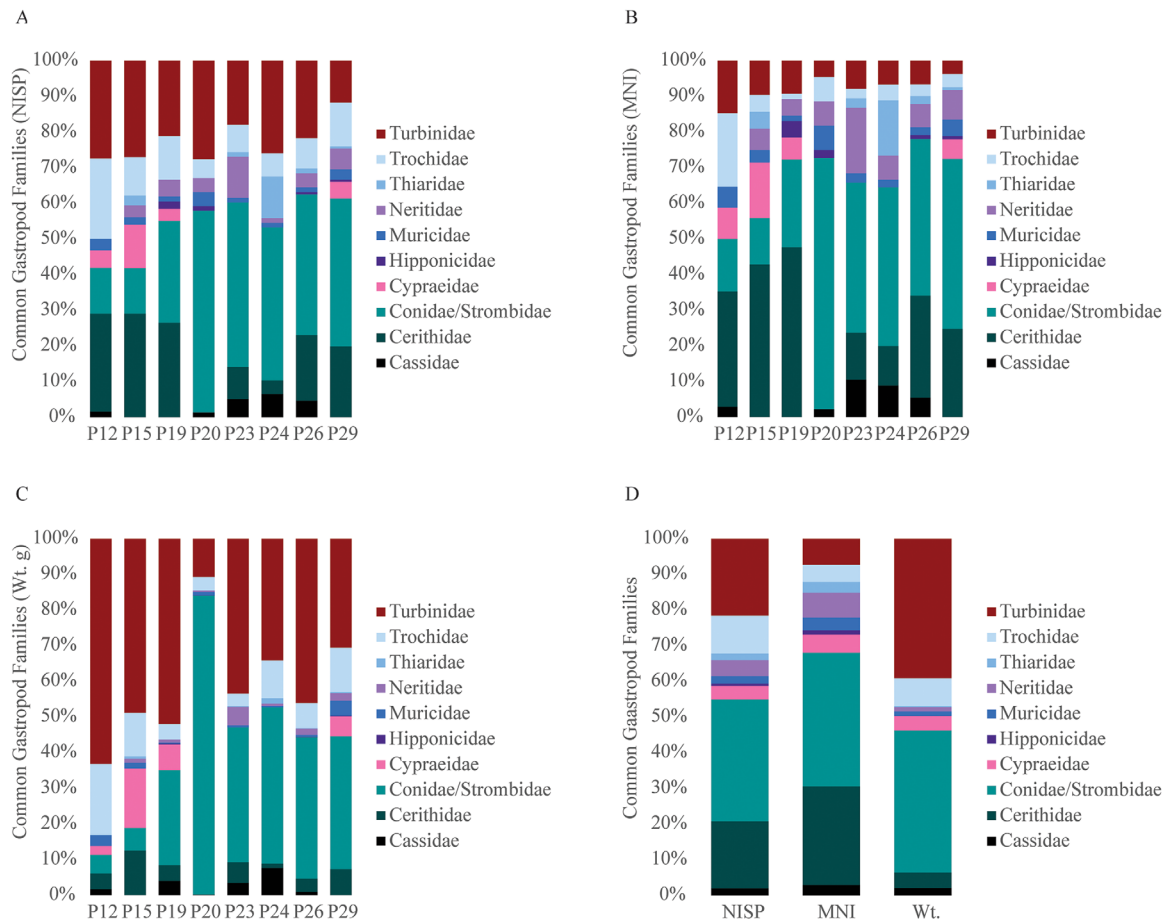


FIGURE 9 | Gastropoda family frequency for plana 12-19 in (a) NISP, (b) MNI, (c) weight (g), and (d) all plana aggregated. *Only families that occur in higher frequencies than 1% NISP were included in this figure.

We compared our analysis to other results from Micronesian atolls. However, only the analysis on Ebon (Harris et al. 2016) and Fais (Ono and Intoh 2011) used similar analytical methods as our study to assess their fish assemblage. As such, it should be taken into account that all other studies mentioned have analysed their fish assemblages, focusing on five, paired cranial bones and some 'special' elements (Leach 1986). Scholars who have compared analyses that include all recovered fish specimens in an assemblage to the 'selective elements approach' have noted that the latter can result in the underrepresentation of Chaetoniids, Pomacentrids, Scombridae, and Belonoidei, species documented ethnographically (Vogel and Anderson 2012). This is potentially due to the fragility of cranial elements in these families, and the exclusion of analysis of vertebrae, by which these families are often identified (Ono and Intoh 2011; Ono and Clark 2012).

Looking at the particular assemblages, it should be noted that Ujae (Weisler 1999a) and Utrok (Weisler 2001a) assemblages did identify Scombridae and Belonidae. Moreover, none of the assemblages, including our Mokil assemblage, as well as the Ebon (Harris et al. 2016) and Fais (Ono and Intoh 2011) assemblages, identified any Chaetoniids or Pomacentrids. As a result, we believe that our comparison should be minimally impacted by these biases and is a useful addition for establishing a preliminary regional comparison.

Our Mokil sample is similar to what has been observed on Utrök and Ujae in the Marshall Islands, where there was a majority of Actinopterygii compared to Mammalia, in addition to a high frequency of both Gastropoda and Bivalvia (Weisler 1999a, 2001b). On Utrök, Weisler (2001b) reported a total of 56 identified families, which is slightly higher than Mokil at 53. Compared to Ujae and Ebon, numbers on Mokil are lower, with at least 87 and 76 families recorded, respectively³ (Harris et al. 2016; Harris and Weisler 2017; Pregill and Weisler 2007; Weisler 1999a).

10.1 | Differential Fractions Between Plana 3 and 8 (post 320 calBP) and 12 Through 29 (1620 – 190 calBP)

While it is possible that the overall diversity on Mokil is lower, given that plana 3 and 8 here were sieved using a finer screen size ($\frac{1}{8}$ inch) than the other plana ($\frac{1}{4}$ inch), this could also mean that smaller taxa were represented in higher frequencies in these plana than in the others, that these taxa might not occur at all in plana older than planum 8, or that there is a differential representation of specific elements of taxa between the plana sieved at $\frac{1}{8}$ inch or $\frac{1}{4}$ inch. However, any element that was encountered in plana 3 and 8 was also recovered in plana 12 through 29, regardless of taxon. There were no elements from smaller or larger taxa represented in plana 3 or 8 that were not

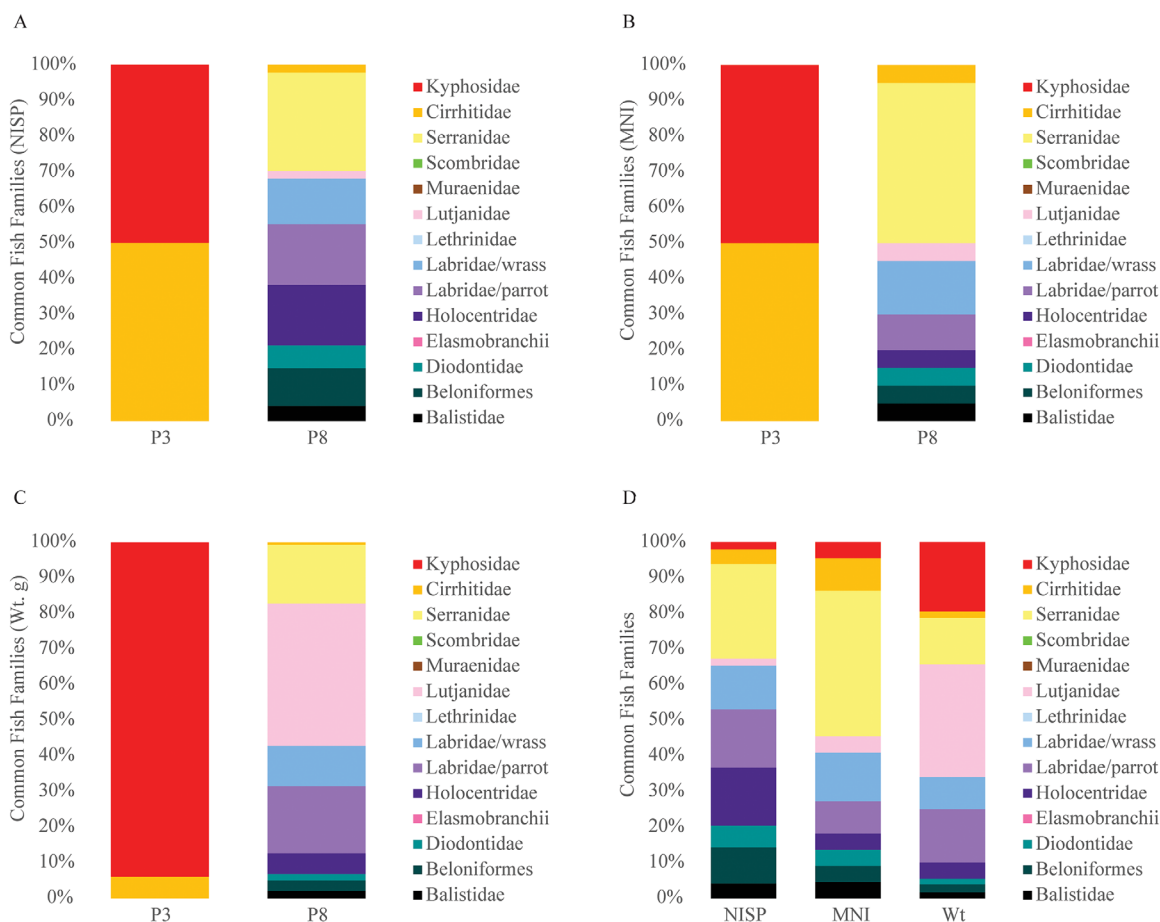


FIGURE 10 | Fish family frequency for plana 3 and 8 in (a) NISP, (b) MNI, (c) Weight (g), and (d) all plana aggregated. *Only families that occur in higher frequencies than 0.05% NISP were included in this figure, as well as Kyphosidae and Cirrhitidae.

present in plana 12 through 29 (See Supplementary information 3 and 6). Cirrhitidae, a family of smaller fish species, was found in plana 3, 8, and 24 (NISP = 1 in each plana). This could indicate that Cirrhitidae were potentially missed in other plana given their generally smaller sized bones. Holocentridae were represented by the cleithrum, the maxilla, and the quadrate throughout the assemblage; however, the premaxilla was only encountered in planum 8, which could be due to a smaller sieve size being used. However, this taxon is generally smaller too, and these elements do not differ in size much from one another. Mugilidae are only represented in planum 8, by one vertebra. They do not appear in any other planum, which could indicate that a smaller sieve size was necessary to recover this species or that taphonomic factors such as bone density impacted preservation in older plana.

10.2 | Invertebrates

Bivalvia frequency is lower than Gastropoda on Ujae (Weisler 1999a) and Ebon (Harris et al. 2016), which is similar to the Mokil assemblage; however, this is the inverse for the Utrök assemblage (Weisler 2001b). Gastropoda frequency for Mokil fluctuates over time, reaching lower frequencies in plana 20 and 12, where Actinopterygii or, in the latter, potentially Bivalvia, compensate for the decrease. Overall, for Mokil, Bivalvia occurs in relatively similar frequencies through time except when weight

is considered for planum 12. However, the main contributors here are Tridacninae, which are big, heavy shells, which helps explain a skew in the weight frequency over NISP and MNI numbers for Bivalvia. Six species of Bivalvia were identified on Mokil, with Mesodesmatidae, Tridacninae, and Tellinidae being the most common taxa throughout time. Two plana are void of Tridacninae: plana 19 and 12. After planum 12, there is also a shift as Mesodesmatidae disappear and are replaced by Lucinidae and Arcidae on Mokil. On Utrök, Tridacninae were by far the most common, accounting for 80% of Bivalvia weight, which was similar to Ujae (Weisler 1999a), while on Ebon, Tridacninae, Psammobiidae, Cardiidae, and Tellinidae made up the majority of the bivalve assemblage (Harris et al. 2016).

Twenty taxa were identified for Gastropoda on Mokil, which, together with our Bivalvia count, comprises a total of 26 families compared to 34 on Utrök, 32 families on Ujae (Weisler 1999a), and 47 on Ebon (Harris et al. 2016). Although this lower number could potentially be due to our smaller sample size. Strombidae/Conidae, Turbinidae, Cerithiidae, and Trochidae seem most prevalent in the Mokil assemblage and all occur through time except for Cerithiidae, which are missing from Planum 20. In planum 20, Strombidae/Conidae also increase significantly in frequency over all other taxa present on Mokil. On Utrök, Weisler (2001b) reports Strombidae, Cerithiidae, and Muricidae/Turbinellidae to be the most common, while for

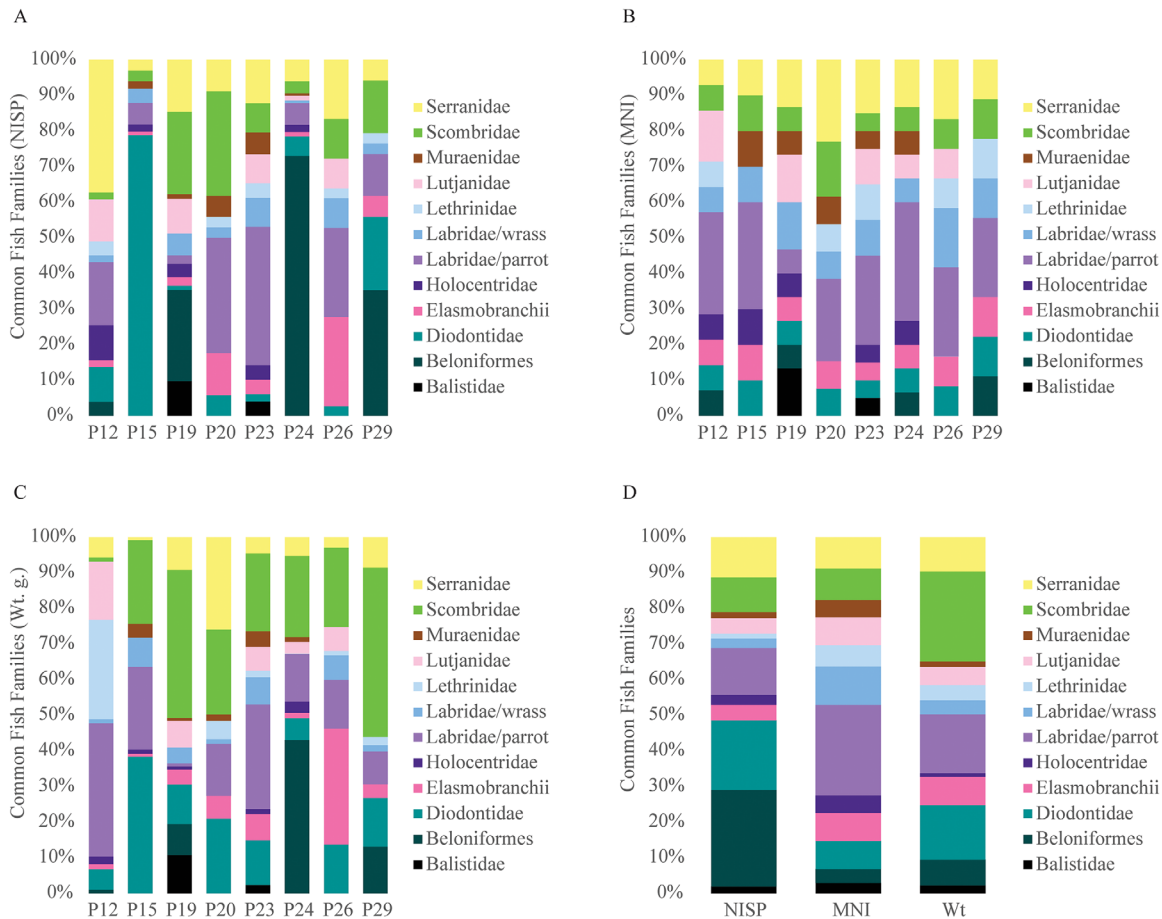


FIGURE 11 | Fish family frequency for plana 12-29 in (a) NISP, (b) MNI, (c) Weight (g), and (d) all plana aggregated.* Only families that occur in higher frequencies than 0.05% NISP were included in this figure.

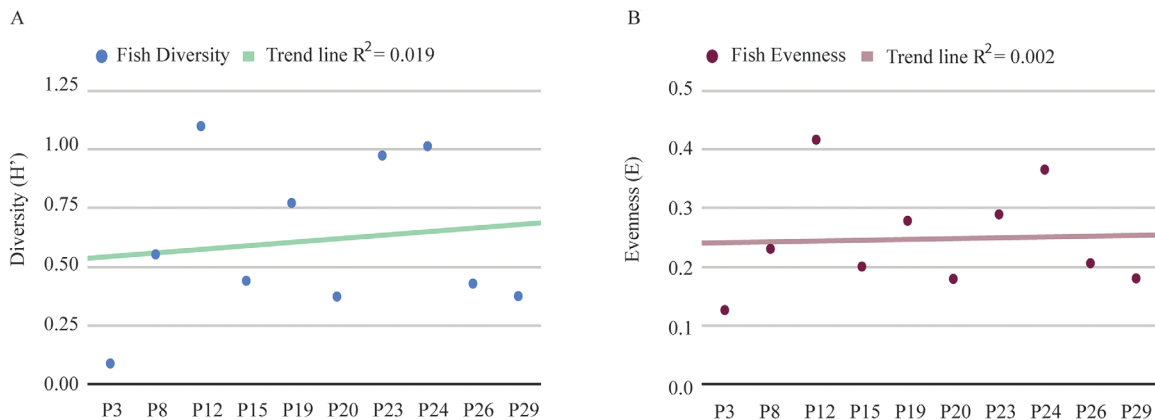


FIGURE 12 | Fish (a) diversity (H') and (b) evenness (E) per planum.

Ujae, Cerithiidae and Turbinellidae, along with Neritidae and Turbinidae, are the most common Gastropoda (Weisler 1999a). For Ebon, the most common families were Ranellidae, Neritidae, Muricidae, Cypraeidae, Cerithiidae, Conidae, Psammobiidae, Trochidae, Cardiidae, Turbinidae, Turbinellidae, Strombidae, and Veneridae (Harris et al. 2016). Cypraeidae on Mokil are absent between plana 26 and 20, between approximately 1550 – 970 calBP. *Cypraeacassis rufa*, belonging to the Cypraeidae family, became extinct on Utrök (Weisler 2001b). Given the absence of this species

for a longer period of time in our sample from Mokil, it is possible that this species was either overharvested but recovered with time or was avoided for a period of time. However, since our sample is small, further research is needed to see if this pattern replicates itself on Mokil when a larger sample size is considered. In addition, Turbinellidae disappear after planum 20. Keeping in mind that plana 3 and 8 were sieved using a smaller mesh size, the presence of some of the smaller gastropods in mostly these plana may be the result of recovery bias. This could certainly be

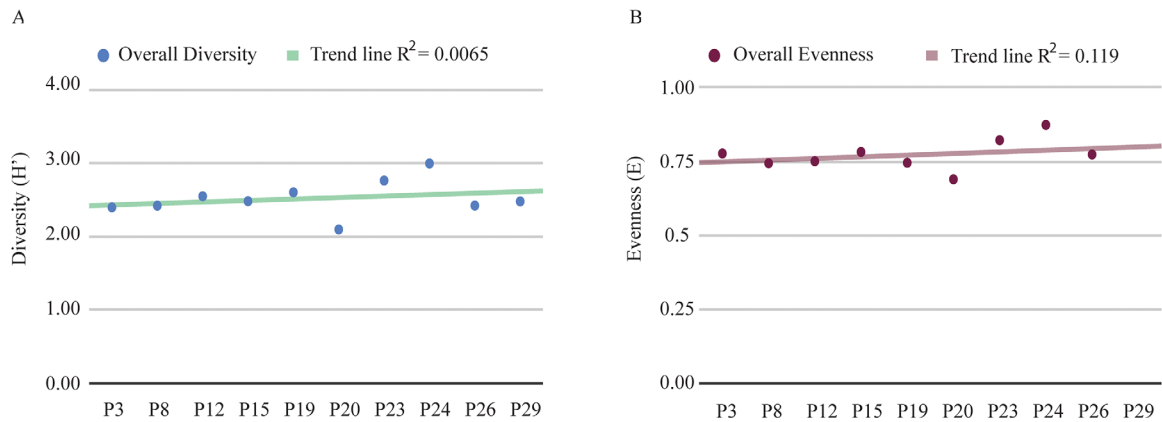


FIGURE 13 | Overall (a) diversity (H') and (b) evenness (E) per planum.

the case for Helenicidae (Helenicids) (planum 3: 2 NISP; 2 MNI) and Achatinidae (Giant African snails) (planum 3: 1 NISP; 1 MNI), although their frequencies are low.

10.3 | Fish

Twenty-three fish taxa were identified on Mokil, compared to 24⁴ on Utrök (Weisler 2001a), 27 on Ebon (Harris et al. 2016), 20 on Ujae (Weisler 1999a), 18 on Fais (Ono and Intoh 2011), and 24 on Nukuoro and Kapingamarangi (Leach and Davidson 1988). On Mokil, Scaridae are the most common, with Scaridae/wrasse together with Scaridae/parrotfish making up 64% MNI of all fish found. On Utrök (Weisler 2001a), Ebon (Harris et al. 2016), and Ujae (Weisler 1999a), Scaridae also make up the majority of fish. On Nukuoro, Scaridae are most prevalent after Serranidae, while on Kapingamarangi they are most important after Balistidae (Leach and Davidson 1988). Notably, on Fais, Serranidae, Carcharinidae, and Scombridae are more prevalent than Scaridae (MNI) (Ono and Intoh 2011), which could perhaps be due to the lack of a lagoon here. Other common species on Mokil include Serranidae, Diodontidae, Beloniformes, Lutjanidae, Scombridae, and Elasmobranchii. This is similar for Utrök, Ujae, and Ebon; however, Carangidae, Ostraciidae, and Acanthuridae seem to be more prevalent here than in the Mokil assemblage. Other commonalities can be seen between Mokil and Kapingamarangi where Scaridae, Elasmobranchii, Serranidae, Scombridae and Lutjanidae also occur most prominently, with the difference that Kapingamarangi's most common family is Balistidae, with Diodontidae and Belonidae much less common (Leach and Davidson 1988). Little similarity can be found with the Nukuoro assemblage where Serranidae and Scaridae are most prevalent but are followed by Anguillidae, Balistidae, Carrangidae, Nemphrid and Holocentridae, none of which are common on Mokil (Leach and Davidson 1988).

Across time, there are no major shifts in fish occurrence on Mokil. Subtle differences in NISP, MNI, and Wt. can be seen in Beloniformes and Lutjanidae, which are common in many plana, but do not occur in planum 20. Labridae/wrasses also drop in frequency in this planum. Subsequently, there is a slight increase of Serranidae and Scombridae in planum 20. Scombridae and Elasmobranchii disappear in plana 8 and 3 on Mokil. The absence of these taxa in plana 8 and 3 is interesting in that this

cannot be due to a recovery bias, given that a smaller sieve size would capture more remains, not less. Because the Mokil sample size is relatively small, further investigation would be required before more resolute conclusions could be drawn. Considering that plana 3 and 8 were sieved at a smaller size, the occurrence of some of the smaller fish families in mostly just these plana may be due to recovery bias. This could be the case for Cirrhitidae, although they occur in very low frequency (1 NISP in each layer) even in these plana.

Fish diversity is variable through time, however, it remains low throughout the assemblage, with a maximum of $H' = 1.09$. Diversity and evenness together indicate potentially alternating patterns of more specialised targeted fishing practices during plana 29 (1620 – 1440 calBP), 26 (between 1620 – 1400 calBP), 20 (between 1550 – 910 calBP), 15 (between 970 – 190 calBP) and 8 (after 320 calBP), and more generalised ones (or the use of nets), where there is no intention of selecting specific species across time periods associated with plana 24, 23, 19, and 12. However, evenness across the board is closer to 0 than to 1, which is relatively weak (Figure 12).

10.4 | Mammals

There are only two mammalian species found on Mokil: *Rattus* sp. and *Canis familiaris*. The occurrence of *Canis familiaris* in some of the oldest plana (planum 26), dating to between 1550 – 1400 calBP, suggests that dogs may have been introduced during the earliest stages of settlement, although this could be earlier given that plana 27 and 28 were not included in our sample. The movement of commensals—in which animal dispersal is facilitated by human movement either purposefully or accidentally (Storey et al. 2012, p. 39)—is known for other islands in Eastern Micronesia (Athens 1990; Davidson 1971, 1992).

Canis familiaris is thought to have first been introduced to Central-Eastern Micronesia and spread to Western Micronesia since they are mostly absent in the earlier periods in the latter (Intoh 1999), with the exception of remains found on Fais dating to 1730–1500 calBP (Intoh and Shigehara 2004). As such, there are still many questions surrounding the introduction of dogs generally into both Near and Remote Oceania (Intoh and Shigehara 2004; Matisoo-Smith 2007). This avenue of investigation is

particularly important as these movements can shed light on early human dispersal routes if commensals are found in the earliest occupation layers (Cramb 2022; Cramb and Hadden 2020; Oskarsson et al. 2012; Williams et al. 2018).

There are several theories regarding the number of dog introductions and the interrelation between identified haplotypes (e.g. Cramb 2022; Greig et al. 2016; Greig et al. 2018; Williams et al. 2018). Further genetic research, including determining whether the Mokil dog specimens belong to one of the known haplotypes, could help in determining population origins (Cramb and Hadden 2020; Matisoo-Smith 2007; Oskarsson et al. 2012). Dog occurs in all other discussed islands, albeit also in low frequencies (Harris et al. 2016; Ono and Intoh 2011; Weisler 1999a, 2001a), with Intoh and Shigehara (2004) speculating that they could have originated from a broad range of potential source areas, including the eastern Caroline Islands, Philippines, Indonesia, or northern Melanesia.

Rattus sp. does not occur until later in planum 23 (ca. 1400 – 970 calBP), which is not uncommon for Micronesia. For example, rats in the Marianas do not seem to appear until more than 2000 years after human settlement (Pregill and Steadman 2009), unlike Polynesia where the occurrence of rats usually coincides with the initial presence of humans (Matisoo-Smith et al. 1998; Matisoo-Smith 2009; Wickler 2004). However, their absence in the earliest layers from Mokil may be influenced by sampling bias, as the assemblage derives from select plana within a single 1×1 m unit. Additionally, the larger sieve size ($\frac{1}{4}$ inch) used up until planum 8 may have resulted in the loss of smaller bones, potentially obscuring their presence in earlier contexts. Notably, in other areas in Micronesia, the absence of *Rattus* sp. in the oldest layers coincides with the presence of many endemic Aves species (Pregill and Steadman 2009). This is not the case for Mokil, where we have identified only five Aves specimens. Rat also occurs on Utrök, Ebon, Ujae, and Fais (Harris et al. 2016; Steadman and Intoh 1994; Weisler 1999a, 2001a).

Overall, information about the dispersal of *Rattus exulans* and *Rattus tanezumi* is sparse for Micronesia, particularly information from a securely dated context (e.g. Wickler 2004). As a result, this information—in combination with further investigation into the particular species found in our assemblage—provides an important contribution to understanding the history of the genus *Rattus* in Micronesia and the Caroline Islands more broadly, and could be potentially helpful in clarifying human population expansion (Matisoo-Smith and Robins 2004; Wickler 2004).

10.5 | Other

Pig was not encountered on Mokil but has been found in pre-contact contexts on Fais (Intoh and Shigehara 2004) and on Ujae but in historic deposits (Weisler 1999a). Additionally, lizards were also not encountered on Mokil, while multiple species were found on Ebon (Pregill and Weisler 2007). Bird on Mokil was not identified further, but seabirds, migratory shorebirds, and land birds were found on Utrök, Ujae, and Fais (Harris et al. 2016; Steadman and Intoh 1994; Weisler 1999a, 2001a). Further analyses, including aDNA and ZooMS, would be useful for identifying the various bird bones found to elucidate if they

are endemic, migratory, or perhaps chicken, which, to date, has not been found in this part of Micronesia.

10.6 | Overall Patterns

Through time on Mokil, it appears that there was a potential period of disruption around planum 20 (between ca. 1550 – 910 calBP). Prior to this, there was a general decrease in gastropods and an increase in fish; by planum 20, this phenomenon reverses again, with gastropods again starting to increase and fish declining. A similar pattern was observed at the site of Chelechol ra Orrak in Palau, where starting around 1700 calBP, there was a pronounced decrease in fishing and an increase in exploitation of inshore littoral molluscs (Giovas et al. 2016). Further investigation has seemed to rule out overexploitation as a cause (Giovas et al. 2016).

Despite the decrease in fish frequency on Mokil in planum 20, it shows the highest frequency of Serranidae and Scombridae but is devoid of Beloniformes and Lutjanidae, which occur in most other plana. The diversity ($H = 0.37$) and evenness ($E = 0.18$) of harvested fish are also some of the lowest in the assemblage, potentially indicating more targeted practices when it came to fishing. In planum 20, there is also a sudden increase in Conidae/Strombidae compared to the previous or subsequent period, and this is one of the only plana where Cerithiidae are completely absent. Turbinellidae disappear after planum 20.

Lastly, the overall diversity and evenness indices decrease in planum 20, with a lower-than-average diversity score of 2.1 (average $H' = 2.52$) and evenness score of 0.69 (average $E = 0.77$), indicating that fewer species were harvested in uneven quantities, which could indicate a more specialist approach (Figure 13).

In planum 12 (± 250 calBP), some other notable changes occur. Here, bivalves like Mesodesmatidae decrease dramatically in favour of newly appearing Arcidae and Lucinidae, while the overall fish component increases with a corresponding decline in Gastropoda. Given that radiocarbon dates are missing for these two plana, it is difficult to connect these potential changes with other factors.

Overall, we were able to observe some similarities between the Utrök, Ujae, Ebon, Fais, Kapingamarangi, and Mokil assemblages, but the difference in gastropod/bivalve ratios between Utrök and Mokil, the latter for which that number was much higher (as well as the disparities in the number of identified families between Mokil, and Ujae, and Ebon) could prove interesting in further research. It also appears that Utrök, Ujae, and Fais were much richer in avian remains than Mokil. Further research, however, should be conducted to investigate whether Mokil was indeed more impoverished in avian fauna at the beginning of human settlement, whether the absence of birds is potentially due to a sampling bias, or whether people arrived earlier and had already begun overexploiting the bird population. There could also be other reasons for this pattern, including differential processing of birds or using other deposition areas.

Thus far, Mokil follows a tradition in Remote Oceania of rats not being among the first animals brought by humans during

initial settlement (Wickler 2004), while dogs are among the earliest (Athens 1990, 1995; Davidson 1971, 1992). Given general questions regarding the spread, origin, and dispersal route(s) of these animals, the specimens for both these genera from Mokil could be useful in future studies.

11 | Conclusion

The faunal assemblage from Mokil provides a critical, and analytically expansive, comparative dataset for understanding pre-contact subsistence practices and human settlement strategies on atolls in the Central Caroline Islands. The Mokil assemblage includes 53 distinct families and has high frequencies of invertebrates and fish, with lower frequencies of mammals and birds. Invertebrate remains comprise 26 taxa, with Strombidae/Conidae, Turbinidae, Cerithiidae, and Trochidae being the most common taxa. Fish remains are diverse, comprising twenty-three different taxa, with Scaridae (parrotfish and wrasse) comprising the majority, and taxa such as Serranidae, Lutjanidae, and Scombridae appearing throughout the sequence.

There are some notable shifts, such as a broader subsistence transition with a reduction in fish and an increase in mollusc exploitation around planum 20 (between 1550 – 990 calBP), as well as shifts to more targeted fishing practices, as indicated by diversity and evenness metrics. This is a pattern that was also observed at the Chelechol ra Orrak site in Palau, starting around 1700 calBP (Giovas et al. 2016). In planum 12 ($\pm$ 250 calBP), several notable shifts are evident as well. Bivalves such as Mesodesmatidae decline sharply, while Arcidae and Lucinidae appear for the first time. Additionally, the overall fish component increases, coinciding with a decrease in Gastropoda.

Canis familiaris is present in some of the oldest plana, supporting the idea that dogs were introduced early in the settlement sequence, consistent with broader patterns across Remote Oceania. In contrast, *Rattus* sp. appears much later, post-dating initial settlement, aligning with trends observed across other Micronesian sites. While Mokil appears relatively poor in avian remains, this could reflect sampling or recovery bias.

Taken together, these findings have provided a much-needed contribution to the zooarchaeological literature of the region and has enhanced our understanding of early atoll settlement timing and strategies. These data have also contributed to documenting the presence and diversity of taxa on Mokil during the pre-contact era, which are useful for examining human-environmental interactions in the past (Mondini et al. 2003; Rick and Erlandson 2008; Swift et al. 2017) and our current understanding of local and regional ecologies (Braje et al. 2017; Pauly et al. 1998; Thomas 2019). They also highlight the importance of using consistent sampling and analytical methods, increasing sample size, and further taxonomic analysis—including genetic studies of dog and rat specimens—to refine our understanding of early transoceanic dispersals across the Pacific. Future research will be dedicated toward aDNA and/or collagen peptide mass fingerprinting analysis of dog and rat remains from Mokil to identify haplotype and further parse out how these commensals dispersed into and beyond Micronesia.

Acknowledgements

We thank Michelle LeFebvre for editing and providing important feedback on earlier drafts of the paper. We also thank Aaron Poteate and Adam Thompson who excavated the material and provided other records and useful information. In addition, we thank Aimee Miles for communication regarding the pending zooarchaeological investigation of the Pingelap assemblage. Thanks go to University of Oregon undergraduate students Annika McNair, Audrey Keane, Allison Croyle, Isabella Fehringer, Lily Reisner, Emma Ruby, and Miles Berry for their assistance in sorting and identifying faunal material in the Island and Coastal Archaeology Lab.

Conflicts of Interest

The authors report there are no competing interests to declare.

Data Availability Statement

The authors confirm that all data underlying the findings are included within the supplementary materials of the manuscript.

Endnotes

¹The first article that was published on this assemblage (Poteate et al. 2016) used this terminology, and it was also used on the find bags and other documentation from that excavation. The use of the term “planum” to describe the excavation of arbitrary units (akin to using “level” or “spits”) is not uncommon and can be found in the archaeological literature elsewhere (e.g. Rösch 2021; Hegyi et al. 2025). To maintain unity across these sources, we have decided to retain this terminology.

²Fais consists of an elevated coral platform. Technically, it would not be considered an atoll as it does not have a central lagoon. However, many scholars (e.g. Flannery 1995; Connell 1986; Spennemann 2006) do refer to it as an atoll given its general similarity to classic atolls considering geological and ecological attributes.

³For Ebon, only numbers were reported for the classes of molluscs and fish, with these alone totalling 76 different families (Harris et al., 2016).

⁴Includes fish, Elasmobranchii and Muraenidae or Anguillidae (Weisler, 2001a).

References

- Anderson, A. 2009. “The Rat and the Octopus: Initial human Colonization and the Prehistoric Introduction of Domestic Animals to Remote Oceania.” *Biological Invasions* 11, no. 7: 1503–1519. <https://doi.org/10.1007/s10530-008-9403-2>.
- Athens, J. S. 1990. “Nan Madol Pottery, Pohnpei.” *Micronesica* 2: 17–32.
- Athens, J. S. 1995. *Landscape Archaeology: Prehistoric Settlement, Subsistence, and Environment of Kosrae, Eastern Caroline Islands, Micronesia: Archaeological Data Recovery Investigations for the Kosrae Wastewater Project*. International Archaeological Research Institute.
- Athens, J. S. 2018. “Archaeology of the Eastern Caroline Islands.” In *The Oxford Handbook of Prehistoric Oceania*, edited by T. L. Hunt, and E. E. Cochrane, 271–301. Oxford University Press.
- Athens, J. S., M. F. Dega, and J. V. Ward. 2004. “Austronesian Colonization of the Mariana Islands: The Paleoenvironmental Evidence.” *Indo-Pacific Prehistory Association Bulletin* 24, no. 2: 21–30.
- Athens, J. S., and J. Stevenson. 2012. “Pohnpei Coring Records: The Natural Distribution of *Cyrtosperma chamissonis*.” *Journal of Pacific Archaeology* 3, no. 1: 35–48.
- Ayres, W. S. 1990. “Pohnpei’s Position in Eastern Micronesian Prehistory.” *Micronesica Supplement* 2: 187–212.

- Balick, M. J. 2009. *Ethnobotany of Pohnpei: Plants, People, and Island Culture*. University of Hawaii Press.
- Bascom, W. R. 1965. *Ponape: A Pacific Economy in Transition*. University of California Press.
- Bergbauer, M., and M. Kirschner. 2020. *Reef Fishes of the Indo-Pacific*. John Beaufoy Publishing.
- Blust, R. 2010. "Malaita-Micronesian Once Again." *Oceanic Linguistics* 49, no. 2: 559–567.
- Braje, T. J., T. P. Leppard, S. M. Fitzpatrick, and J. M. Erlandson. 2017. "Archaeology, Historical Ecology and Anthropogenic Island Ecosystems." *Environmental Conservation* 44, no. 3: 286–297. <https://doi.org/10.1017/S0376892917000261>.
- Bryson, R. U. 1989. *Ceramics and spatial archaeology at Nan Madol, Pohnpei* [Ph.D., University of Oregon]. <https://www.proquest.com/docview/303736111/abstract/AC58AAC412664484PQ/1>.
- Butler, V. L., S. K. Campbell, K. M. Bovy, and M. A. Etnier. 2019. "Exploring Ecodynamics of Coastal Foragers Using Integrated Faunal Records From Āixwīcōn village (Strait of Juan de Fuca, Washington, USA)." *Journal of Archaeological Science: Reports* 23: 1143–1167.
- Carson, M. T. 2013. *First Settlement of Remote Oceania: Earliest Sites in the Mariana Islands*, (Vol. 1). Springer International Publishing. <https://doi.org/10.1007/978-3-319-01047-2>.
- Clark, G., A. Anderson, and D. Wright. 2006. "Human Colonization of the Palau Islands, Western Micronesia." *The Journal of Island and Coastal Archaeology* 1, no. 2: 215–232. <https://doi.org/10.1080/15564890600831705>.
- Clark, G. R. 2005. "A 3000-Year Culture Sequence From Palau, Western Micronesia." *Asian Perspectives* 44, no. 2: 349–380.
- Cochrane, E., and T. Hunt. 2018. *The Oxford Handbook of Prehistoric Oceania*. Oxford University Press.
- Connell, J. 1986. "Population, Migration, and Problems of Atoll Development in the South Pacific." *Pacific Studies* 9, no. 2: 41–58.
- Cramb, J. 2022. "The Dogs of Remote Oceania: An Archaeological and Ethnohistorical View of Domestic Dog Introduction and Loss in the South Pacific." *Archaeology in Oceania* 57, no. 1: 28–38. <https://doi.org/10.1002/arco.5252>.
- Cramb, J., and C. S. Hadden. 2020. "From Land and Sea: Overcoming the Challenges of Directly Dating Dog Remains on Polynesian Islands." *Radiocarbon* 62, no. 6: 1651–1665.
- Dance, P. 1976. *The Collector's Encyclopedia of Shells*. McGraw-Hill.
- Davidson, J. 1971. "Archaeology on Nukuoro Atoll." *Bulletin of the Auckland Institute and Museum* 9: 25–108.
- Davidson, J. 1992. "New Evidence about the Date of Colonisation of Nukuoro Atoll, a Polynesian Outlier in the Eastern Caroline Islands." *The Journal of the Polynesian Society* 101, no. 3: 293–298.
- Davidson, J. M. 1967. "Preliminary Archaeological Investigations on Ponape and Other Eastern Caroline Islands." *Micronesica* 3, no. 2: 81–95.
- Descantes, C. 1998. "Integrating Archaeology and Ethnohistory: The Development of Exchange between Yap and Ulithi, Western Caroline Islands." PhD diss., University of Oregon.
- Dickinson, W. R. 2003. "Impact of Mid-Holocene Hydro-isostatic Highstand in Regional Sea Level on Habitability of Islands in Pacific Oceania." *Journal of Coastal research* 489–502.
- Di Piazza, A. 1999. "Te Bakoa Site: Two Old Earth Ovens From Nikunau Island (Republic of Kiribati)." *Archaeology in Oceania* 34: 40–42.
- Dye, T. 1987. *Archaeological Survey and Test Excavations on Arno Atoll, Marshall Islands*. In T. Dye (ed.), *Marshall Islands Archaeology*, pp. 271–399. Pacific Anthropological Records 38. B. P. Bishop Museum.
- Fitzpatrick, S. M. 2003. "Early Human Burials in the Western Pacific: Evidence for c.3000 Year Old Occupation on Palau." *Antiquity* 77, no. 298: 719–731. <https://doi.org/10.1017/S0003598X00061664>.
- Fitzpatrick, S. M., and M. F. Napolitano. 2023. "The Influence and Efflorescence of Ancient Micronesia." In *The Oxford Handbook of Island and Coastal Archaeology*, edited by S. M. Fitzpatrick and J. Erlandson. Oxford University Press.
- Fitzpatrick, S. M., V. D. Thompson, A. S. Poteate, M. F. Napolitano, and J. M. Erlandson. 2016. "Marginalization of the Margins: The Importance of Smaller Islands in Human Prehistory." *The Journal of Island and Coastal Archaeology* 11, no. 2: 155–170. <https://doi.org/10.1080/15564894.2016.1192568>.
- Flannery, T. F. 1995. *Mammals of the South-West Pacific & Moluccan Islands*. Cornell University Press.
- Froese, R., and D. Pauly. 2021. *FishBase: A Global Information System on Fishes*. <https://fishbase.se/home.htm>.
- Gakuhari, T., M. Intoh, T. Nakano, and M. Yoneda. 2013. "Strontium Isotope Analysis of Prehistoric Faunal Remains Excavated From Fais Island in Micronesia." *People and Culture in Oceania* 29: 69–81.
- Galipaud, J. C. 2001. "Le Peuplement Initial De Pohnpei." *Journal de la Société des Océanistes* 112: 49–60.
- Giovas, C. 2018. "Impact of Analytic Protocols on Archaeofish Abundance, Richness, and Similarity: A Caribbean-Pacific Crossover study." In *Zooarchaeology in Practice: Case Studies in Methodology and Interpretation in Archaeofaunal Analysis*, edited by M. Lefebvre, and C. Giovas, 59–89. Springer International Publishing.
- Giovas, C. M. 2006. "No Pig Atoll: Island Biogeography and The Extirpation of a Polynesian Domesticated." *Asian Perspectives* 45, no. 1: 69–95.
- Giovas, C. M. 2013. *Foraging Variability in the Prehistoric Caribbean: Multiple Foraging Optima, Resource Use, and Anthropogenic Impacts on Carriacou, Grenada [Thesis]*. <https://digital.lib.washington.edu/443/researchworks/handle/1773/23391>.
- Giovas, C. M., S. M. Fitzpatrick, O. Kataoka, and M. Clark. 2016. "Prey Body Size and Anthropogenic Resource Depression: the Decline of Prehistoric Fishing at Chelechol ra Orrak, Palau." *Journal of Anthropological Archaeology* 41: 132–146. <https://doi.org/10.1016/j.jaa.2015.12.001>.
- Grayson, D. K. 2014. *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Elsevier.
- Green, R. C., and M. I. Weisler. 2004. "Prehistoric Introduction and Extinction of Animals in Mangareva, Southeast Polynesia." *Archaeology in Oceania* 39, no. 1: 34–41.
- Greig, K., A. Gosling, C. J. Collins, et al. 2018. "Complex History of Dog (*Canis familiaris*) Origins and Translocations in the Pacific Revealed by Ancient Mitogenomes." *Scientific Reports of Otago, Studies in Prehistoric Anthropology, Volume 16* reports 8, no. 1: 9130.
- Greig, K., R. Walter, and E. A. Matisoo-Smith. 2016. "Dogs and People in Southeast Asia and the Pacific." In *The Routledge Handbook of Bioarchaeology in Southeast Asia and the Pacific Islands*. Routledge.
- Grouard, S. 2001. "Faunal Remains Associated With Late Saladoïd and Post-Saladoïd Occupations at Anse À la Gourde, Guadeloupe, West Indies: Preliminary Results." *Archaeofauna* 10: 71–98.
- Harris, M., A. B. J. Lambrides, and M. I. Weisler. 2016. "Windward vs. leeward: Inter-site Variation in Marine Resource Exploitation on Ebon Atoll, Republic of the Marshall Islands." *Journal of Archaeological Science: Reports* 6: 221–229. <https://doi.org/10.1016/j.jasrep.2016.02.012>.
- Harris, M., and M. Weisler. 2017. "Intertidal Foraging on Atolls: Prehistoric Forager Decision-Making at Ebon Atoll, Marshall Islands." *The Journal of Island and Coastal Archaeology* 12, no. 2: 200–223. <https://doi.org/10.1080/15564894.2016.1167140>.
- Harris, M., and M. Weisler. 2018. "Two Millennia of Mollusc Foraging on Ebon Atoll, Marshall Islands: Sustained Marine Resource Use on a Pacific Atoll." *Archaeology in Oceania* 53, no. 1: 41–57. <https://doi.org/10.1002/arco.5134>.

- Haun, A. E. 1984. *Prehistoric Subsistence, Population, and Sociopolitical Evolution on Ponape, Micronesia*. University of Oregon. <https://www.proquest.com/openview/386d627b87ec6010d17fc498aa5da0ba/1?pq-origsite=gscholar&cbl=18750&diss=y>.
- Hegyi, A., S. Gridan, L. Angheluta, et al. 2025. "On the Fringes of the Empire: Multidisciplinary Investigations at the Roman Fort in Ungra, Transylvania." *Journal of Field Archaeology* 50, no. 5: 425–443.
- Horrocks, M., and M. I. Weisler. 2006. "Analysis of Plant Microfossils in Archaeological Deposits From Two Remote Archipelagos: The Marshall Islands, Eastern Micronesia, and the Pitcairn Group, Southeast Polynesia." *Pacific Science* 60, no. 2: 261–280. <https://doi.org/10.1353/psc.2006.0004>.
- Hunter-Anderson, R. 1991. "A Review of Traditional Micronesian High Island Horticulture in Belau, Yap, Chuuk, Pohnpei, and Kosrae." *Micronesica* 24, no. 1: 1–56.
- Hunter-Anderson, R. L., and M. W. Graves. 1990. "Coming From Where? An Introduction to Recent Advances in Micronesian Archaeology." *Micronesica Supplement* 2: 5–16.
- Intoh, M. 1999. "Cultural Contacts Between Micronesia and Melanesia." In *Pacifique de 5000 à 2000 Avant Le Present: Suppléments à L'Histoire d'une Colonisation*, edited by J. C. Galipaud, and I. Liley, 407–422. Editions de IRD (Institut de Recherche pour le développement).
- Intoh, M., and N. Shigehara. 2004. "Prehistoric Pig and Dog Remains From Fais Island, Micronesia." *Anthropological Science* 112, no. 3: 257–267. <https://doi.org/10.1537/ase.040511>.
- Irwin, G. 1992. *The Prehistoric Exploration and Colonisation of the Pacific*. Cambridge University Press.
- Kayanne, H., T. Yasukochi, T. Yamaguchi, H. Yamano, and M. Yoneda. 2011. "Rapid settlement of Majuro Atoll, central Pacific, following its emergence at 2000 years CalBP." *Geophysical Research Letters* 38, no. 20. <https://doi.org/10.1029/2011gl049163>.
- Kirch, P. V. 2000. "Pigs, Humans, and Trophic Competition on Small Oceanic islands." In *Australian Archaeologist: Collected Papers in Honour of Jim Allen*, edited by A. Anderson, and T. Murray, 427–439. Coombs Academic Pub., the Australian National University.
- Kirch, P. V. 2017. *On the Road of the Winds: An Archaeological History of the Pacific Islands before European Contact, Revised and Expanded Edition*. Univ of California Press.
- Klein, R. G., and K. Cruz-Uribe. 1984. *The Analysis of Animal Bones From Archeological Sites*, edited by K. W. Butzer and L. G. Freeman. Prehistoric Archaeology and Ecology Series University of Chicago Press.
- Lambrides, A. B., and M. I. Weisler. 2015. "Assessing Protocols for Identifying Pacific Island Archaeological Fish Remains: The Contribution of Vertebrae." *International Journal of Osteoarchaeology* 25, no. 6: 838–848.
- Leach, B. F., and J. M. Davidson. 1988. "The Quest for the Rainbow Runner: Prehistoric Fishing on Kapingamarangi and Nukuoro Atolls, Micronesia." *Micronesica* 21, no. 1: 2.
- Leach, F. 1986. "A Method for the Analysis of Pacific Island Fishbone Assemblages and an Associated Database Management System." *Journal of Archaeological Science* 13, no. 2: 147–159.
- Leach, F., and G. Ward. 1981. *Archaeology on Kapingamarangi Atoll: a Polynesian Outlier in the Eastern Caroline Islands*, Vol 16. University of Otago, Studies in Prehistoric Anthropology.
- Leonard, R. D., and G. T. Jones. 1989. *Quantifying Diversity in Archaeology*. Cambridge University Press.
- Levin, M. J., K. Seikel, and A. Miles. 2018. *Subsistence and Settlement on Pingelap Atoll: Results from the 2017 Field Season* [Technical]. www.researchgate.net/publication/324507113.
- Lieske, E., and R. Myers. 2001. *Coral Reef Fishes: Indo-Pacific and Caribbean*. Harper Collins Publishers.
- Liu, Y. C., R. Hunter-Anderson, O. Cheronet, et al. 2022. "Ancient DNA Reveals Five Streams of Migration Into Micronesia and Matrilocality in Early Pacific Seafarers." *Science* 377, no. 6601: 72–79.
- Lyman, R. L. 1994a. "Quantitative Units and Terminology in Zooarchaeology." *American Antiquity* 59, no. 1: 36–71. <https://doi.org/10.2307/3085500>.
- Lyman, R. L. 1994b. *Vertebrate Taphonomy*. Cambridge University Press.
- Lyman, R. L. 2008. *Quantitative Paleozoology*. Cambridge University Press.
- Lyman, R. L. 2019. "A Critical Review of Four Efforts to Resurrect MNI in Zooarchaeology." *Journal of Archaeological Method and Theory* 26, no. 1: 52–87. <https://doi.org/10.1007/s10816-018-9365-3>.
- Lyman, R. L., and S. Wolverton. 2023. "Quantification in Zooarchaeology and Palaeoethno(Archaeo)botany." In *Handbook of Archaeological Sciences* 1211–1225. John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781119592112.ch60>.
- Masse, W. B. 1990. "Radiocarbon Dating, Sea-level Change and the Peopling of Belau." *Micronesica Supplement* 2, no. 21: 3–30.
- Matisoo-Smith, E. 2007. "Animal Translocation, Genetic Variation, and the Human Settlement of the Pacific." In *Genes, Language, & Culture History in the Southwest Pacific*, edited by J. S. Friedlaender, 157–170. Oxford University Press.
- Matisoo-Smith, E. 2009. "The Commensal Model for Human Settlement of the Pacific 10 Years On—What Can We Say and Where to Now?" *The Journal of Island and Coastal Archaeology* 4, no. 2: 151–163. <https://doi.org/10.1080/15564890903155273>.
- Matisoo-Smith, E., R. M. Roberts, G. J. Irwin, J. S. Allen, D. Penny, and D. M. Lambert. 1998. "Patterns of Prehistoric Human Mobility in Polynesia Indicated by mtDNA From the Pacific Rat." *Proceedings of the National Academy of Sciences* 95, no. 25: 15145–15150. <https://doi.org/10.1073/pnas.95.25.15145>.
- Matisoo-Smith, E., and J. H. Robins. 2004. "Origins and Dispersals of Pacific Peoples: Evidence From mtDNA Phylogenies of the Pacific Rat." *Proceedings of the National Academy of Sciences* 101, no. 24: 9167–9172. <https://doi.org/10.1073/pnas.0403120101>.
- McCoy, M. D., H. A. Alderson, and A. Thompson. 2015. "A New Archaeological Field Survey of the Site of Nan Madol, Pohnpei." *Rapa Nui Journal* 29, no. 1: 5–22.
- Mondini, M., S. Munoz, and S. Wickler. 2003. *Colonisation, Migration, and Marginal Areas: A Zooarchaeological Approach*. Oxbow Books, Limited. <http://ebookcentral.proquest.com/lib/uoregon/detail.action?docID=4812232>.
- Morris, P. A. 1966. *A Field Guide to Shells of the Pacific Coast and Hawaii*. Houghton Mifflin Company.
- Moss, M. L., R. Minor, and K. Page-Botelho. 2017. "Native American Fisheries of the Southern Oregon Coast: Fine Fraction Needed to Find Forage Fish." *Journal of California and Great Basin Anthropology* 37, no. 2: 169–182.
- Murphy, R. E. 1950. "The Economic Geography of a Micronesian Atoll." *Annals of the Association of American Geographers* 40, no. 1: 58–83. <https://doi.org/10.2307/2561018>.
- Napolitano, M. F., S. M. Fitzpatrick, G. Clark, and J. H. Stone. 2019. "New Investigations of Early Prehistoric Settlement on Yap, Western Caroline Islands." *The Journal of Island and Coastal Archaeology* 14, no. 1: 101–107. <https://doi.org/10.1080/15564894.2017.1335661>.
- Nunn, P. D. 1994. *Oceanic Islands*. Blackwell Publishers, Oxford.
- Ono, R., and D. J. Addison. 2013. "Historical Ecology and 600 Years of Fish Use on Atafu Atoll, Tokelau in." In *Prehistoric Marine Resource Use in the Indo-Pacific Regions*, edited by D. J. Addison, R. Ono, and A. Morisson, 59–84. ANU E Press.
- Ono, R., and G. Clark. 2012. "A 2500-year Record of Marine Resource Use on Ulong Island, Republic of Palau." *International Journal of Osteoarchaeology* 22, no. 6: 637–654.

- Ono, R., and M. Intoh. 2011. "Island of Pelagic Fishermen: Temporal Changes in Prehistoric Fishing on Fais, Micronesia." *The Journal of Island and Coastal Archaeology* 6, no. 2: 255–286. <https://doi.org/10.1080/15564894.2010.540531>.
- Oskarsson, M. C. R., C. F. C. Klütsch, U. Boonyaparakob, A. Wilton, Y. Tanabe, and P. Savolainen. 2012. "Mitochondrial DNA Data Indicate an Introduction Through Mainland Southeast Asia for Australian Dingoes and Polynesian Domestic Dogs." *Proceedings of the Royal Society B: Biological Sciences* 279, no. 1730: 967–974. <https://doi.org/10.1098/rspb.2011.1395>.
- Parker, P. L., and T. F. King. 1981. "Recent and Current Archaeological Research on Moen Island, Truk." *Asian Perspectives* 24, no. 1: 11–26.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. "Fishing down Marine Food Webs." *Science* 279, no. 5352: 860–863. <https://doi.org/10.1126/science.279.5352.860>.
- Peres, T. M. 2010. "Methodological Issues in Zooarchaeology." In *Integrating Zooarchaeology and Paleoethnobotany*, edited by A. M. VanDerwarker, and T. M. Peres, 15–36. Springer. https://doi.org/10.1007/978-1-4419-0935-0_2.
- Peres, T. M. 2023. "Zooarchaeology of Foodways." In *Foodways Archaeology—Methods and Cases*, edited by T. M. Peres, 11–25. Springer International Publishing. https://doi.org/10.1007/978-3-031-41017-8_2.
- Petersen, G. 2006. "Micronesia's Breadfruit Revolution and the Evolution of a Culture Area." *Archaeology in Oceania* 41, no. 2: 82–92. <https://doi.org/10.1002/j.1834-4453.2006.tb00611.x>.
- Poteate, A. S. 2013. "Mokil3 Fieldnotes." Unpublished fieldnotes.
- Poteate, A. S., S. M. Fitzpatrick, W. S. Ayres, and A. Thompson. 2016. "First Radiocarbon Chronology for Mwoakilloa (Mokil) Atoll, Eastern Caroline Islands, Micronesia." *Radiocarbon* 58, no. 1: 169–178. <https://doi.org/10.1017/RDC.2015.16>.
- Pregill, G. K., and D. W. Steadman. 2009. "The Prehistory and Biogeography of Terrestrial Vertebrates on Guam, Mariana Islands." *Diversity and Distributions* 15, no. 6: 983–996. <https://doi.org/10.1111/j.1472-4642.2009.00603.x>.
- Pregill, G. K., and M. I. Weisler. 2007. "Lizards From Prehistoric Sites on Ebon Atoll, Marshall Islands." *Micronesica* 39, no. 2: 107–116.
- Prendergast, M. E., and P. J. Lane. 2010. "Middle Holocene Fishing Strategies in East Africa: Zooarchaeological Analysis of Pundo, a Kansyore Shell Midden in northern Nyanza (Kenya)." *International Journal of Osteoarchaeology* 20, no. 1: 88–112.
- Ragone, D. 1997. "Breadfruit: Artocarpus Altilis (Parkinson) Fosberg—Promoting the Conservation and use of Underutilized and Neglected Crops. 10 (Vol. 10)." *Bioversity International*.
- Rainbird, P. 2004. *The Archaeology of Micronesia*. Cambridge University Press.
- Ramsey, C. B. 2009. "Bayesian Analysis of Radiocarbon Dates." *Radiocarbon* 51, no. 1: 337–360.
- Reimer, P. J., E. Bard, A. Bayliss, et al. 2013. "IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years Cal BP." *Radiocarbon* 55, no. 4: 1869–1887.
- Reitz, E. J., and E. S. Wing. 2008. *Zooarchaeology*. Cambridge University Press.
- Richards, Z. T., C. C. Shen, J. P. A. Hobbs, C. C. Wu, X. Jiang, and F. Beardsley. 2015. "New Precise Dates for the Ancient and Sacred Coral Pyramidal Tombs of Leluh (Kosrae, Micronesia)." *Science advances* 1, no. 2: e1400060.
- Rick, T. C., and J. M. Erlandson. 2008. *Human Impacts on Ancient Marine Ecosystems: A Global Perspective*. University of California Press.
- Rindos, D. 1989. "Diversity, Variation and Selection." In *Quantifying Diversity in Archaeology*, edited by R. D. Leonard, and G. T. Jones, 13–24. Cambridge University Press.
- Rösch, F. 2021. "From Drawing Into Digital: On the Transformation of Knowledge Production in Postexcavation Processing." *Open Archaeology* 7, no. 1: 1506–1528.
- Rosendahl, P. 1977. *Archaeological Survey in the Marshall and Eastern Caroline Islands*. Dept. of Anthropology, Bishop Museum. Mss. 080577.
- Sabelli, B. 1980. *Simon and Schuster's Guide to Shells*. Simon and Schuster.
- Schneider, M. J., T. Ardren, B. Bertelli, P. Jorissen, and S. J. Purkis. 2024. "The Spanish Wells: Freshwater Lenses and the Florida Keys." *The Journal of Island and Coastal Archaeology*. <https://www.tandfonline.com/doi/abs/10.1080/15564894.2021.2021332>.
- Shun, K. S., and J. S. Athens. 1990. "Archaeological Investigations on Kwajalein Atoll, Marshall Islands, Micronesia." *Micronesica Suppl* 2: 231–240.
- Spennemann, D. H. R. 2006. "Extinctions and Extirpations in Marshall Islands Avifauna Since European Contact—a Review of Historic Evidence." *Micronesica* 38, no. 2: 253–266.
- Steadman, D. W., and M. Intoh. 1994. "Biogeography and Prehistoric Exploitation of Birds From Fais Island, Yap State, Federated States of Micronesia." *Pacific Science* 48, no. 2: 116–135.
- Storey, A. A., J. S. Athens, D. Bryant, et al. 2012. "Investigating the Global Dispersal of Chickens in Prehistory Using Ancient Mitochondrial DNA Signatures." *PLoS ONE* 7, no. 7: e39171. <https://doi.org/10.1371/journal.pone.0039171>.
- Streck, C. S. 1990. "Prehistoric Settlement in Eastern Micronesia: Archaeology on Bikini Atoll, Republic of the Marshall Islands." *Micronesica Supplement* 2: 247–260.
- Swift, J. A., M. J. Miller, and P. V. Kirch. 2017. "Stable Isotope Analysis of Pacific Rat (*Rattus exulans*) From Archaeological Sites in Mangareva (French Polynesia): The Use of Commensal Species for Understanding Human Activity and Ecosystem Change." *Environmental Archaeology* 22, no. 3: 283–297. <https://doi.org/10.1080/14614103.2016.1216933>.
- Taborosi, D., and M. Collazo Sanchez. 2009. "Mwoakilloa Atoll: Freshwater Resources and Their Usage, State, and Infrastructure." *Palikir, Pohnpei: Island Research & Education Initiative*. <https://www.weriguam.org/pdf/2012/mwoakilloa-report.pdf>.
- Takayama, J., and R. Shutler. 1978. "Preliminary Report of a Pottery Site on Fefan Island, Truk, central Caroline Islands." *Archaeology & Physical Anthropology in Oceania* 13, no. 1: 1–9.
- Temminck. 1844. In National Museum of Natural History, Smithsonian Institution. Mammal Species of the World. Checklist dataset. <https://doi.org/10.15468/csfquc> accessed via GBIF.org on 2024-12-05.
- Thaman, R. R. 2008. "Atolls—the "Biodiversity Cool Spots" vs Hot Spots: A Critical New Focus for Research and Conservation." *Micronesica* 40, no. 1/2: 33–61.
- Thomas, F. 2015. "Marginal Islands and Sustain Ability: 2,000 Years of Human Settlement in Eastern Micronesia." *Economic and Ecohistory* 11, no. 1: 64–74.
- Thomas, F. 2019. "Atoll Archaeology in the Pacific." In *Encyclopedia of Global Archaeology*. Springer. https://doi.org/10.1007/978-3-319-51726-1_3409-1.
- Thomas, F. R. 2002. "An Evaluation of central-place Foraging Among Mollusk Gatherers in Western Kiribati, Micronesia: Linking Behavioral Ecology With Ethnoarchaeology." *World Archaeology* 34, no. 1: 182–208.
- Thomas, F. R. 2009. "Historical Ecology in Kiribati: Linking Past With Present." *Pacific Science* 63, no. 4: 567–600. <https://doi.org/10.2984/049.063.0406>.
- Thompson, A. 2011. *The Early Settlement of Mwoakilloa Atoll* [Fiscal Report].
- Thompson, A. 2016. "Ancient Bones in Honor of the Goddess Sinlaku: New Findings on the Island of Kosrae, Eastern Micronesia." *Rapa Nui Journal* 30, no. 1: 43–51.

- Thompson, S. 1982. *Cyrtosperma Chamissonis* (Araceae): Ecology, Distribution, and Economic Importance in the South Pacific. <https://doi.org/10.3406/jatba.1982.3868>.
- Tinker, S. W., and K. Tinker. 1989. *Pacific Sea Shells*. Tuttle Publishing.
- Vogel, Y., and A. J. Anderson. 2012. "Prehistoric Fishing on Rapa Island." In *Taking the High Ground: The Archaeology of Rapa, a Fortified Island in Remote Polynesia*, edited by A.J. Anderson, and D.J. Kennett, 115–133. ANU E Press.
- Ward, J. V. 1988. "Palynology of Kosrae, Eastern Caroline Islands: Recoveries From Pollen Rain and Holocene deposits." In *Quaternary Palynology of Tropical Areas*, edited by J. V. Ward, and K. B. Liu, [Special issue] 55 (1-3), 157–176.
- Weisler, M. I. 1999a. "Atolls as Settlement Landscapes: Ujae, Marshall Islands." *Atoll Research Bulletin* 460: 1–51. <https://doi.org/10.5479/si.00775630.460.1>.
- Weisler, M. I. 1999b. "The Antiquity of Aroid Pit Agriculture and Significance of Buried A Horizons on Pacific Atolls." *Geoarchaeology* 14, no. 7: 621–654. [https://doi.org/10.1002/\(SICI\)1520-6548\(199910\)14:7<621::AID-GEA2>3.0.CO;2-2](https://doi.org/10.1002/(SICI)1520-6548(199910)14:7<621::AID-GEA2>3.0.CO;2-2).
- Weisler, M. I. 2001a. "Life on the Edge: Prehistoric Settlement and Economy on Utrök Atoll, northern Marshall Islands." *Archaeology in Oceania* 36, no. 3: 109–133. <https://doi.org/10.1002/j.1834-4453.2001.tb00486.x>.
- Weisler, M. I. 2001b. "Precarious Landscapes: Prehistoric Settlement of the Marshall Islands." *Antiquity*. <https://www.proquest.com/docview/217562646?pq-origsite=gscholar&fromopenview=true&sourcetype=Scholarly%20Journals>.
- Weisler, M. I., H. Yamano, and Q. Hua. 2012. "A Multidisciplinary Approach for Dating Human Colonization of Pacific Atolls." *The Journal of Island and Coastal Archaeology* 7, no. 1: 102–125.
- Wheeler, A. C., and A. K. G. Jones. 1989. *Fishes*. Cambridge University Press.
- White, T. E. 1953. "A Method of Calculating the Dietary Percentage of Various Food Animals Utilized by Aboriginal Peoples*." *American Antiquity* 18, no. 4: 396–398. <https://doi.org/10.2307/277116>.
- Wickler, S. 2004. "Modelling Colonisation and Migration in Micronesia From a Zooarchaeological Perspective. Colonisation, Migration, and Marginal Areas: A Zooarchaeological Approach." In *Colonisation, Migration, and Marginal Areas: A Zooarchaeological Approach*, edited by M. Mondini, S. Wickler, and S. Munoz, 28–40. Oxbow Books. <https://www.torrossa.com/en/resources/an/4914344#page=37>.
- Williams, C., S. Mazzola, G. Curone, and G. Pastorino. 2018. "What We Have Lost: Domestic Dogs of the Ancient South Pacific." *Annual Research & Review in Biology* 25, no. 2: 1–11. <https://doi.org/10.9734/ARRB/2018/40377>.
- Yamaguchi, T., M. Chikamori, H. Kayanne, H. Yamano, H. Yokoki, and Y. Najima. 2006. "Conditions and Activities Supporting Early Prehistoric human Settlement on Majuro Atoll in Marshall Islands, Eastern Micronesia." In *Proceedings of the 10th International Coral Reef Symposium*, edited by Y. Suzuki, T. Nakamori, M. Hidaka, H. Kayanne, B. E. Casareto, K. Nadaoka, H. Yamano, and M. Tsuchiya, 1549–1555.
- Yamaguchi, T., H. Kayanne, and H. Yamano. 2009. "Archaeological Investigation of the Landscape History of an Oceanic Atoll: Majuro, Marshall Islands I." *Pacific Science* 63, no. 4: 537–565.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supporting File 1: arco70021-sup-0001-SuppMat.docx