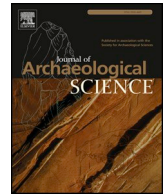




Contents lists available at ScienceDirect

## Journal of Archaeological Science

journal homepage: [www.elsevier.com/locate/jas](http://www.elsevier.com/locate/jas)

# Shape does matter: A geometric morphometric approach to shape variation in Indo-Pacific fish vertebrae for habitat identification

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## ARTICLE INFO

## Keywords:

Geometric morphometrics  
Fish habitat  
Wallacea  
Zooarchaeology  
Ichthyoarchaeology  
Vertebrae

## ABSTRACT

Traditional fish vertebrae identification relies on the availability of comprehensive reference collections that include every element from the neural spine for each taxon. In regions with great taxonomic diversity, such as the Indo-Pacific, the identification of fish vertebrae to species is difficult. This results in taxonomic lists with many skeletal elements identified only to family. However family level identifications often tell us little about the environmental preferences of the fish and thus, by inference, human fishing practices. Here we apply geometric morphometrics (GM) to examine shape variations within vertebrae in modern specimens of a variety of pelagic and reef species to determine if this method can be used to reliably inform on habitat preferences. Digitized vertebral elements of reef (Acanthuridae, Balistidae, Labridae, Lethrinidae, Lutjanidae and Serranidae) and pelagic/open water (Scombridae and Carangidae) families were scored using 2D landmarks. These were subjected to Generalized Procrustes Analysis and discriminatory multivariate analyses (Linear Discriminant Analysis and Discriminant Function Analysis) in order to assess whether shape can be used to differentiate habitats. Our results suggest that geometric morphometrics do allow the differentiation of habitat in vertebrae and provide an alternative method for the classification of archaeological fish assemblages. These analyses were applied to a sample of archaeological fish remains from a site in Alor Island (Nusa Tenggara Timur, Indonesia) and compared with the results of an earlier traditional comparative ichthyoarchaeological analysis. We found that the main component of the Pleistocene marine human diet comprised reef species, with the sporadic addition of open water species, supporting the pattern recorded with traditional analyses. This methodology could be widely applied to archaeological fish material from across the Indo-Pacific allowing a greater number of bones in assemblages to contribute to insights into human exploitation of coastal habitats and fishing techniques over time.

## 1. Introduction

Fish bones often dominate Indo-Pacific zooarchaeological assemblages. In most cases, fish vertebrae constitute the largest component of these assemblages, although until recently these elements were largely excluded from lower level taxonomic identifications (e.g. Desse and Desse, 1976; Lambrides and Weisler, 2015a, 2015b; Guillaud et al., 2016). The identification of fish vertebrae to family requires a comprehensive reference collection, with complete fish vertebral columns as well as broad species representation within families. Despite such difficulties, the importance of vertebrae when analysing archaeological fish remains is well recognised, as their inclusion increases the number

of elements (NISP) and number of individuals (MNI) in an assemblage, and provides a means for estimating fish size and seasonality of capture, in both archaeological and non-archaeological studies (Gabriel et al., 2012; Granadeiro and Silva, 2000; Lambrides and Weisler, 2015a, 2016; Samper Carro et al., 2017; Van Neer et al., 1999). Moreover, comparisons between the representation of cranial and post-cranial elements may provide insights about fish processing and fishing techniques (Butler, 1993; Zohar and Biton, 2011; Zohar and Cooke, 1997; Zohar and Dayan, 2001; Zohar et al., 2008).

Geometric morphometrics (GM), commonly used in biology to study shape variation (Zelditch et al., 2004), has frequently been applied to the analysis of morphometric differences in *Homo* and animal species.

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Some examples of the application of GM include the identification of domestic traits and evolutionary history in ISEA pigs based on molar and cranial shape differences (Cucchi et al., 2009; Evin et al., 2013; Ottoni et al., 2013; Owen et al., 2014); diversity and similarities of domestic and wild canids and feeding habits based on skull shape (Drake, 2011; Drake and Klingenberg, 2010; Meloro et al., 2015); taxonomic classification of Indonesian Pleistocene cervids (Gruwier et al., 2015); and methodological and morphological analyses of bone and dental morphology on great apes and humans (Gómez-Robles et al., 2007; Lockwood et al., 2002; Pérez et al., 2006). These methods have also been applied to non-archaeological fish remains, especially fish otoliths and scales, to assess taxonomic differences (e.g. Ponton, 2006; Ibañez et al., 2007; Duarte et al., 2017), or the origin of specimens in fish markets to address food safety policies (Ibañez, 2015). Recent research has also applied GM for the taxonomic identification of fish vertebrae from modern and archaeological assemblages (De Schepper et al., 2007; Guillaud et al., 2016). However, such studies have yet to examine fish habitat, a subject particularly pertinent to arguments regarding the maritime technological abilities of late Pleistocene peoples in Wallacea.

Claims of pelagic fishing ca. 42 ka cal BP at Jerimalai shelter in Timor-Leste indicated that the first humans to reach the Wallacean archipelago were already in possession of complex maritime and fishing technology and were able to carry out sustained fishing of pelagic species. This claim was based on the high proportion of Scombridae (tuna and mackerels) in the Pleistocene levels of the site (O'Connor et al., 2011). However, Anderson (2013a; 2013b) pointed out that claims for pelagic fishing at Jerimalai are problematic as the fish bones found in the Pleistocene levels were identified only as Scombridae, and as identifications were based entirely on vertebrae, sub-family, tribe, genus or species within Scombridae were not positively identified in the assemblage. As more than 22 scombrid species are currently found in the waters around Timor, and neritic tunas and mackerels outnumber oceanic tunas such as yellowfin, albacore and skipjack, Anderson (2013a) argued that the claims for both tuna fishing and pelagic fisheries in the Pleistocene at Jerimalai are unsustainable.

Here we apply GM to identify shape variation of fish vertebrae and examine to what extent shape can inform on fish preferred habitats. We evaluate how shape variations along the vertebral column could reflect differences in habitat. In doing so, we provide a benchmark for the quantitative identification of fish vertebrae. This methodology may allow more reliable identification of vertebrae based on shape, and thus a better grounding for the identification of pelagic versus in-shore fishing, with important implications for interpreting human fishing technology and behaviour from Pleistocene archaeological sites in the Indo-Pacific region. We examine fish vertebrae preserved in Tron Bon Lei, Alor, Indonesia, a late Quaternary fish-rich site, to in order to examine the presence and role of pelagic fishing at this site.

## 2. Material and methods

### 2.1. Modern reference material

Modern reference material is housed in the Department of Archaeology and Natural History, College of Asia and the Pacific, at the Australian National University (ANU). For this analysis, we selected every species available from six inshore-reef herbivore, omnivore and carnivore fish families (Acanthuridae, Balistidae (including two species in the Monacanthidae family), Labridae, Lethrinidae, Lutjanidae and Serranidae; Table 1) and two open water families (Carangidae and Scombridae; Table 2), classified according to species' environmental and biological information from FishBase (Froese and Pauly, 2017) and the California Academy of Sciences' catalog of fishes (Eschmeyer et al., 2017). These families are some of the most commonly documented in zooarchaeological assemblages from Indonesia and Timor-Leste (O'Connor et al., 2011; Ono and Clark, 2012; Samper Carro et al., 2016,

2017). A total of 66 specimens representing 43 species were included in our analysis (Tables 1 and 2), comprising 666 precaudal and 1216 caudal vertebrae (including both cranial and caudal sides).

### 2.2. Archaeological material

The archaeological fish assemblage was recovered from Tron Bon Lei, a rock shelter located on Alor Island, Indonesia (Fig. 1). Three test pits were excavated at the rock shelter in 2014, with Test Pit B yielding the largest amount of archaeological material. Three occupational phases were identified based on radiocarbon dates and stratigraphic changes, ranging from the late Holocene to the late Pleistocene (Fig. 1). In addition to large quantities of cultural material, this assemblage provided thousands of fish remains (O'Connor et al., 2017; Samper Carro et al., 2016, 2017). Due to fragmentation and the high taxonomic diversity in the region, the ichthyoarchaeological elements were identified only to family. The presence/absence of fish families was based on the identification of cranial (five paired bones and "special bones") and a few postcranial remains (Samper Carro et al., 2017). Acanthuridae, Balistidae, Scaridae, Labridae, Lethrinidae, Lutjanidae, Serranidae and Carangidae yielded the largest number of individuals, while Scombridae presence is limited to layer 11 and 12, dated to the late Pleistocene (Table 3). The Tron Bon Lei assemblage suggested that reef/inshore families were more commonly exploited throughout the sequence, while the sporadic presence of open-water/pelagic fish families increased during the late Pleistocene (Samper Carro et al., 2016, 2017). This trend was similar to that observed in the nearby island of Timor where, as mentioned above, the presence of Scombridae vertebrae from the lower layers of Jerimalai (dated to ca. 42 ka cal BP) suggested an emphasis on pelagic fishing in the Pleistocene (O'Connor et al., 2011).

From the total of 27,441 fish remains identified in Tron Bon Lei, 9803 are vertebrae (Samper Carro et al., 2017). The complete zooarchaeological assemblage was temporarily transported to ANU to conduct the taxonomical and anatomical identification of the fish remains. Due to time constraints, the taxonomical identification focused on the elements easier to identify, which for vertebral remains, were limited to the 1st vertebrae of a small part of the assemblage (layers 11 and 12). The rest of vertebrae were classified by width into four categories to track general size trends: less than 3 mm; 3–6 mm; 6–10 mm; larger than 10 mm.

For this study, we selected vertebrae from the two layers where both of the families including open-water/pelagic species (Carangidae and Scombridae) were documented, layer 11 (dated to 10,110–12,545 cal BP) and layer 12 (18,890–21,000 cal BP). Based on the five paired cranial elements traditionally used and the 1st vertebrae, Serranidae ( $n = 38$ ), Lutjanidae ( $n = 22$ ), Labridae ( $n = 17$ ), Carangidae ( $n = 16$ ), Lethrinidae ( $n = 13$ ), Balistidae ( $n = 10$ ) and Scombridae ( $n = 3$ ) yielded the largest MNI in layer 11, which is the layer with a largest number of remains in the whole assemblage. The same families were identified in layer 12, although the number of remains is lower (Samper Carro et al., 2017). Small vertebrae (< 3 mm and 3–6 mm in width) are the most abundant, with vertebrae larger than 10 mm in width being more common in the terminal Pleistocene layers (Samper Carro et al., 2017). For our analysis, we did not consider the smallest vertebrae (< 3 mm), and focused on complete vertebrae from the other three size ranges: 3–6 mm width; 6–10 mm width; and larger than 10 mm width. A total of 81 precaudal and 238 archaeological caudal vertebrae (including cranial and caudal sides) were thus analysed.

### 2.3. Methods

For each individual fish, precaudal and caudal vertebrae were selected, and the cranial and caudal sides of each photographed using a Nikon D5100 camera with macro lens AF-S Micro NIKKOR 60 mm. Vertebrae were fixed with plasticine on a supporting platform and levelled using a spirit level. The camera was systematically placed at 90°

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