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# Applications of vertebral morphometrics in Pacific Island archaeological fishing studies

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**Abstract:** Significant differences between fish bone identification protocols in Pacific Island archaeology and other regions (e.g., Europe and North America) have influenced the use of vertebral morphometrics for the reconstruction of fish length and weight. Fish vertebral morphometrics using vertebrae identified to taxon and type (e.g., caudal, thoracic) are routinely reported in the archaeological literature outside of the Pacific Islands. Conversely, in Pacific Island archaeological fishing studies, vertebrae that are not identified to taxon have been utilised to assess change in average fish vertebrae size, and to reconstruct changes in fish length and weight over time. Using a fish bone assemblage from a prehistoric habitation site on Ebon Atoll, Republic of the Marshall Islands, we report false trends when vertebrae—not identified to taxon and type—are used to assess differences in average vertebrae size among cultural layers. These results are compared to the same assemblage where taxon and vertebra type are used to more accurately determine fish size. It is essential that vertebrae from Pacific Island fish bone assemblages are identified to taxon and type prior to assessing change in fish size over time, especially when investigating human impacts to finfish resources, capture technology or charting environmental change.

*Keywords:* faunal analysis, fish vertebrae, morphometric measures, Marshall Islands, Pacific fishing

## Introduction

Protocols for archaeofaunal identifications and the subsequent quality of these analyses structure all inferences regarding prehistoric subsistence systems, diet, foraging patterns and human impacts to terrestrial and marine ecosystems. Fish bone identification protocols in Pacific Island archaeology are unique when compared to other regions (e.g., the United Kingdom (UK), Europe and North America) as only a restricted range of cranial elements, the so-called “five-paired cranial elements”—dentary, premaxilla, articular, quadrate and maxilla—and “special” or unique bones have been routinely used for taxonomic identification. More recently, Pacific Island faunal analysts have incorporated an expanded range of cranial elements, resulting in more complete determinations of species richness and diversity (e.g., Jones O’Day 2004; Vogel 2005; Walter 1998; Weisler and Green 2013; Weisler et al. 2010). The routine taxonomic identification of fish vertebrae is the latest advance in Pacific fishing studies (e.g., Lambrides and Weisler 2013; Ono and Clark 2012). Yet, in other regions, a wider range of cranial and post-cranial elements have been routinely incorporated into identification protocols for decades (e.g., Butler 1993; Colley 1984; Desse-Berset and Desse 1994; Joslin 2011; Morales 1984; Moss 2011; Robson et al. 2013; Van Neer 1986; Zohar et al. 2001).

The distinction between taxonomic identification protocols used in the Pacific Islands and other regions can be attributed to a few key reasons:

1. The emphasis outside of the Pacific Islands on identifying butchery and processing techniques, with element representation central to these analyses; for example, the removal of fish heads for preservation (Bruschi and Wilkens 1996; Carenti 2013; Desse-Berset 1993), the pickling of fish (Van Neer et al. 2007) or the use of cut mark morphology to determine the presence of stockfish (i.e., unsalted fish that were dried for preservation) (Brinkhuizen 1994; Cerón-Carrasco 1994).
2. The preservation of a restricted range of elements at certain sites, which has directed the development of taxonomic identification protocols specific to a region; for example, the frequent representation of salmon vertebrae from sites in the North American Pacific Northwest, which has resulted in the development of methods focused predominately on vertebrae for assessing human diet, site occupation and seasonality (e.g., Butler and Chatters 1994; Campbell and Butler 2010; Cannon 2000; Ewonus et al. 2011; Gobalet 2012; Gobalet et al. 2004; Moss 2011; Orchard and Szpak 2011).
3. The effectiveness of vertebrae for conducting seasonality studies through the establishment of age profiles and growth rates (e.g., Cannon 1988; Casteel 1976; Desse and Desse-Berset 1992; Grier et al. 2013; Van Neer et al. 1999, 2004).
4. Finally, distinctions in regional methodologies can also be attributed to historical precedent, as disciplinary leaders (e.g., Casteel in the Pacific Northwest, Wheeler in the UK and Leach in the

Pacific Islands) have advocated for variable fish bone taxonomic identification protocols, which has produced regional training legacies. This is evident in Pacific archaeology, where Leach (1986) advocated for the identification of the five-paired cranial elements and “special” bones to the exclusion of other bones, including most vertebrae.

Fish vertebral morphometrics are routinely reported in the archaeological fishing literature outside of the Pacific Islands, given the ubiquity of vertebrae in cultural deposits and their use for reconstructing fish length and weight based on specific measurements (e.g., Casteel 1976; Colley 1990; Desse and Desse-Berset 1996c; Enghoff 1994; Gabriel et al. 2012; Gobalet 1989; Huber et al. 2011). Yet, in Pacific Island archaeological fishing studies, vertebrae that are not identified to taxon, but rather to the category of “fish” or group (Osteichthyes), have been utilised to assess change in average fish vertebrae size, and reconstruct changes in fish length and weight over time (e.g., Jones 2009; Jones and Quinn 2009; Rolett 1998). This approach is argued to provide a cross-section of the sizes of fish represented in the archaeological deposit (following Newsom and Wing 2004: 52–3, 67–72). Rigorous protocols exist for the systematic application of vertebral morphometrics, but species-level identifications are often required to provide accurate fish size (weight and length) reconstructions. Given that some regions of the tropical Pacific have more than 3000 marine fish taxa, which is amongst the highest biodiversity in the world (Briggs 2005; Veron et al. 2009), reconstructive methods that require species- or genus-level identifications of vertebrae cannot always be directly applied to Pacific Island archaeological assemblages, where family-level identifications are more routine.

In this paper, we briefly review the global literature on fish vertebral morphometrics and contrast these methods with those applied to Pacific Island assemblages. Using a fish bone assemblage from Ebon Atoll, Republic of the Marshall Islands, we contrast three protocols that use fish vertebrae to estimate fish size: (1) all taxa and vertebrae types to simulate methods commonly used in Pacific Island archaeology; (2) controlling for the taxon (i.e., Scombridae, Scaridae and Carangidae) but including all vertebrae types as a single category; and (3) controlling for both taxon and vertebra type (i.e., caudal vertebrae from Scombridae only). We show that combining all vertebral measurements irrespective of taxon or vertebra type—a method routinely used in the Pacific Islands—can produce false trends. Differences in vertebrae size among cultural layers commonly associated with decreases in fish size over time in the Pacific fishing literature are more likely tracking alternative trends (e.g., change in species composition across cultural layers). We therefore suggest future research directions for the systematic incorporation and development of vertebral morphometrics in Pacific Island archaeology.

## **Background**

### *Global applications of vertebral morphometrics*

Casteel (1974a, b, 1976) and Morales and Rosenlund (1979) provided systematic and replicable methods for measuring archaeological fish bones for reconstructing live fish weight and length. Since these pioneering works, pursuits have focused on refining approaches for assessing changes in fish populations over time, including seasonality, resource depression and changes in trophic structure (e.g., Desse and Desse-Berset 1996a, b; Gabriel et al. 2012; Leach et al. 1997a; Van Neer et al. 1993). Fishing studies outside of the Pacific Islands from the 1980s onwards routinely incorporated vertebral morphometrics using only those vertebrae identified to taxon and in some cases, most importantly, with type identified (i.e., atlas, caudal, precaudal etc.). Yet, these protocols were inconsistently applied across regions (i.e., variations in the taxonomic level vertebrae were identified prior to fish size reconstructions). For example, using an archaeological assemblage from Spain, Morales (1984: 53–6) acknowledged the variability of fish vertebrae along the vertebral column and recorded measurements of only those vertebrae that were identified to taxon and type prior to size reconstructions. Furthermore, Enghoff (1994), when investigating Danish fishing practices during the Ertebølle period, consistently measured only the first and second vertebrae of those identified to species to reconstruct fish size. In contrast, Gobalet (1989) identified minnows and carps (Cyprinid) to family and reconstructed fish size based on vertebral width measurements, without identifying vertebra type (see also Bertrando and McKenzie 2011; Broughton et al. 2000; Butler and Delacorte 2004; Zabilska 2013).

Nathalie Desse-Berset, George Desse and Jean Desse have each made exceptional contributions to the development and systematisation of archaeofish bone morphometrics and, of particular relevance here, vertebral morphometrics (e.g., Desse 1984; Desse and Desse 1983; Desse and Desse-Berset 1992, 1993, 1997, 1999b, 2000; Desse-Berset 1997, 2011). Desse and Desse-Berset (1996c) argued that vertebrae should be identified to species with vertebra type and position on the vertebral column known (i.e., first thoracic, tenth caudal) prior to making allometric reconstructions of weight and length. Desse and Desse-Berset (1989, 1994, 1999a) also developed the “Global Rachidian Profiles” (GRP) method, which maximised the calculation of the minimum number of individuals (MNI) values and size reconstructions based on vertebral morphometrics. Determining the exact position of vertebrae along the vertebral column is critical to the application of the GRP method. More recently, Radu et al. (2008: 361–2) applied the GRP method at Tappeh Hesar (Damghan, Iran) and using 29 cyprinid vertebrae were able to isolate small (174–250 mm) and large (400–500 mm) individuals based on fork length measurements (see also Clavel and Arbogast 2007). While Radu et al. (2008) only completed family-level identifications of the archaeological vertebrae, Desse and Desse-Berset (1996b: 176) argue for what they term “taxonomic proximity”, as “the relationship estimated between

various bone measurements and fish length, is a general one for the species, often valid for the genus and, occasionally, for a whole family as well". The GRP method is an improvement on earlier approaches in the Pacific Islands that utilised morphometrics of unidentified fish vertebrae, and by considering only measurements of identified vertebrae, it can provide coarse-grained reconstructions of fish size; for this reason, it should be considered by researchers working in the Pacific Islands.

It is critical that the exact position of each vertebra along the vertebral column be determined prior to reconstructions of fish length and weight (e.g., Desse and Desse-Berset 1989, 1999a). Gabriel et al. (2012) investigated meagre (*Argyrosomus regius*), a taxon common in many archaeological sites in Portugal, Spain, Greece, the eastern Mediterranean, Mauritania and the North Sea. Extensive identification criteria were provided to ensure that each meagre vertebra could be distinguished along the vertebral column and the appropriate regression equation was applied to reconstruct total length (TL) (Gabriel et al. 2012: table 1). Furthermore, Ritchie (2010: 177) measured the width of the posterior centrum of all atlas vertebrae identified to species to calculate weight and length determinations (see also Carder and Crock 2012; Carder et al. 2007; Orchard 2003). In contrast, Pletka (2011: 154) incorporated all "caudal" vertebrae measurements and did not determine the exact position along the vertebral column; however, statistical protocols were implemented to distinguish vertebrae from separate individuals (see also LeFebvre 2007).

At a number of Pacific Northwest sites, the ubiquity of salmon (*Oncorhynchus* spp.) vertebrae has provided the opportunity to develop innovative methods for obtaining high-resolution data from the analysis of vertebrae. Discussion has focused on methods for completing species-level identifications of salmon, critical for reconstructions of diet, site use, seasonality studies, and conservation and management practices (e.g., Gobalet 2012). Radiographic analysis, once used for identifications of salmon vertebrae (Cannon 1988), has been shown to be of limited use (Cannon and Yang 2006: 128). Subsequently, Huber et al. (2011) developed a method for making species-level identifications of salmon using vertebral morphometrics (for application of the identification protocol, see Lubinski and Partlow 2012). While aDNA has been successfully extracted to identify Pacific Northwest archaeological assemblages of salmon vertebrae, its application is often limited to small samples due to cost (Butler and Bowers 1998; Cannon and Yang 2006; Ewonus et al. 2011; Grier et al. 2013; Kemp et al. 2014; Moss et al. 2014; Speller et al. 2005; Yang et al. 2004; for related work on herring DNA, see also McKechnie et al. 2014; Speller et al. 2012). According to Moss et al. (2014), aDNA methods still appear to be the most accurate method of identifying salmon vertebrae to species, with the morphometrics protocols of Huber et al. (2011) requiring further refinement. Given the difficulties of species-level identifications in the Pacific Islands, a combination of morphometrics and aDNA or

peptide mass fingerprinting may be required to confidently implement fish size reconstructions (Richter et al. 2011).

#### *Pacific Island fishing studies and vertebral morphometrics*

Although not widely adopted in the tropical Pacific Islands, morphometric analysis of cranial elements in temperate New Zealand is more routine, particularly measurements of the five-paired cranial elements as well as key “special” bones, such as the upper and lower pharyngeal grinding plates of parrotfish (Scaridae) and wrasse (Labridae). New Zealand has a greatly reduced marine biodiversity compared to the subtropical and tropical Pacific Islands, where the species richness of ichthyofauna hinders species-level identifications that are ideal for accurate size reconstructions (e.g., Leach and Boocock 1994, 1995; Leach and Davidson 2000; Leach et al. 1997a,c, 1999a,b,c). However, these methods have been applied in other regions of the Pacific Islands (e.g., Fraser 1998; Leach et al. 1997b; Masse et al. 2006; Ono and Clark 2012; Weisler 2004).

There has been limited application of vertebral morphometrics in Pacific Island archaeology. Commonly, maximum width measurements of unidentified vertebrae are used to document vertebrae size and then to infer fish size changes over time (Jones O’Day 2001; Rolett 1998: 142; Weisler et al. 2010: 139–40). Conversely, Jones and Quinn (2009: 2745) measured the anterior width of unidentified vertebrae and reconstructed average weight, as “this procedure is based on the assumption that the fish vertebrae represent a cross-section of the species present in the assemblage”. This method was adapted from Wing (2001: 116–7) and Newsom and Wing (2004: 68–71) for application in the Caribbean based on a known allometric formula ( $\log Y = 2.53(\log X) + 0.872$ , where  $Y$  is the body weight and  $X$  is the vertebral width) developed using local fish species. The use of this allometric formula for Pacific Island archaeological assemblages is problematic, given that a unique regression equation is required for each vertebra along the vertebral column for every identified taxon (Gabriel et al. 2012; Seymour 2004).

These protocols have been acknowledged as coarse-grained (Weisler et al. 2010: 139–40), as the inclusion of unidentified elements can not only create false trends but also mask actual trends in the size of fish taxa over time. These approaches do not place sufficient focus on individual variation (at the family, genus and species level), sexual dimorphism and ecological factors that can influence growth rates and sizes (e.g., Robertson 1998). For example, male Mediterranean rainbow wrasse (*Colis julis*) are larger than females of the same age due to their sequential hermaphroditism; specifically, the fish that change sex are already the larger individuals in their age group and a growth spurt also occurs after the sex change (Linde et al. 2011). Ecological factors can also affect fish growth rate, with research on the bicour damselfish (*Stegastes partitus*) suggesting that temperature

shapes growth-related traits and can influence the intensity of selective mortality (Rankin and Sponaugle 2011). For these reasons, it is critical that an extensive fish reference collection be available for morphometrics; ideally, this would include male and female specimens of a variety of ages and also captured from variable ecological zones (e.g., juvenile fish from sheltered habitats such as mangrove forests and seagrass beds and adults from exposed coral reefs). Furthermore, issues of bone preservation must be considered, including bone structure, processing, ingestion, weathering and dissolution (Gabriel et al. 2012: 2864).

Given the influence of ontogenic growth and depositional and post-depositional taphonomic factors, it is critical that elements are identified to taxon prior to assessing changes in fish populations over time. For these reasons, Ono and Intoh (2011: 267) measured the width of identified tuna, bonito and mackerel (Scombridae) vertebrae only, but as only family-level identifications were possible, size reconstructions were not completed. The most comprehensive application of vertebral morphometrics in Pacific Island archaeology using identified vertebrae was conducted by Fraser (1998: 131–4), who used only the ultimate vertebra of Scombridae to reconstruct live fork length (FL) (see also Leach et al. 1997b). The importance of species-level identifications for the improvement of osteometric reconstructions was emphasised by Fraser (1998), as only family-level identifications were implemented in the study. Critically, Fraser (1998) considered change in reconstructed fork length (as determined by ultimate vertebrae measurements) to evaluate change over time rather than analysing change using the raw measurement data (but see Jones and Kirch 2007; Jones O'Day 2001; Rolett 1998). According to Gabriel et al. (2012: 2862–4), there is substantial variability in the relationship between bone size and fish size, and as such comprehensive reference collections that represent a variety of growth stages/age, sex and capture environments are required to develop “mathematical models that explicitly account for such variability” and will facilitate reconstructions of fish length and weight and assessments of change.

Methods are required that allow broad trends to be investigated if position along the vertebral column cannot be consistently determined for all taxa. For example, the average number of vertebrae varies between 31 and 66 for Scombridae and of that total, an average of 20 + are caudal vertebrae. In such cases it can be difficult to determine the precise location along the vertebral column. This issue is compounded by the often poor preservation of Scombridae remains in Pacific Island archaeological fish bone assemblages. Alternatively, the use of only those vertebrae types that can be confidently identified to a position on the vertebral column due to unique morphology may be necessary, such as proatlas, atlas, antepenultimate, penultimate and ultimate.

It has been demonstrated that fish vertebrae identified to taxon are routinely used for fish size reconstructions outside of the Pacific Islands and it is critical that Pacific Island vertebral morphometrics adopt similar protocols.

## Case Study

Comprising 29 coral atolls and five limestone islands without a lagoon, the Republic of the Marshall Islands (RMI) has a total land area of 181 km<sup>2</sup>, spread over 2000000 km<sup>2</sup> of ocean in eastern Micronesia, and is situated 3850 km south-west of Hawai'i. Ebon Atoll (4°38'24.67"N, 168°42'23.56"E) is the southernmost atoll in the Marshall Islands and has 22 islets, with a total land area of 5.75 km<sup>2</sup>, surrounding a 104 km<sup>2</sup> lagoon (Figure 1). Prehistoric village sites in the RMI are generally located parallel to the lagoon shoreline and characterised by surface and subsurface deposits of marine shellfish, fish bone, shell artefacts and coral gravel pavements. Aroid pit systems, for the cultivation of giant swamp taro (*Cytosperma* sp.), are often located at the inland extent of habitation zones, near the centre of larger islets (Weisler 1999, 2001). Site MLEb-1 is situated ~25 to 200 m from the lagoon beach and, along with other habitation sites, forms a near-continuous site that parallels the islet for nearly 2 km. A 2 × 2 m unit (TP 17, 18, 19 and 20, each 1 m<sup>2</sup>) was excavated just back from the lagoon beach. Cultural deposits were encountered to a depth of 1.75 m (Weisler 1999: fig. 4; Weisler 2002: 20). The stratigraphy was divided into three main prehistoric layers, capped by thin ~4 cm thick relatively sterile beach sand with historical artefacts and midden. Layer I is a black (Munsell 5Y2.5/1, taken moist in shade) gravelly sand with dense prehistoric midden and humanly transported gravel spread for village pavements. This layer was further divided into an upper layer IA, which was slightly darker and compact than IB. These combined layers were ~60 cm thick. Layer II, which was also divided into an upper IIA and lower IIB based on increasing sand and mottled pockets with depth, is a very dark grey (5Y3/1) sandy gravel midden with a combined thickness of ~118 cm. Layer IIIA consists of grey (5Y5/1) sand that is almost completely sterile. This overlies palaeo-beach deposits of coarse sand and coral chunks to ~190 cm below surface. The densest fish bone recovered during the 2011/2012 field season was in the 2 × 2 m unit, so it was the most suitable for the application of morphometrics. The fish bone concentration index was 6782 bones per m<sup>3</sup> (6.4 mm and 3.2 mm combined).

## Materials and Methods

### *Taxonomic identifications*

The following analyses are based on the fish bone retained from the 6.4 mm sieves from the 2 × 2 m unit (total volume of excavated cultural layers = 4.1 m<sup>3</sup>) from site MLEb-1, Ebon Islet and the 3.2 mm material retained from TP 17 (total volume of excavated cultural layers = 1 m<sup>3</sup>). Only TP 17 was

sampled using 3.2 mm sieves, due to time constraints on the fieldwork. Wet-sieving was consistently used during the excavations for all deposits. Faunal remains were sorted into major categories: fish, rat, bird, other vertebrates (e.g., sea turtle, lizard, dog etc.) and shell; only fish bone is discussed here.

Fish remains were identified by Lambrides to the lowest taxonomic level, however, only the vertebrae are relevant to this paper. Identifications are presented to family level only, for ease of comparison between datasets and to effectively demonstrate the implications of utilising unidentified vertebrae for size reconstructions of an assemblage; more specific taxonomic identifications are required for accurate fish size reconstructions. Taxonomic identifications were completed using comparative collections held by Weisler (2001: appendix 3) at the University of Queensland, including additional specimens added to the collection over the past decade. The Pacific Islands fish reference collection currently comprises 45 families, 93 genera and 168 species. The number of individuals represented in the collection for a given species ranges from 1 to 20; on average there are 2–3 individuals for a given species. In the comparative collection there is a good representation of fish size, geographical variability (e.g., Hawai‘i, Marshall Islands, Pitcairn Group etc.), ecological variability and capture technique. There are targeted efforts to expand the comparative collection and improve the representation of species, sex and size.

Definitions of vertebral types were adapted from Casteel (1976: 77–8) and include the following: (1) proatlas, the vertebral face on the posterior end of the basioccipital; (2) atlas, the vertebra immediately posterior to the proatlas; (3) thoracic, those vertebrae with a fused neural spine and usually lacking haemal spines (cf. Acanthuridae); (4) precaudal, those vertebrae with a fused neural spine and with well-developed parapophyses; (5) caudal, those vertebrae with fused neural and haemal arches; (6) antepenultimate—this vertebra is known in the ichthyology literature as the last caudal vertebra and is immediately anterior to the penultimate vertebra, and it was incorporated due to observed variation between reference specimens (Lambrides and Weisler 2013); (7) penultimate, the vertebra (in most cases) lacking a permanently attached haemal spine, and posterior to the antepenultimate and immediately anterior to the ultimate vertebra; and (8) ultimate, the last vertebra along the vertebral column, also defined as the urostyle. Figure 2 illustrates the individual characteristics of each vertebra type, but also see Lambrides and Weisler (2013: fig. 2) for an articulated vertebral column with the eight types marked.

All vertebrae were considered for identification based on protocols outlined in Lambrides and Weisler (2013), with the exception of those identified as fragmented. Fragmentation (defined as < 50% of an individual vertebra) was quantified for all vertebrae. Fragmented vertebrae could not be assigned to a specific type (e.g., atlas, thoracic, caudal etc.) and identified to taxon. The proatlas (basioccipital), atlas, antepenultimate, penultimate and ultimate can be particularly useful for vertebral

morphometrics, as their position on the vertebral column can be accurately determined. Only the number of identified specimens (NISP) was calculated for each taxon and used to complete the morphometric analyses to assess differences among cultural layers.

### *Morphometric protocols*

For each archaeological vertebra, three measurements were recorded to the nearest 0.01 mm using digital calipers (Mitutoyu Digimatic). Recorded measurements of the anterior centrum face include the maximum dorso-ventral height of the centrum (M1) and the maximum mediolateral width of the centrum (M2). The maximum craniocaudal length of the centrum (M3) was also recorded. Only M1 and M2 could be measured on the ultimate vertebra (or urostyle) (after Desse and Desse-Berset 1996a; Gabriel et al. 2012) (Figure 3). M1, M2 and M3 were each measured three times, and the mean of each of the three measurements was used for the analysis and to address measurement error. Given the high correlation between measurements on the same fish bone (Desse and Desse-Berset 1996b: 172), in future it may not be necessary to measure M1, M2 and M3 for each archaeological vertebra. However, relationships between fish size (length and weight) and bone size (M1, M2 and M3) should be developed for each taxon based on reference specimen metrics (e.g., Gabriel et al. 2012: table 12) to increase the likelihood that a measurement can be recorded (M1, M2 or M3) given the influence of pre- and post-deposition alterations to bone (e.g., fragmentation, dissolution, processing etc.). All statistical analyses were run using IBM SPSS Statistics Desktop 20.0 and Past version 3.2.

## **Results**

### *The fish vertebrae remains of MLEb-1 (TP17, 18, 19 and 20)*

Rank order abundance, taxonomic diversity and evenness (6.4 mm and 3.2 mm)

A total of 10245 (6.4 mm) and 17559 (3.2 mm) fish bones was recovered from a 2 × 2 m unit from site MLEb-1. The assemblage recovered from the 6.4 mm sieves comprised (including fragments) weighing 475 g; this is compared to the material recovered from the finer mesh sieves (3.2 mm) with 15115 non-vertebrae weighing 357 g and 2444 vertebrae (including fragments) weighing 77 g. Of all vertebrae, 35% (6.4 mm) and 58% (3.2 mm) were identified as fragmented. A high proportion of the archaeological vertebrae were identified to taxon: 63% (6.4 mm) and 40% (3.2 mm).

Table 1 lists key distinctions in rank order abundance between the two recovery methods as determined by the identification of vertebrae (6.4 mm and 3.2 mm), with data aggregated from all test pits of the 2 × 2 m unit. The most abundant taxa by NISP for the 6.4 mm sieves were tuna, mackerel and bonito (Scombridae), parrotfish (Scaridae), jack (Carangidae) and grouper (Serranidae). Based solely on the material recovered from the 3.2 mm sieves (TP 17), flying fish (Exocoetidae,

NISP = 252) were the top-ranked taxon and mojarras (Gerreidae) were added to the taxonomic list (Figure 4).

Taxonomic evenness was determined using the complement of Simpson's index ( $1 - D$ ) and the Shannon–Weiner indices of diversity ( $H'$ ) and evenness ( $e = H' / \ln S$ ) (Hayek and Buzas 2010; Lyman 2008; Magurran 2004). Values of  $1 - D$  range from 0 to 1, with higher values suggesting that the assemblage is more even and not dominated by a single taxon. The Shannon–Weiner index of diversity tends to vary between 1.5 and 3.5, with higher values indicating greater heterogeneity in a faunal assemblage; however, these values can be affected by sample size (Lyman 2008: 192). Finally, the Shannon–Weiner index of evenness ranges from 0 to 1, with a value of 1 suggesting that all taxa are equally abundant. These measures of diversity and evenness were considered for the entire fish bone assemblage from the  $2 \times 2$  m unit (both 6.4 mm and 3.2 mm) to assess the entire assemblage irrespective of cultural layer. It was determined that the assemblage was diverse or heterogeneous ( $H' = 2.734$ ), but also very even, with both many taxa represented and many individuals from each taxon ( $1 - D = 0.915$ ;  $H' / \ln S = 0.849$ ). This is significant as one taxon is not dominating the archaeological fish bone assemblage from the site, when compared to sites from other regions that are dominated by a single taxon or few taxa, such as the high abundance of salmon remains in the Pacific Northwest (Moss 2012), carp in Hungary (Bartosiewicz et al. 1994: 55), or snapper and barracouta in many South Island, New Zealand sites (Leach and Boocock 1995; Leach et al. 1999c). This may have implications for the application of morphometrics to tropical and subtropical Pacific Island assemblages, as a statistically meaningful sample size is critical for assessing change in fish assemblages over time.

### *Vertebral morphometrics*

#### Sieve size and vertebral morphometrics

Figure 5 illustrates the distribution of the maximum mediolateral widths of the centrum (M2) for all vertebrae types recovered from the 6.4 mm and 3.2 mm sieves; of the identified vertebrae, it was not possible to measure M2 ( $n = 2436$ ) for 183 specimens. The mean maximum width of the 6.4 mm vertebrae is  $6.58 \pm 2.76$  mm (range = 1.07–30.89 mm) and the 3.2 mm mean maximum width is reported as  $3.47 \pm 0.98$  mm (range = 1.44–6.95 mm). It is evident that finer mesh sizes (i.e.,  $\leq 6.4$  mm) are critical for determining variation in vertebrae size and to accurately represent the contribution of each size category in the archaeological assemblage. As all cultural layers of the  $2 \times 2$  m unit were systematically sampled with 6.4 mm sieves, this larger assemblage was used for vertebral morphometrics.

#### Impact of data resolution

The following section demonstrates the importance of determining taxon, vertebra type and position along the vertebral column prior to conducting vertebral morphometrics and assessing temporal changes in fish size. Prior to exploratory data analyses, initial data analysis was implemented to ensure that all statistical assumptions were met. Datasets were each examined for normality (skewness and kurtosis). As the data was not normally distributed, non-parametric statistics (i.e., Kruskal–Wallis one-way analysis of variance and effect size) were used. A key assumption of Kruskal–Wallis is that homogeneity of variances is met; this assumption was tested and not violated for any of the tested datasets. An effect size ( $\eta^2$ ) was also calculated to assess the magnitude of the difference between groups based on the sorting variable (i.e., taxon or vertebra type). Post hoc tests were not run, as it was not necessary to determine pairwise differences (i.e., follow up tests between pairs of groups, often using Mann–Whitney U tests) or if there was temporal ordering to the differences, as change over time in fish populations was not being tested. Rather, it was an attempt to track the presence of trends as they relate to data resolution and demonstrate the problems of considering unidentified vertebrae.

All taxa and all vertebrae types: The analysis of all vertebrae types and taxa combined provided a proxy for methods applied in Pacific Island archaeology; that is, the measurement of unidentified vertebrae that, irrespective of type, are collapsed into a single category for analysing change over time in fish size. In the Pacific fishing literature only descriptive statistics (e.g., range, mean and standard deviation) are used to assess changes in average vertebrae size over time. A general decrease in M1, M2 and M3 vertebrae measurements over time (cultural layers: IIIA to Historical) is evident when analysis is restricted to descriptive statistics (Table 2 and Figure 6). A Kruskal–Wallis test was conducted to evaluate differences among the six cultural layers (Historical, IA, IB, IIA, IIB and IIIA) on median change in vertebrae measurements (M1, M2 and M3) (i.e., are there statistically significant differences in M1, M2 and M3 vertebrae measurements between cultural layers?). Each test was significant: M1,  $\chi^2(5, N = 1478) = 114.09, p \leq 0.0005$ ; M2,  $\chi^2(5, N = 1479) = 133.68, p \leq 0.0005$ ; M3,  $\chi^2(5, N = 1415) = 100.84, p \leq 0.0005$ , but with comparatively low effect sizes – M1,  $\eta^2 = 0.08$ ; M2,  $\eta^2 = 0.09$ ; M3,  $\eta^2 = 0.07$ .

Individual taxon and all vertebrae types: A comparison of datasets where the taxon was known but all vertebrae types were grouped as a single “uniform” category was completed. The three top-ranked taxa (Scombridae, Scaridae and Carangidae) as determined by NISP were used to provide examples of this approach (Table 3 and Figure 7). Kruskal–Wallis tests were conducted to evaluate differences among the six cultural layers (Historical, IA, IB, IIA, IIB and IIIA) on median change in vertebrae measurements (M1, M2 and M3), but controlling for taxon (i.e., Scombridae, Scaridae and Carangidae). The tests for each taxon provided variable outcomes across the three measurements. For

Scombridae, only M2 and M3 were significantly different based on median change among cultural layers: M1,  $\chi^2(4, N = 364) = 6.91, p = 0.141$ ; M2,  $\chi^2(4, N = 366) = 15.26, p = 0.004$ ; M3,  $\chi^2(4, N = 355) = 14.36, p = 0.006$ , with low effect sizes – M1,  $\eta^2 = 0.019$ ; M2,  $\eta^2 = 0.042$ ; M3,  $\eta^2 = 0.041$ . For Scaridae, only M1 and M3 were significantly different based on median change among cultural layers: M1,  $\chi^2(4, N = 210) = 10.12, p = 0.039$ ; M2,  $\chi^2(4, N = 210) = 9.40, p = 0.052$ ; M3,  $\chi^2(4, N = 201) = 12.91, p = 0.012$ , with low effect sizes – M1,  $\eta^2 = 0.048$ ; M2,  $\eta^2 = 0.045$ ; M3,  $\eta^2 = 0.065$ . Finally, for Carangidae, only M1 was significantly different based on median change among cultural layers: M1,  $\chi^2(3, N = 134) = 10.83, p = 0.013$ ; M2,  $\chi^2(3, N = 133) = 7.72, p = 0.052$ ; M3,  $\chi^2(3, N = 127) = 5.00, p = 0.172$ , with small effect sizes – M1,  $\eta^2 = 0.081$ ; M2,  $\eta^2 = 0.058$ ; M3,  $\eta^2 = 0.040$ . The variability in the outcomes of the Kruskal–Wallis tests for each taxon based on the measurements recorded (M1, M2 and M3) is problematic, as theoretically each of the measurements should correlate well with live fish size and should be tracking similar trends. While the M1, M2 and M3 measures for each taxon are correlated ( $p \leq 0.05$ ), there is variation in the  $r^2$  values, which we suggest relates to the error introduced by grouping non-congruent variables: (1) family, genera and species; and (2) all vertebrae irrespective of type.

Individual taxon and individual vertebra type: The final stage of analysis controlled for taxon and vertebra type. Scombridae was the top-ranked taxon and Scombridae caudal vertebrae were the most abundant by NISP (Table 4 and Figure 8). The genera present among the Scombrids are all tribe Thunnini: cf. *Katsuwonus* sp. (skipjack) and *Thunnus* spp. (Marshall Islands: albacore, bigeye, Pacific bluefin and yellowfin). Ideally, the proatlas (NISP = 0), atlas (NISP = 4), antepenultimate (NISP = 8), penultimate (NISP = 6) or ultimate vertebra (NISP = 11) would have been used for this analysis, given the importance of determining position along the vertebral column prior to size reconstructions. However, due to small sample sizes across all cultural layers and the difficulty in determining the position along the vertebral column for Scombridae caudal vertebrae, the type was grouped to provide coarse-grained outcomes. Yet, this approach is appropriate for analysing the implications of considering a single vertebra type, which is necessary for this study. Kruskal–Wallis tests were conducted to evaluate differences among the five cultural layers that had Scombridae (IA, IB, IIA, IIB and IIIA) on median change in vertebrae measurements (M1, M2 and M3), but testing for the impact of controlling taxon and vertebra type. No tests were statistically significant: M1,  $\chi^2(4, N = 213) = 2.48, p = 0.649$ ; M2,  $\chi^2(4, N = 213) = 7.35, p = 0.119$ ; M3,  $\chi^2(4, N = 215) = 6.22, p = 0.184$ , with low effect size – M1,  $\eta^2 = 0.012$ ; M2,  $\eta^2 = 0.035$ ; M3,  $\eta^2 = 0.030$ . Therefore, there is no evidence based on key measurements of Scombridae caudal vertebrae that there is a statistically significant difference in vertebrae size among cultural layers.

Importantly, the successive refinement in analytical protocols when controlling for taxon and type resulted in a reduction in sample size. To determine whether sample size was sufficient to detect such a small effect when controlling for taxon and type (i.e., Scombridae caudal vertebrae) subsampling procedures were implemented. First, using the dataset that contained all vertebrae irrespective of taxon and type, we randomly drew specimens until the sample size was equivalent to the subset, which controlled for taxon and type. For example, from the original dataset of M1 measurements (Table 2), 98 specimens were randomly sampled from Layer IA, 28 from Layer IB, 23 from Layer IIA, 62 from Layer IIB and 2 from Layer IIIA, which is equivalent to the sample size of measured Scombrid caudal vertebrae (Table 4). This process was repeated 1000 times. The Kruskal–Wallis test was then run on each of the subsampled assemblages to verify if it is possible to detect such a small effect (i.e., statistically significant outcome) with reduced sample sizes. For each analysis (or Kruskal–Wallis test of the subsampled population), the outcome was still highly significant ( $p \leq 0.0005$ ). This suggests that the reduction in sample size does not explain why we fail to get a significant result when we control for taxon and type.

An application of the “Global Rachidian Profiles” method: The “Global Rachidian Profiles” (GRP) method proposed by Desse and Desse-Berset (1989, 1999a) maximises the calculation of MNI and, relevant here, size reconstructions based on vertebral morphometrics. Further analysis of the GRP method may provide a more useful approach for incorporating vertebral morphometrics into Pacific Island fishing studies. The archaeological assemblage of *Selar* spp. (Carangidae) from the  $2 \times 2$  m unit was used to provide an example of the GRP approach. There are two species of *Selar* found in the Marshall Islands, bigeye scad (*S. crumenophthalmus*) and oxeye scad (*S. boops*). Figure 9 provides an example of the GRP method for a bigeye scad reference specimen (no. 325) graphed using the M1, M2 and M3 measurements (*S. boops* is not represented in the comparative collection). Based on determinations of standard deviation ( $\sigma$ ) and the coefficient of variation ( $C_v$ ) for each of the three measurements (M1, M2 or M3), the most suitable was used to predict the fork length of measured *Selar* spp. archaeological vertebrae. Ideally, the recorded measurement (M1, M2 or M3) with the least deviation from the mean—this can be supported by graphing the measurements—will be used to examine the archaeological vertebrae. In this example, M1 was determined as the most suitable measurement to analyse the archaeological vertebrae and predict fork length (no. 325,  $\sigma = 0.501$ ;  $C_v = 0.095$ ; no. 406,  $\sigma = 0.384$ ;  $C_v = 0.091$ ). The archaeological vertebral measurements (M1) recorded for *Selar* spp. were plotted over the equivalent vertebra type (i.e., T1 = first thoracic, P2 = second precaudal, C7 = seventh caudal etc.) as determined by measurements of vertebrae from reference specimens with known length measurements (in this case, fork length) (Figure 9). Therefore, the archaeological *Selar* spp. vertebrae probably derived from specimens that range

between 23 and 29 cm in fork length with a few outliers; this example was grouped at the level of TP, so change over time cannot be assessed.

## **Discussion**

### *Data resolution and vertebral morphometrics in Pacific Island archaeology*

Analyses were completed to document the implications of controlling for taxon and vertebra type when investigating changes in vertebrae size over time. These were as follows: (1) all taxa and vertebrae types to simulate methods commonly used in Pacific Island archaeology, (2) controlling for the taxon (i.e., Scombridae, Scaridae and Carangidae) but including all vertebrae types as a single category; and (3) controlling for both taxon and vertebra type (i.e., Scombridae caudal vertebrae only).

When all vertebrae were considered together, irrespective of taxon and vertebra type, the results of the Kruskal–Wallis test were statistically significant for each of the three measurements (M1, M2 and M3), suggesting that there are differences in vertebrae size among the groups (i.e., cultural layers); however, post hoc tests are required to determine whether there is temporal ordering to these differences. As the taxonomic composition of the sample and variation in vertebral morphometry were increasingly controlled for, the outcomes of the analyses became increasingly variable. When evaluating the three top-ranked taxa according to NISP—Scombridae, Serranidae and Carangidae—the outcomes of the Kruskal–Wallis tests were inconsistent with comparatively low effect size determinations, indicating a relatively low magnitude of difference between the cultural layers based on each measurement (M1, M2 and M3). Finally, when only a single vertebra type for a taxon was evaluated (i.e., Scombridae caudal vertebrae), there was no observed variation among cultural layers for the key vertebrae measurements (M1, M2 and M3).

The comparison between these three datasets highlights the importance of identifying the exact position of a vertebra on the vertebral column prior to reconstructions of fish size (Desse and Desse-Berset 1996c; Gabriel et al. 2012). In the case of Scombridae, it is often difficult to distinguish caudal from precaudal archaeological vertebrae due to preservation, let alone determine position of an individual caudal vertebra along the vertebral column. There was not a sufficient sample of the other vertebrae types (i.e., atlas, penultimate etc.) to track change in vertebrae size among cultural layers for an individual vertebra type. This analysis has demonstrated that it is problematic to use unidentified fish vertebrae for assessing changes in fish size over time, as it is possible to document false trends using a method that is routinely used in the Pacific Islands (e.g., Jones and Quinn 2009; Jones O’Day 2001; Rolett 1998). This issue is enhanced in Pacific Island archaeology due to the number of taxa represented in archaeological fish bone assemblages and the need for comprehensive

reference collections to facilitate species-level identifications. These approaches have been acknowledged as “coarse-grained”, but we suggest that it is better to exclude measurements of unidentified vertebrae if taxonomic identifications cannot be made.

Methods for reconstructing fish size based on vertebral morphometrics require species-level identifications, which is difficult given the high biodiversity of fish in the tropical Pacific Islands. Desse and Desse-Berset (1996b: 176) argue for “taxonomic proximity”, where relationships between a bone measurement and fish length are generally consistent for the species, and often (cautiously) applicable to the genus and family. Therefore, a method of vertebral morphometrics is required that can be applied to Pacific Island fish bone assemblages even when species-level identifications are not possible. The GRP method can provide “coarse-grained” reconstructions of fish length based on vertebral measurements. In this example, only two reference specimens were considered (nos. 325 and 406) for comparison with the archaeological vertebrae; however, the inclusion of more reference specimens will improve the accuracy of archaeological fish length predictions by accounting for intra-taxonomic variation (e.g., age, sex etc.) (Bartosiewicz and Takács 1997).

## **Conclusions**

Outside of the Pacific Islands, unidentified vertebrae are rarely used for fish size reconstructions. Unidentified vertebrae have been utilised only as an adjunct to data obtained from identified vertebrae to provide a coarse-grained method of assessing change over time (e.g., LeFebvre 2007; Newsom and Wing 2004; Wing 2001). Prior to reconstructions of fish length and weight: (1) all vertebrae should be identified to taxon and assigned to type; and (2) the exact position on the vertebral column should be determined. This ensures that any changes in reconstructed fish size are identified using a specific vertebra type. Consequently, variability across a vertebra type (i.e., thoracic, precaudal and caudal) is not influencing trends. As previously discussed, certain vertebra types are easier to identify (i.e., accurately determine their position on the vertebral column), thereby enhancing their utility for size reconstructions (i.e., proatlas, atlas, antepenultimate, penultimate and ultimate).

Species-level identifications are preferable but, in regions with high biodiversity, even genus-level identifications can be difficult with extensive comparative collections. For archaeological fish bone assemblages that are taxonomically rich, such as the Pacific Islands, or where species-level identifications are critical (e.g., the Pacific Northwest), a combination of approaches may be necessary, such as aDNA analysis/peptide mass fingerprinting and morphometrics. We encourage archaeologists working in the Pacific Islands to continue developing and implementing methods for identifying fish bone to species (e.g., aDNA analysis: Nicholls et al. 2003) to ensure high-resolution assessments of both temporal change in fish size and the contribution of finfish to prehistoric diet.

Ideally, the protocols used by Gabriel et al. (2012) are the optimum and while we currently do not have the ability to replicate this study in the tropical Pacific, it should be the objective of future research. However, the GRP method does produce “coarse-grained” reconstructions of fish length, which are more useful for assessing changes in fish size over time than an analysis of unidentified vertebrae.

In this paper, we have demonstrated that false trends can be produced when unidentified vertebrae are measured to infer changes in fish size among cultural layers, which is a method routinely used in Pacific Island archaeology. Differences in vertebrae size across cultural layers commonly associated with decreases in fish size over time in the Pacific fishing literature are more likely to be tracking alternative trends (e.g., change in species composition across cultural layers). It is hoped that future collaboration between researchers will enhance these methods through the development of an open source database where morphometric data from modern comparative collections can be shared. Finally, it is important to acknowledge the limitations of morphometrics: (1) adequate samples of archaeological vertebrae are required for assessing fish or vertebrae size over time; and (2) a comprehensive comparative collection—with multiple specimens of each species representing a variety of ages and sex—is essential for size reconstructions. It is possible that vertebral morphometrics will not be suitable for all regions and archaeological assemblages. However, a clear rationale for its use should be made in addition to presenting a detailed account of the methods of measurement and the quality of the reference collection for conducting the fish size reconstructions.

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**Table 1.** (a) The rank order abundance of fish taxa from site MLEb-1, TP17, 18, 19 and 20 (aggregated by test pit). Identifications are family-level only and represent the vertebrae remains recovered from the 6.4 mm sieves. A total of 37% of all vertebrae were unidentified. (b) Rank order abundance of fish taxa from site MLEb-1, TP17 (aggregated by test pit). Identifications are presented to family-level and represent the vertebrae remains recovered from the 3.2 mm sieves. Some 60% of all vertebrae were unidentified.

(a)

Taxon	NISP
Scombridae	440
Scaridae	228
Carangidae	169
Serranidae	160
Siganidae	84
Acanthuridae	81
Lutjanidae	76
Lethrinidae	62
Mullidae	62
Kyphosidae	58
Balistidae	54
Exocoetidae	51
Labridae	24
Holocentridae	21
Bothidae	15
Fistulariidae	10
Sphyraenidae	10
Chaetodontidae	9
Belonidae	8
Mugilidae	6
Cirrhitidae	5
Kuhliidae	4
Pomacentridae	4
Muraenidae	3
Total	1644

(b)

Taxon	NISP
Exocoetidae	252
Serranidae	102
Carangidae	74
Lutjanidae	61
Holocentridae	59
Lethrinidae	58
Mullidae	54
Acanthuridae	53
Belonidae	42
Cirrhitidae	38
Muraenidae	27
Bothidae	26
Kyphosidae	22
Balistidae	15
Kuhliidae	15
Scaridae	13
Scombridae	13
Pomacentridae	12
Siganidae	10
Fistulariidae	7
Gerreidae	6
Labridae	6
Mugilidae	5
Chaetodontidae	4
Sphyraenidae	1
Total	975

**Table 2.** Vertebral measurements (mm) (M1, M2 and M3) with all identified taxa and vertebrae types grouped from site MLEb-1 (TP17, 18, 19 and 20), 6.4 mm, all cultural layers.

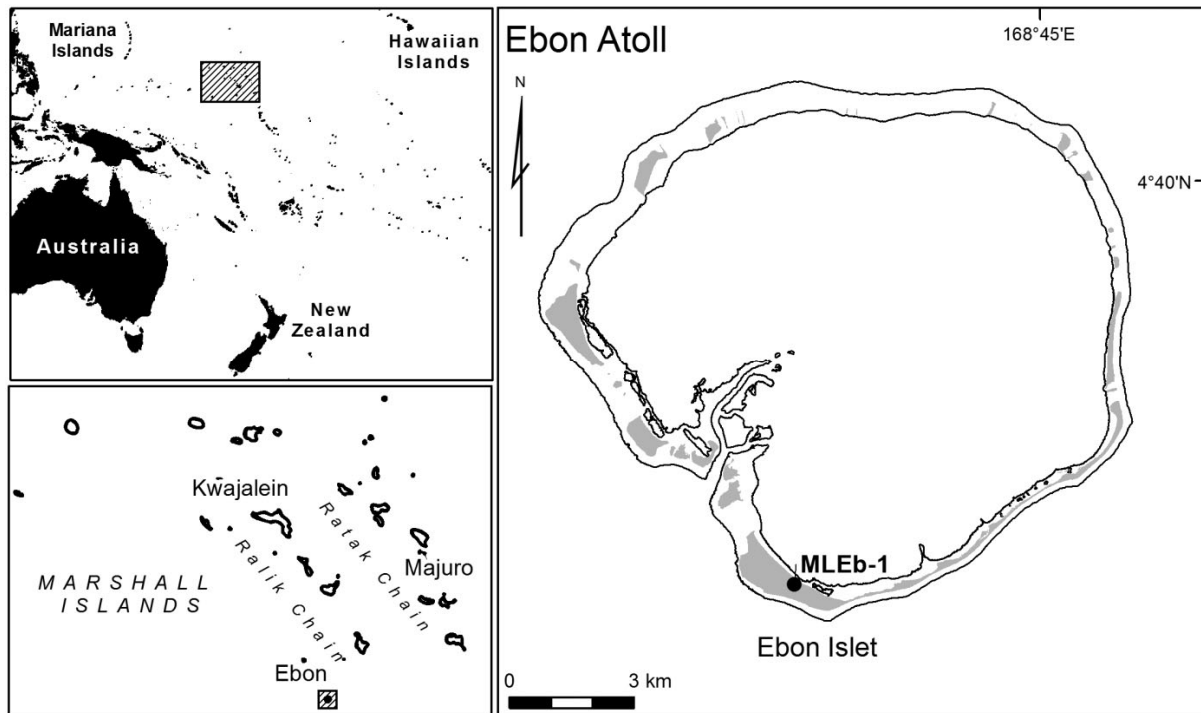
Layer	<i>n</i>			Mean (mm)			Range $\pm$ s.d. ( $\sigma$ ) (mm)		
	M1	M2	M3	M1	M2	M3	M1	M2	M3
Historical	55	55	52	4.88	5.11	6.16	2.24 - 8.28 $\pm$ 1.59	2.28 - 8.90 $\pm$ 1.75	3.44 - 10.24 $\pm$ 1.76
IA	1072	1070	1025	5.94	6.35	7.21	0.82 - 24.16 $\pm$ 2.41	1.07 - 30.89 $\pm$ 2.67	0.84 - 36.55 $\pm$ 2.89
IB	167	167	158	5.69	6.21	6.69	2.23 - 13.56 $\pm$ 2.28	2.31 - 12.54 $\pm$ 2.52	1.80 - 12.58 $\pm$ 2.54
IIA	53	54	52	7.06	7.91	8.13	2.51 - 11.73 $\pm$ 2.45	2.73 - 14.56 $\pm$ 2.95	2.91 - 12.47 $\pm$ 2.69
IIB	122	124	119	8.21	9.11	9.40	2.18 - 13.20 $\pm$ 2.40	2.20 - 14.35 $\pm$ 2.59	2.77 - 12.93 $\pm$ 2.46
IIIA	9	9	9	6.48	7.11	6.80	3.78 - 11.02 $\pm$ 2.44	4.83 - 10.74 $\pm$ 2.32	3.27 - 11.30 $\pm$ 2.79

**Table 3.** Vertebral measurements (mm) (M1, M2 and M3) for top three ranked taxa by NISP (Scombridae, Scaridae and Carangidae) with vertebrae types grouped from site MLEb-1 (TP17, 18, 19 and 20), 6.4 mm, all cultural layers.

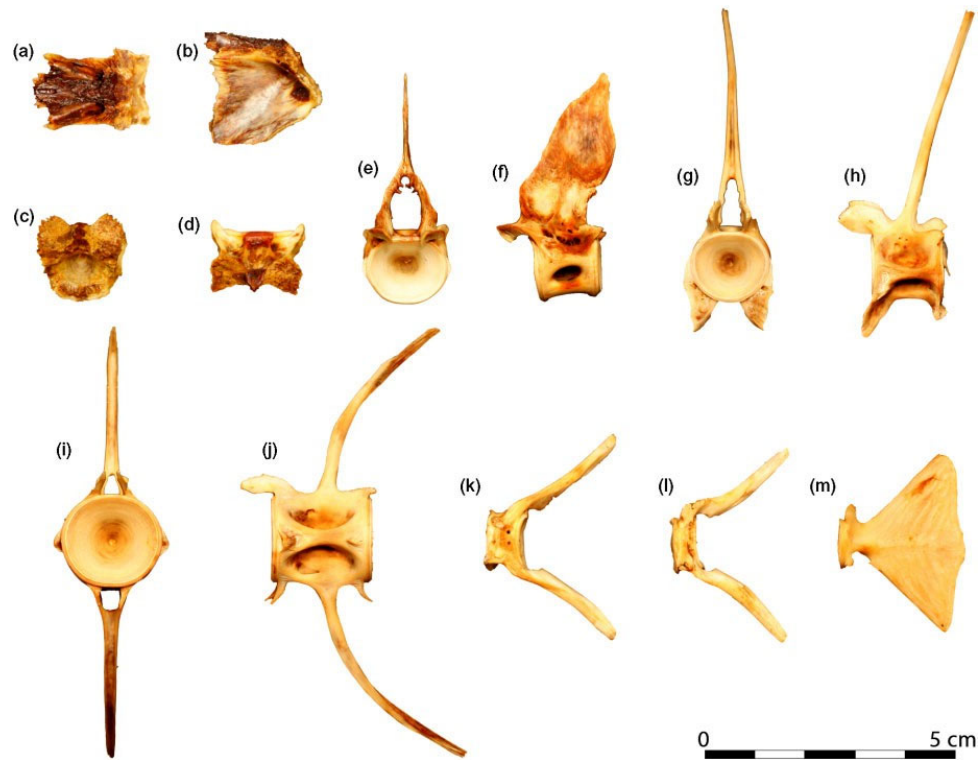
Layer	<i>n</i>			Mean (mm)			Range $\pm$ s.d. ( $\sigma$ ) (mm)		
	M1	M2	M3	M1	M2	M3	M1	M2	M3
Scombridae									
IA	188	187	182	8.40	9.12	9.45	4.29-24.16 $\pm$ 2.13	3.64-30.89 $\pm$ 2.61	3.24-36.55 $\pm$ 2.70
IB	41	41	37	8.14	9.12	9.05	4.64-12.16 $\pm$ 1.73	4.30-12.54 $\pm$ 1.82	2.76-12.58 $\pm$ 1.90
IIA	34	35	36	8.37	9.51	9.17	5.68-11.73 $\pm$ 1.65	5.81-14.56 $\pm$ 1.90	2.91-12.13 $\pm$ 1.95
IIB	98	100	97	8.82	9.79	9.73	4.52-13.20 $\pm$ 2.02	4.77-14.35 $\pm$ 2.14	2.77-12.93 $\pm$ 2.26
IIIA	3	3	3	9.16	9.94	9.89	6.44-11.02 $\pm$ 2.41	8.41-10.74 $\pm$ 1.33	7.44-11.30 $\pm$ 2.13
Scaridae									
Historical	6	6	6	7.74	7.25	8.10	4.59-7.97 $\pm$ 1.51	5.18-8.90 $\pm$ 1.59	6.24-10.24 $\pm$ 1.66
IA	185	185	176	6.78	7.49	8.18	2.73-10.54 $\pm$ 1.59	2.82-13.62 $\pm$ 1.91	2.39-12.53 $\pm$ 2.21
IB	12	12	12	7.31	7.94	9.07	3.49-9.75 $\pm$ 1.73	3.59-11.04 $\pm$ 2.11	4.66-11.93 $\pm$ 1.93
IIA	3	3	3	7.56	8.66	8.10	6.83-8.45 $\pm$ 0.92	7.20-9.43 $\pm$ 1.27	7.39-9.33 $\pm$ 1.06
IIB	4	4	4	9.30	9.94	11.61	8.80-10.72 $\pm$ 0.95	9.09-10.68 $\pm$ 0.66	11.30-12.06 $\pm$ 0.32
Carangidae									
IA	107	106	100	5.87	6.46	8.32	3.21-11.14 $\pm$ 1.58	3.31-11.93 $\pm$ 1.67	2.73-18.17 $\pm$ 3.03
IB	17	17	17	4.84	5.60	6.95	3.24-6.80 $\pm$ 0.78	4.63-8.53 $\pm$ 0.95	3.36-9.36 $\pm$ 1.70
IIA	1	1	1	N/A	N/A	N/A	5.78	6.59	3.85
IIB	9	9	9	4.97	5.67	7.98	4.25-6.03 $\pm$ 0.54	5.24-6.95 $\pm$ 0.53	5.58-10.97 $\pm$ 1.62

**Table 4.** Vertebral measurements (mm) (M1, M2 and M3) for Scombridae caudal vertebrae, from site MLEb-1 (TP17, 18, 19 and 20), 6.4 mm, all cultural layers.

Layer	<i>n</i>			Mean (mm)			Range $\pm$ s.d. ( $\sigma$ ) (mm)		
	M1	M2	M3	M1	M2	M3	M1	M2	M3
IA	98	97	97	8.75	9.60	9.90	5.59-24.16 $\pm$ 2.51	6.72-30.89 $\pm$ 3.01	6.10-36.55 $\pm$ 3.31
IB	28	28	27	8.57	9.63	9.51	5.43-12.16 $\pm$ 1.58	6.58-12.54 $\pm$ 1.31	6.04-12.58 $\pm$ 1.31
IIA	23	24	24	8.47	9.73	9.55	6.18-11.73 $\pm$ 1.79	7.56-12.38 $\pm$ 1.68	7.41-12.13 $\pm$ 1.31
IIB	62	62	65	8.96	10.04	10.07	4.52-13.20 $\pm$ 2.13	5.53-14.35 $\pm$ 1.96	5.75-12.93 $\pm$ 1.65
IIIA	2	2	2	8.24	9.58	9.37	6.44-10.03 $\pm$ 2.54	8.41-10.74 $\pm$ 1.65	7.44-11.30 $\pm$ 2.73



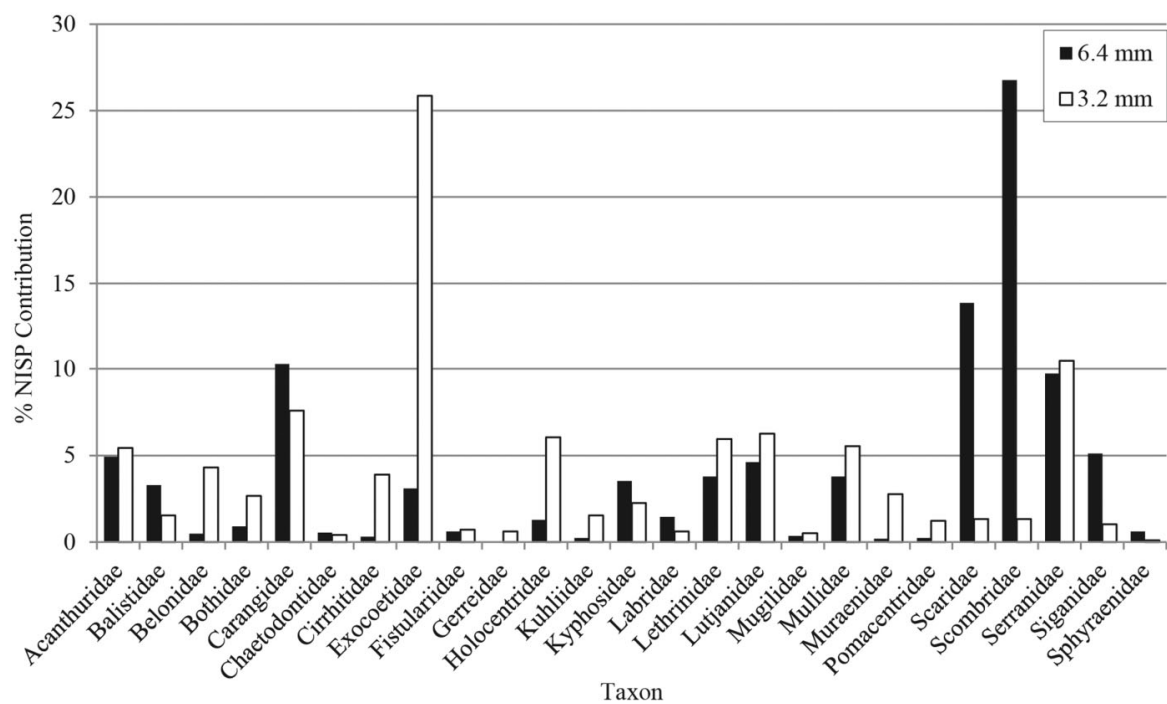
**Figure 1.** A map of the Republic of the Marshall Islands, with Ebon Atoll and the location of site MLEb-1.



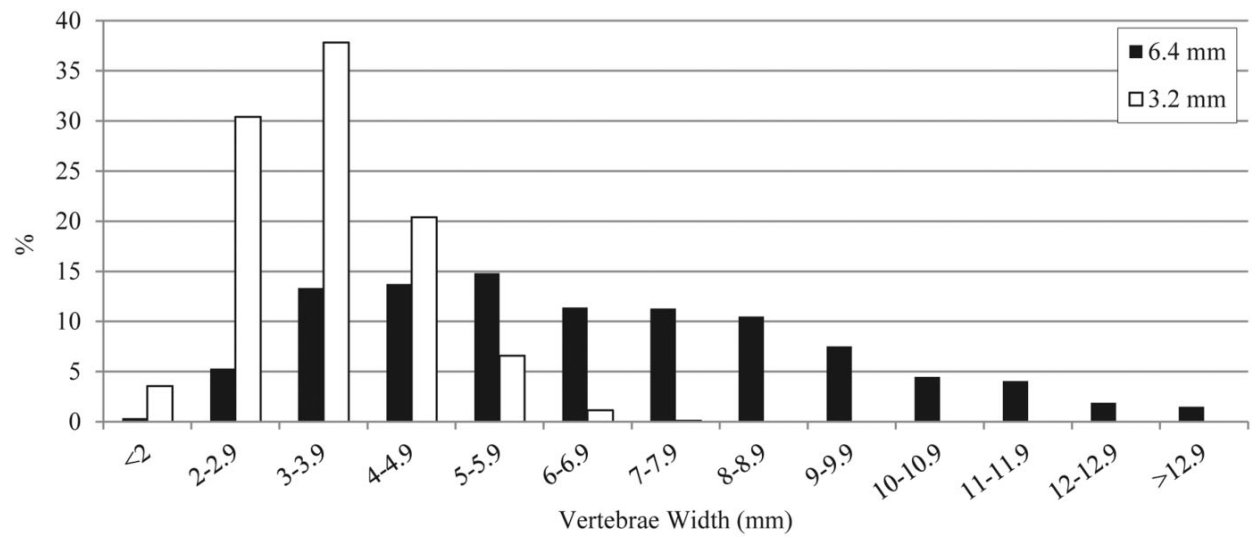
**Figure 2.** Vertebrae types as characterised by yellowfin tuna (*Thunnus albacares*, Scombridae): (a) dorsal and (b) lateral views of the basioccipital with a proatlas vertebral face; (c) anterior and (d) dorsal views of the atlas; (e) anterior and (f) lateral views of the first thoracic; (g) anterior and (h) lateral views of the second precaudal; (i) anterior and (j) lateral views of the 14th caudal; (k) a lateral view of the antepenultimate; (l) a lateral view of the penultimate; (m) a lateral view of the ultimate (or hypural).



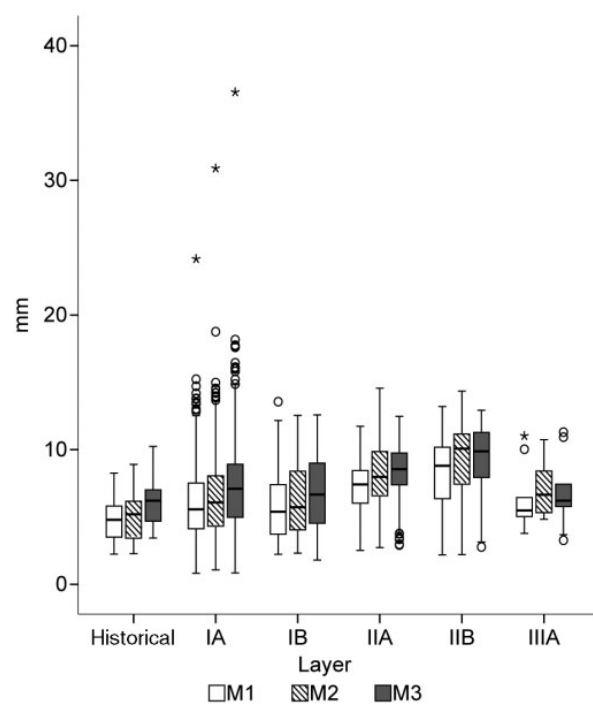
**Figure 3.** The honeycomb grouper (*Epinephelus merra*, Serranidae) first thoracic vertebra. Vertebral measurements after Desse and Desse-Berset (1996a) and Gabriel et al. (2012): the maximum dorso-ventral height of the centrum (M1), the maximum mediolateral width of the centrum (M2) and the maximum craniocaudal length of the centrum (M3).



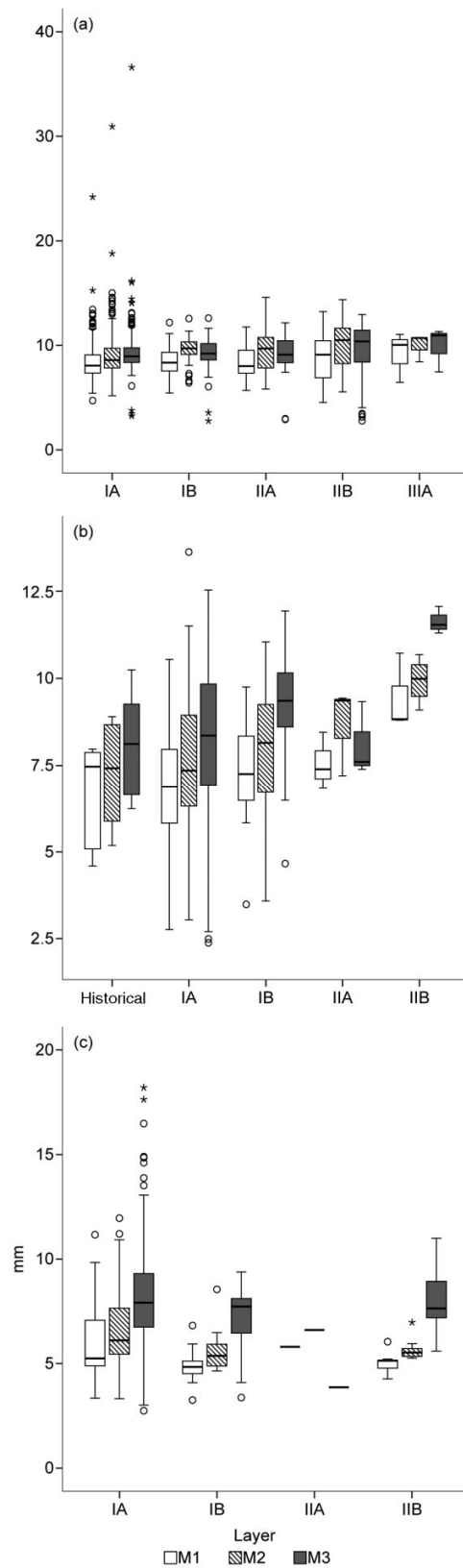
**Figure 4.** The percentage contribution to total NISP by taxon and sieve size (vertebrae only).



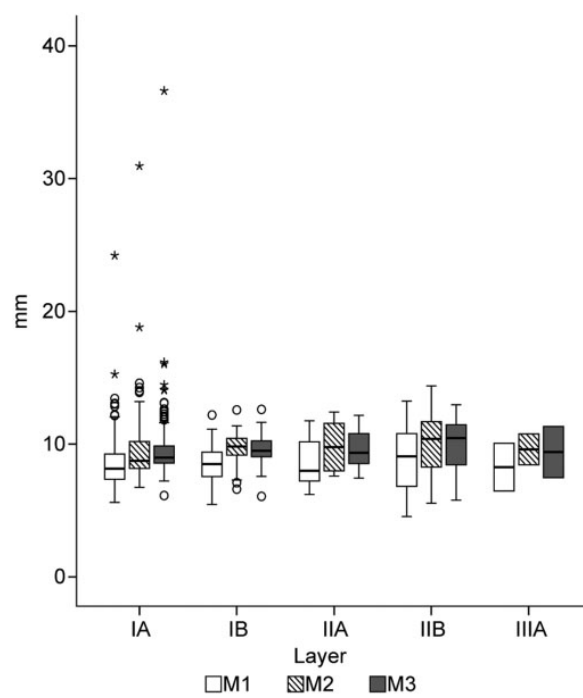
**Figure 5.** The distribution of the maximum mediolateral widths of the centrum (M2) for all vertebrae types identified to taxon from 6.4 mm and 3.2 mm ( $n = 2436$ ).



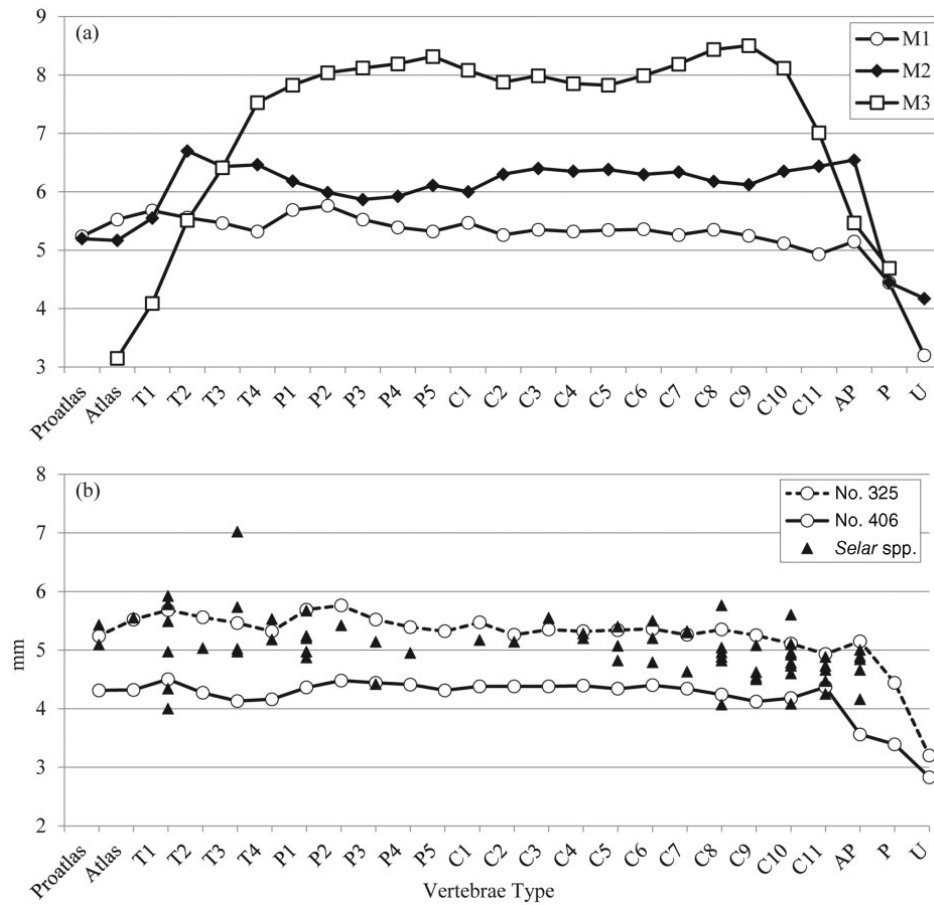
**Figure 6.** The range of vertebral measurements (mm) for all identified taxa and vertebrae types grouped from site MLEb-1 (TP17, 18, 19 and 20), 6.4 mm, all cultural layers.



**Figure 7.** The range of vertebral measurements (mm) for the three top-ranked taxa according to NISP: (a) Scombridae, (b) Scaridae and (c) Carangidae, with all vertebrae types grouped from site MLEb-1 (TP17, 18, 19 and 20), 6.4 mm, all cultural layers.



**Figure 8.** The range of vertebral measurements (mm) for Scombridae caudal vertebrae, from site MLEb-1 (TP17, 18, 19 and 20), 6.4 mm, all cultural layers.



**Figure 9.** Global Rachidian Profiles: (a) *Salar crumenophthalmus* (M1, M2 and M3 from modern specimen no. 325); (b) *Salar* spp. M1 measurements of all vertebrae types from MLEb-1 (TP17, 18, 19 and 20), 6.4 mm, all cultural layers. No. 325, fork length = 290 mm; no. 406, fork length = 230 mm: T, thoracic; P, precaudal; C, caudal; AP, antepenultimate; P, penultimate; U, ultimate.