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Size and weight estimations of the spangled emperor (Teleostei: Lethrinidae: *Lethrinus nebulosus*) from bones measurements elucidate fishing grounds exploited and ancient seasonality at Akab (United Arab Emirates)

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Abstract

The presence of emperor fishes has been reported in several archaeo-ichthyological studies in Eastern Arabia. The spangled emperor (*Lethrinus nebulosus*) is one of the main species currently composing annual landings in the central and southern Persian Gulf. Its presence outlines the importance of the coastal environments exploited during different life cycle stages, such as open-water reefs and sheltered embayments, including grass beds. Osteometrical methods for estimating the life-size from bones were developed during the last few decades. Measurements taken from the bones of 32 fresh spangled emperors, collected from a fish market in Umm al-Quwain (United Arab Emirates) in February 2017, were exploited to calculate regression equations (power fits), allowing size estimations from archaeological remains. Because of the difficulties in identifying emperor species using bones, we also tested and discussed the validity of a generic model.

The Neolithic site of Akab has provided more than 37 000 fish remains, mostly belonging to kawakawa tunas, trevallies and seabreams, which suggest that fishing was essentially carried out during the winter. Relatively few bones (totalling 100 measurements) were identified as belonging to spangled emperors. However, because of the ecological features of this species, estimated sizes permitted investigations into which fishing grounds were exploited, and even provided new evidence regarding ancient seasonality of coastal occupation in Eastern Arabia.

Keywords: osteometry, fishing, spangled emperor, United Arab Emirates

Introduction

Emperor fishes constitute a family (Lethrinidae) of Perciformes native to the Indo-West Pacific – excepting the eastern Atlantic species, *Lethrinus atlanticus*. They are mostly reported in coastal environments of tropical and subtropical seas, from the seashore to 600 m deep. This family includes 5 genera: *Lethrinus*, *Gymnocranius*, *Monotaxis*, *Gnathodentex*, and *Wattsia*. The genus *Lethrinus* is the more speciose and comprises 27 species, according to FishBase (Froese & Pauly, 2017).

The spangled emperor, *Lethrinus nebulosus* (Forsskål, 1775), is widely distributed from Eastern Africa to Samoa and southern Japan, including semi-enclosed seas like the Red Sea and the Persian Gulf (Carpenter, 2001; Carpenter & Allen, 1989; Young & Martin, 1982).

It is readily identified by its yellowish-brown to bronze body with blue spots or wavy streaks – sometimes dark – radiating forward and ventrally from the eyes and sidebands; many scales also have a whitish or light blue spot in their centre. Fins are generally yellow to orange. This species can reach about 86 cm total length (TL), 75 cm fork length (FL) and 8.4 kg; however, specimens mainly range from 20 to 50 cm TL (Carpenter, 2001; Randall, 1995).

The spangled emperor is the commonest species of emperor occurring in the Persian Gulf, especially from the eastern coast of Qatar up to the northern United Arab Emirates, UAE (Figure 1). Nowadays, it is a prized fish, locally called a *sheary*; indeed, in 1973 and 1996 the UAE coined a special issued bronze 5 Fils coin to emphasise its importance for national fisheries and cultural identity. These fish are well adapted to live in the coastal environments of the southern Persian Gulf. Juveniles are numerous in sheltered bays, where the bottom is soft and facilitates the development of large grass beds; whereas mature fish are more commonly encountered in offshore reefs and close to lagoon inlets, as in Umm al-Quwain and Kalba (UAE), during the spawning season. Cage traps, especially the local dome-shaped traps called *garagir*, and longlines are extremely efficient for their capture.

Osteometrical studies on fish have multiplied over the last few decades (Desse, 1984; Desse *et al.*, 1989). And the estimation of their life-size, from the measurement of their skeletal parts, has found application in several studies: the diet and ecology of ichthyophagous fauna (Masson *et al.*, 2011; Prenda *et al.*, 2002), and the reconstruction of ancient fisheries from archaeological food waste (Thieren & Van Neer, 2016; Lambrides & Weisler, 2015; Yeomans, 2015). Ancient fishing techniques can also be approached by the identification of fish species whose ecological features are known, by giving substantial data regarding the localisation of fishing grounds and seasonality. But ecological behaviours can also change according to the maturity stages of certain species. Therefore, because specific identification from bone remains is difficult within the genus *Lethrinus*, the suitability of a generic model was also tested and discussed.

1. Ichthyological assessments

Because of commercial interests, several studies have been conducted on the geographic repartition, feeding habits, ecological behaviours, reproduction and biological aspects of the

spangled emperor; length-weight allometric relations have also been studied (see Borsa *et al.*, 2009 for a complete review).

Ecological behaviour

Juveniles over 70 mm are encountered in sheltered shallow waters, mostly over soft bottoms; in estuaries (Blaber, 1980), around coastal coral reefs (Allen, 1997; Froese & Pauly, 2007; Laboute & Grandperrin, 2000; Randall, 2005) but mostly over grass and algal beds where they abound during the peak of productivity, in the warm season.

When they are mature, spangled emperors migrate to deeper waters, but remain on the continental shelf. In New Caledonia, they are usually seen off the barrier reef. In UAE, they are not seen inside lagoons. In Kuwait, Downing (1987) noted that spangled emperors are usually encountered just off the reef's edge, but also sometimes just above it; while snubnose emperors (*Lethrinus borbonicus*) remain closer to the bottom, near the coral shelter. Indeed, Egretaud (1992) suggests that the spangled emperors from Uvea Island shelter in reefs during the day and effectuate expeditions during the night to feed. While migrating behaviours are yet to be clearly identified, it is agreed that this species spawn in shallow waters (< 5 m), especially over grass beds situated around islets, protected waters and even inlets, areas that seem to be advantageous for egg dispersion.

Feeding habits change according to the size, region and availability of prey. According to personal observations (K.L.) of their stomach contents, their diet is comprised of small fishes (e.g. mullets), crabs, shrimps, molluscs (mostly bivalves, like Venus clams), worms and echinoderms (see also Borsa *et al.*, 2009: tab. 11; Fischer & Bianchi, 1984).

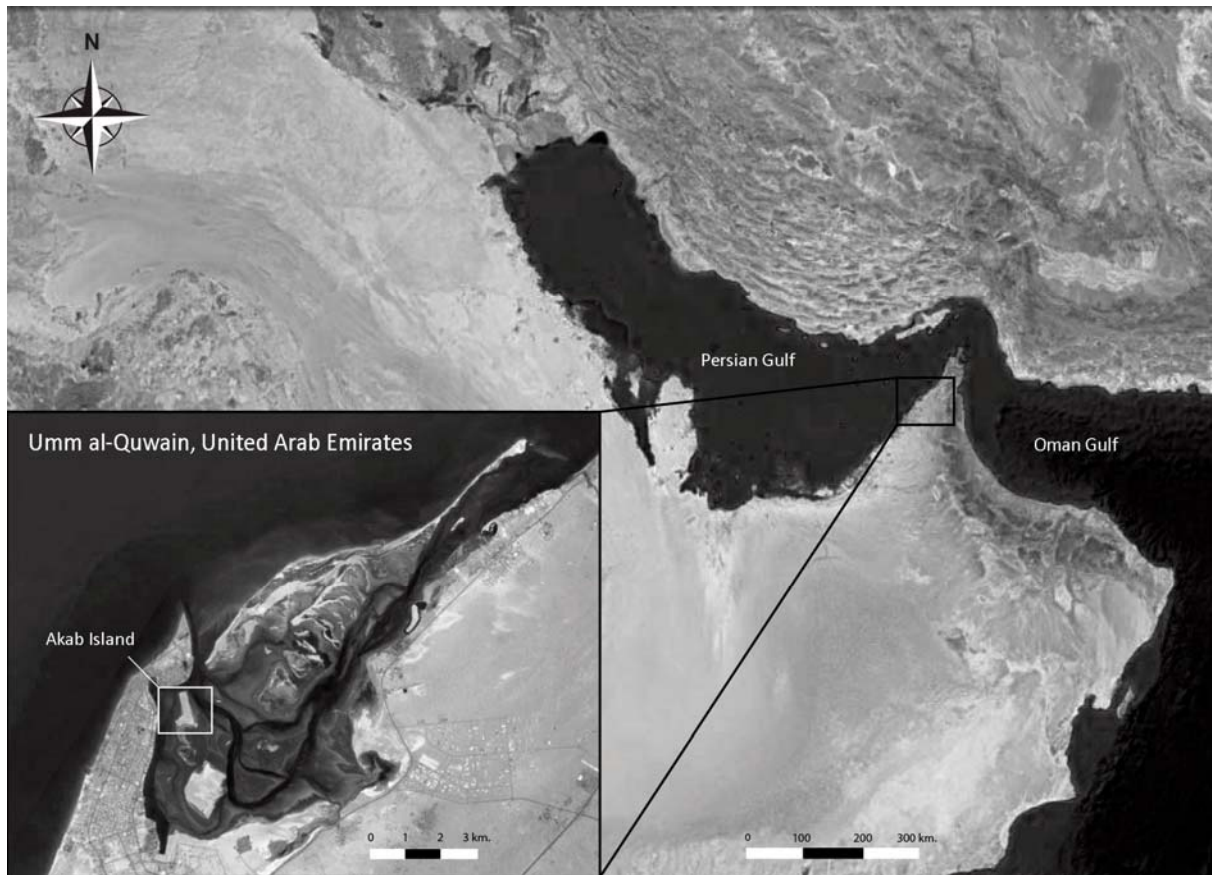


Figure 1. Satellite view of Eastern Arabia and the Umm al-Quwain area, United Arab Emirates © Google Earth 2017

Reproduction and maturity stage

The spangled emperor is a protandrous hermaphrodite, which results in a variation of the sex-ratio to size (Ebisawa, 1990) – males change sex at about 1 year old and 21-24 cm (FL) in the southern Persian Gulf (Grandcourt *et al.*, 2010). However, the percentage of females here seems to be greater (Grandcourt *et al.*, 2006) than in northern Australia and Japan: 71-75% versus 50-60 % (Ebisawa, 1990; Kuo & Lee, 1986).

The spawning season has been well studied by Grandcourt *et al.* (2006; 2010) in the southern Persian Gulf. According to their gonad development studies, spawning occurs once a year between March and early May and is completed within three tidal cycles, which corresponds to increasing/decreasing activities and coincides with higher and lower tides (Grandcourt *et al.*, 2010). The peak of activity was recorded during the month of April. Similar conclusions were obtained on the southeastern Iranian coast (Taghavi Motlagh *et al.*, 2010a; 2010b). Ebisawa (1990) suggests that the spangled emperors' spawning is linked more to the water temperature than their photoperiod, which was validated by the otolith study of Grandcourt *et al.* (2006: fig. 3B).

Their mean "effective maturity" size is estimated at 26.7 cm (FL) for undifferentiated sexes: 28.9 cm (FL) for females and 19.4 cm (FL) for males (Grandcourt *et al.*, 2010). This is clearly lower than for other populations, such as in western Australia, where the mean size for maturity has been estimated at 35 cm (FL) for females and 22.5 cm (FL) for males

(Marriott *et al.*, 2010). This results from several differences in growth and reproductive variables between interregional groups (e.g Kulbicki *et al.*, 1996; Letourneur *et al.*, 1997) and corresponds to distinct stocks (Borsa & Kulbicki, 2004), something which was confirmed by a genetic study (Borsa *et al.*, 2009). But it could also result from variations of sea temperature and fishery pressures in these different areas, as was suggested for the trumpet emperor, *Lethrinus miniatus* (Williams *et al.*, 2006).

The periodicity of otolith growth before first spawning – which corresponds to a single seasonal mark each year – has been validated by several authors (Loubens, 1980; Morales-Nin, 1988; Grandcourt *et al.*, 2006). It remains to be validated after the first spawning because the annuli tend to tighten with age making them harder to read. In the Red Sea, the formation of growth marks is well correlated to the age of the individual, although not necessarily linked to the spawning seasons (Morales-Nin, 1988). Whereas, the formation of growth marks on bones is generally interpreted as the result of environmental change, such as an increase of the photoperiod or the sea temperature –from 21 to 35°C between February and June in Umm al-Quwain, United Arab Emirates (Ali & Cherian, 1983). Williams (1986) studied the formation of otolith growth marks on fish from Kuwait and showed that the hyaline zone is formed between the end of autumn and the beginning of winter, and that the deposition of the opaque zone marks occurs at the beginning of spring. This confirms that a decrease in temperature is consistent with a slowdown in fish growth. Similar observations were noted by Grandcourt *et al.* (2006) in Abu Dhabi waters. These data could provide substantial elements for future studies on seasonality and even ancient sea temperatures using archaeological spangled emperor otoliths.

2. Interests for ancient fisheries and archaeology

According to modern fisheries (Figure 2), emperors – generally the spangled emperor and the pink ear emperor (*Lethrinus lentjan*) – constitute a huge part (15%) of the annual landings in the Persian Gulf (Ali *et al.*, 1980; Morgan, 1985; Sivasubramaniam & Ibrahim, 1982). However, because of intensive fishing during the last few decades, the spangled emperor population has reduced. Grandcourt *et al.* (2006; 2010) noted a critical influence of fishing on the age structure of this fish, revealing both recruitment and growth overfishing. Therefore, size reconstructions of individuals from ancient fisheries could provide conclusive data concerning a possible reduction in size because of exploitation during the past millennia.

While less numerous, snubnose emperors and smalltooth emperors (*Lethrinus microdon*) are also frequently encountered in the Persian Gulf. Several archaeological sites from the Neolithic to the Islamic (or pre-modern) period have provided huge proportions of emperors: Umm al-Quwain site 2 (Mashkour *et al.*, 2016), Ed-Dur (Van Neer *et al.*, 2017), Qala'at al-Bahrain (Vorenger, 2016), Umm an-Nar, Tell Abraq, Saar (Uerpmann & Uerpmann 2005), and Julfar (Desse & Desse-Berset 2000). Because the location of emperor grounds varies between immature and mature individuals, and according to the seasons, size reconstructions are essential to understand ancient fishing strategies, techniques and even seasonality. Indeed, it was first suggested that the ancient Arabian population, in particular

during the Neolithic period, followed the same pattern of mobility as Bedouins alternating between summer and winter settlements (Tosi, 1986; Cleuziou & Tosi, 2007), according to ethnographic works (Lancaster & Lancaster, 1995). In modern Arabia, because the summer is very hot and windy on the coast, boat fishing becomes dangerous and inefficient, whereas winter is an easier and more productive season (Van Neer & Gautier, 1993: 113; UAQ Fisheries, 1984). However, several papers affirm that some Neolithic sites could have been inhabited throughout the year (Biagi & Nisbet, 2006; Zazzo *et al.*, 2014; Méry, 2015: 365; Mashkour *et al.*, 2016: fig 10) and palaeoclimatic studies (Berger *et al.*, 2013; Preston *et al.*, 2015), in particular, have revealed that the summers were not as harsh as previously thought; an assertion which could be validated by further bioarchaeological work.

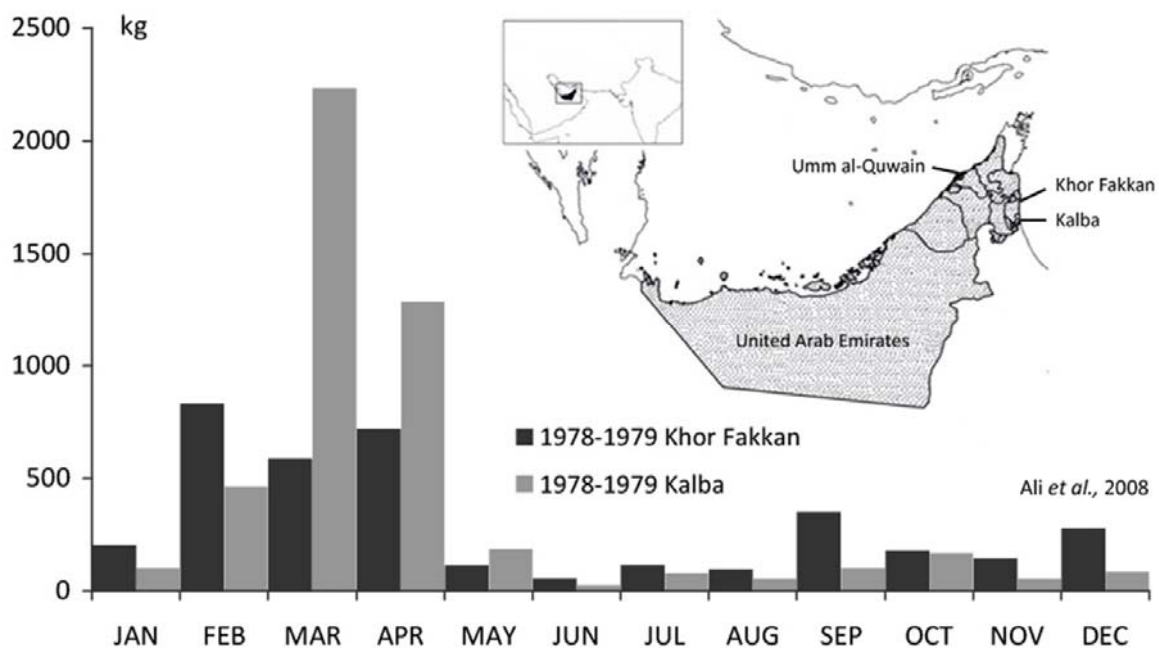


Figure 2. Monthly landings of spangled emperors (*Lethrinus nebulosus*) in Khor Fakkan and Kalba, UAE Eastern Province, 1978–1979, after Ali, Thomas, and Marji (1980)

Archaeological issues

The site of Akab (Late Neolithic period, 4600-4000 BC) is situated on the small sandy island of Khor al-Beidah, bordering the lagoon of the modern city of Umm al-Quwain. Recent excavations have revealed that Akab was inhabited by semi-sedentary herdmen whose economy was primarily focused toward fishing. Semi-circular structures built on posts and many hearths were discovered. The material culture includes Mesopotamian pottery, shell scrapers, and flint tools which were principally involved in personal ornament manufacture, such as beads and pendants, using shells and stones (Charpentier & Méry, 2008). Akab also provides the first Neolithic fish hooks in stratified contexts from the Persian Gulf (Méry *et al.*, 2008). An unprecedented structured platform of dugong bones was also discovered and excavated, which establishes it as the oldest ceremonial site in the whole of Arabia (Méry *et al.*, 2009).

All the excavated sediments were systematically dry sieved using a 3 mm mesh. Fine sieving were also punctually conducted with a 1 mm mesh. This sampling method provided enormous amounts of faunal remains among which about 37 000 fish bones were sorted. A total of 12 550 remains were identified to family level or below (i.e. genus, species). Archaeo-ichthyological investigations have revealed that ancient fishing was carried out both inside and outside the lagoon, in open waters, involving distinct fishing techniques (K.L. unpublished data). Actualistic data suggest that kawakawa tuna fishing was carried out exclusively during the winter months because of the steep rise in sea temperature in mid-spring.

Emperors represents about 6% (NISP = 702) of the whole assemblage, of which 158 remains belong to spangled emperors. Taxonomic identifications are based on comparative anatomy methods and assignments to *Lethrinus nebulosus* are based on the most diagnostic bones (e.g. palatines, maxillae, quadrates, and anguloarticulars). Because we know the effective maturity size of spangled emperors, size estimations could theoretically allow us to differentiate the immature and mature fishes caught at this site. Hence, it would also be possible to determine if Akab fishermen exploited the spawning season of emperors, an activity still in use in Umm al-Quwain today, and therefore extended their effective period of occupation from winter to spring.

3. Material and methods

A total of 32 fresh spangled emperors were collected at the fish market of Umm al-Quwain (UAE) in February 2017, which is an important season for this catch because it corresponds to the spawning season. March and April are closed months, as determined by the UAE Ministry of Environment and Water, to facilitate the renewal of natural stocks. The UAE authorities have also issued a regulation on the minimum length of some fishes, including the spangled emperor, of 22 cm (TL). The specimens collected at the market ranged from 23 to 58 cm and from 179 to 2641 g.

Body measurements were conducted, including total length (TL), standard length (SL) and fork length (FL) in mm, and the total fresh weight (W) in grams. Osteological nomenclature of bones mainly follows Lepiksaar (1994) and Dye & Longenecker (2004). Bone measurements are described in Table 2 and illustrated on Figure 4. They were taken using a digital calliper with a precision of two decimal points and registered in a spreadsheet (Microsoft Excel). Statistical tests and modelisations were conducted with Past 3.10 (Hammer *et al.*, 2001).

Despite the particular interests of working at the species level – because of the application of ecological studies to document ancient fishing (see Cooke & Jimenez, 2004) – we debated whether a generic model for size estimation was suitable because it remains hard to differentiate the different species of the genus *Lethrinus* from bones, except from otoliths. However, a generic model would have needed to be constructed using a representative population assemblage (i.e. 30 individuals) of each species concerned. According to the central limit theorem (CLT), the binomial distribution could have been approximated by a normal distribution. At this stage, the available fish collections do not permit us to conduct this work. It is however possible to construct a statistically valid model for one species;

therefore, we selected *Lethrinus nebulosus* because it is the most prevalent species among the emperor landings in the southern Gulf. This made it possible to empirically test if the equations were suitable for other species by verifying the differences between their estimated size and their real size. However, this approach does not supplant a comparison between representative populations.

The principles of fish size estimation from archaeological bones are outlined by Casteel (1976), including the power regression or allometric approach (see also Tessier, 1948). The bone sizes were generally highly correlated to the life size of the whole fish. Measurements were plotted against the fish's length, and power regression curves were obtained from the point clouds. Their equations are given in Table 3, associated with their corresponding coefficient of determination (r^2). Other individuals of the genus *Lethrinus* (*L. lentjan*, *L. borbonicus*, *L. microdon*, *L. mahsena*, *L. harak* and *L. atlanticus*) were tested with the equations obtained for the spangled emperor to prevalidate the genus model. The application to archaeological bones was made using material from the Neolithic site of Akab (UAE).

Measurements	Abr.	Description
Neurocranium M1	Neu M1	Maximal length of the neurocranium, from the rostral tip of the vomer to the caudal extremity of the basioccipital
Neurocranium M2	Neu M2	Maximal height of the neurocranium, from the ventral part of the basioccipital to the dorsalmost part of the supraoccipital crest
Neurocranium M3	Neu M3	Maximal width of the neurocranium, between the lateralmost extremities of the sphenotics
Vomer M1	Vom M1	Maximal mediolateral width of the vomer
Vomer M2	Vom M2	Distance between the rostral tip and the medial recess between the lateral processes
Basioccipital M1	Boc M1	Maximal width of the articular surface of the basioccipital
Basioccipital M2	Boc M2	Maximal height of the articular surface of the basioccipital
Basioccipital M3	Boc M3	Maximal width of the basioccipital, at level of the two lateral processes for insertion of Baudelot's ligament
Premaxilla M1	Pmx M1	Maximal length of the ascending process of the premaxilla
Premaxilla M2	Pmx M2	Distance between the dorsal tip of the ascending process and the tip of the caudal process
Premaxilla M3	Pmx M3	Rostro-caudal length of the basis of combined ascending and articular processes
Premaxilla M4	Pmx M4	Maximal length of the premaxilla, from the rostral tip to the tip of the caudal process
Maxilla M1	Mx M1	Distance between the dorsal condyle and the ventral tips of the external and internal processes
Maxilla M2	Mx M2	Maximal width of the dorsal condyle
Maxilla M3	Mx M3	Maximal length of the maxilla, from the rostral tip of the external process to the tip of the caudal processes
Dentary M1	Den M1	Height of the symphysis
Dentary M2	Den M2	Maximal width of the rostral extremity
Dentary M3	Den M3	Maximal height, between the coronoid and the ventral processes
Dentary M4	Den M4	Maximal length, from the rostral tip of the dentary to the caudal tips of the coronoid and ventral processes
Anguloarticular M1	Art M1	Distance between the cranio-ventral tip and the little notch situated between the quadrate facet and the post-articular process
Anguloarticular M2	Art M2	Maximal height of the quadrate facet
Anguloarticular M3	Art M3	Maximal width of the quadrate facet
Anguloarticular M4	Art M4	Maximal length between the line joining the quadrate facet and the post-articular process and the rostral tip of the anterior process
Quadrate M1	Qd M1	Distance between the external tip of the lateral condyle and the internal tip of the mesial condyle

Quadrate M2	Qd M2	Distance between the ventral tip of the mesial condyle and the dorsal tip of the ectopterygoid margin
Quadrate M3	Qd M3	Distance between the tip of the mesial condyle and the tip of the preopercular process
Cleithrum D M1	Cl M1	Thickness of the dorsal spine
Cleithrum D M2	Cl M2	Maximal length of the cleithrum
Scapula M1	Sca M1	Maximal width of the condyle
Scapula M2	Sca M2	Maximal height of the condyle
Scapula M3	Sca M3	Maximal length of the dorsal edge of the scapula
Palatine M1	Pal M1	Maximal length of the palatine
Palatine M2	Pal M2	Distance from the rostral tip of the maxillary process to the caudal tip of the dorsal crest
		Distance between the recess situated in the condyle coiling and the cranial tip of the maxilla process
Palatine M3	Pal M3	Distance between the recess situated in the condyle coiling and the cranial tip of the maxilla process
Ceratohyal M1	Ceh M1	Maximal length of the ceratohyal
Ceratohyal M2	Ceh M2	Maximal height of the ceratohyal
Ceratohyal M3	Ceh M3	Maximal width of the articular process of the anterior ceratohyal
Hyomandibular M1	Hm M1	Distance between the sphenotic facet and the opercular process
		Distance between the symplectic facet and the line joining the tips of the sphenotic and pterotic facets
Hyomandibular M2	Hm M2	Distance between the sphenotic facet and the opercular process
Hyomandibular M3	Hm M3	Maximal medio-lateral thickness
		Distance between the rostral edge of the sphenotic facet and the caudal edge of the pterotic facet
Hyomandibular M4	Hm M4	Distance between the little recess posterior to the articular fossa and the supra-articular process
Opercle M1	Op M1	Distance between the little recess posterior to the articular fossa and the supra-articular process
Opercle M2	Op M2	Maximal medio-lateral thickness
Opercle M3	Op M3	Distance from the supra-articular process to the ventral extremity of the opercle
Opercle M4	Op M4	Maximal width, from the articular fossa to the tip of the opercular spine
Preopercle M1	Pop M1	Maximal length of the preopercle
Preopercle M2	Pop M2	Distance between the little inner process and the tip of the rostro-ventral angle
Preopercle M3	Pop M3	Maximal thickness of the quadrate crest
Post-temporal M1	Ptp M1	Distance between the tips of the two processes
Post-temporal M2	Ptp M2	Distance between the tip of the ventral process and the articular facet
Urohyal M1	Uro M1	Maximal width of the hypohyal process
Urohyal M2	Uro M2	Dorsal length of the urohyal
Urohyal M3	Uro M3	Ventral length of the urohyal
First vertebra M1	FV M1	Maximal width of the exoccipital articular surface
First vertebra M2	FV M2	Maximal height of the vertebra
First vertebra M3	FV M3	Maximal height of the centrum (cranial side)
First vertebra M4	FV M4	Maximal width of the centrum (cranial side)
First vertebra M5	FV M5	Maximal width between the lateral processes (cranial side)
Vertebra precaudalis 2 M1	VP2 M1	Maximal height of the centrum (cranial side)
Vertebra precaudalis 2 M2	VP2 M2	Maximal width of the centrum (cranial side)
Vertebra precaudalis 2 M3	VP2 M3	Maximal length of the vertebra (longitudinal or cranio-caudal axis)
Urostyle M1	Ust M1	Maximal height of the centrum (cranial side)
Urostyle M2	Ust M2	Maximal width of the centrum (cranial side)
Sagitta M1	Sag M1	Maximal length (rostro-caudal axis)
Sagitta M2	Sag M2	Maximal height (dorso-ventral axis)
Sagitta Weight	Sag W	Weight (in gram) of the sagitta

Table 1. Descriptions of the bone measurements taken from spangled emperors (*Lethrinus nebulosus*) skeletons

4. Results

Length-weight equation

A total length-weight model was obtained in the form $W = a.TL^b$, with the weight in grams and the total length in cm (Figure 3). The b parameter value is 2.9342, which indicates a slight negative allometry. The FL-weight model is close to those calculated in the same area (Abu Dhabi) by Grandcourt *et al.* (2006) and in the Gulf of Aden by Edwards *et al.* (1985), see Table 1. The present coefficient of determination is high ($r^2 = 0.9875$).

Bones measurements and regression analysis

Equations are given in the form $TL_{fish} = a.M_{bone}^b$ where all the measurements are taken and calculated in mm. The a and b parameters are provided in Table 3; the r^2 is given in the third column. Several equations show a good coefficient of determination, either equal or superior to 0.95 (in bold). For example, the correlations of the palatine measurements ($r^2_{M1} = 0.9842$; $r^2_{M2} = 0.9831$; $r^2_{M3} = 0.9603$) are very good. The lowest coefficients are probably due to an imprecise choice of the relevant osteological points (Vomer M2 and Cleithrum M1, in particular). Four equations were selected for illustrative purposes, due to their high coefficients of correlation and the frequency of corresponding bones in the archaeological contexts.

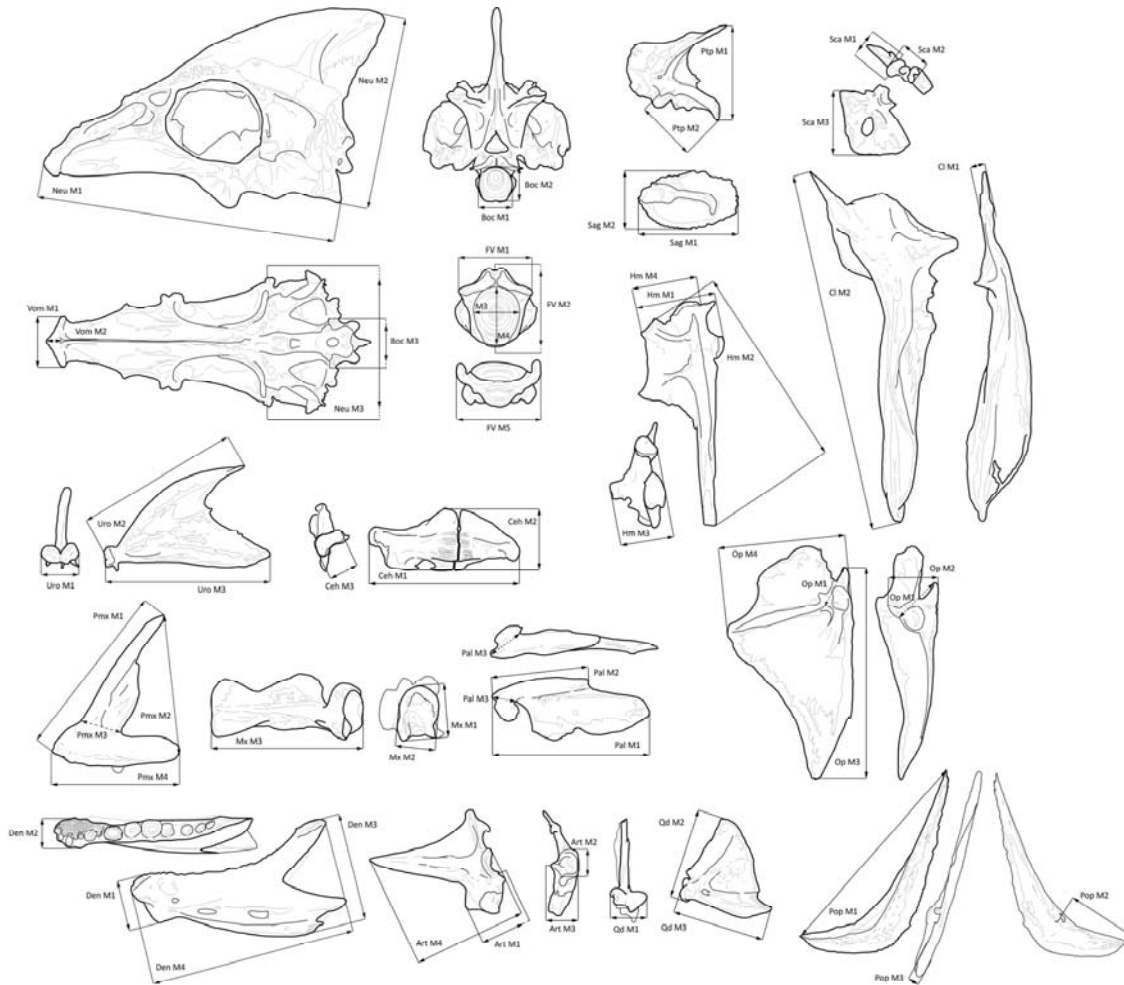


Figure 3. Position of the osteological measurements taken from spangled emperor (*Lethrinus nebulosus*) main bones

The Global Rachidian Profile (GRP)

The present GRP model (Figure 6) was constructed on the basis of the M2 vertebrae measurements (the maximum mediolateral width of the centrum) from 4 different specimens of various sizes – individuals from 270 to 580 mm (TL) were selected. The M2 was selected because, as previously observed (Desse *et al.*, 1989; Vorenger, 2017: 120), it is generally the measurement with the lowest amplitude of variation between the different vertebrae ranks thus facilitating the application of the model – it is not necessary to precisely position the vertebra at the right rank. From the height of an archaeological vertebra, positioned on the ordinate axis, it is possible to roughly estimate in which order of magnitude is the life-size of the individual.

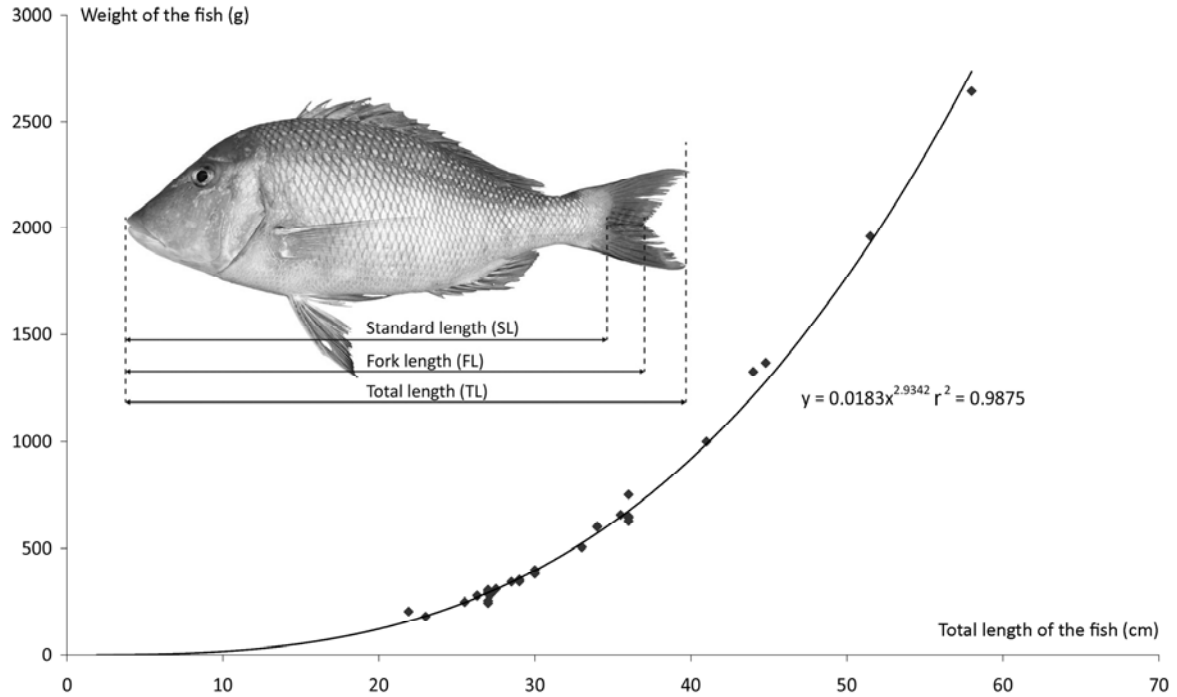


Figure 4. Total length (TL) to weight relationship of the modern sample of spangled emperors (*Lethrinus nebulosus*) studied (N = 32)

Geographic areas	References	a	b	P30	P50
Persian Gulf (UAE UAQ)	Present study	0.0334	2.823	494	2091
Persian Gulf (UAE Abu Dhabi)	Grandcourt <i>et al.</i> , 2006	0.0300	2.880	539	2345
Persian Gulf (Qatar)	Baddar, 1987	0.0173	3.010	484	2253
Persian Gulf (Hormozgan)	Taghavi Motlagh <i>et al.</i> , 2010	0.0518	2.722	543	2182
Gulf of Aden	Edwards <i>et al.</i> , 1985	0.0350	2.810	495	2081
Gulf of Aden	Aldonov & Druzhinin, 1979	0.0432	2.798	586	2449
Red Sea and Aden ♀	al-Sakaff & Esseen, 1999	0.0950	2.615	692	2633
Red Sea and Aden ♂	al-Sakaff & Esseen, 1999	0.0670	2.708	670	2672
Japan	Ebisawa, 1990	0.0252	2.913	507	2243
New Caledonia	Borsa <i>et al.</i> , 2009	0.0293	2.875	517	2246

Table 2. Fork length to weight equation parameters for spangled emperors from the studied area and other regions of the Indo-West Pacific

Measurements	a	b	r ²	N					
Neurocranium M1	3.9693	1.0623	0.9865	30	Ceratohyal M1	15.671	0.9377	0.9844	32
Neurocranium M2	8.3066	1.0015	0.985	30	Ceratohyal M2	34.435	0.9651	0.9699	32
Neurocranium M3	6.9757	1.0987	0.9772	30	Ceratohyal M3	82.948	0.9277	0.9423	32
Vomer M1	35.387	0.9119	0.9512	32	Hyomandibular M1	32.446	0.931	0.9757	32
Vomer M2	132.71	0.7313	0.6073	32	Hyomandibular M2	9.6294	0.9951	0.9865	32
Basioccipital M1	70.079	0.8421	0.964	31	Hyomandibular M3	57.061	0.9384	0.9488	32
Basioccipital M2	65.525	0.8091	0.9304	31	Hyomandibular M4	34.002	1.0083	0.9652	32
Basioccipital M3	66.906	0.8484	0.8902	31	Opercle M1	52.543	0.9594	0.9657	32
Premaxilla M1	14.582	0.9264	0.985	31	Opercle M2	60.884	0.9086	0.9409	32
Premaxilla M2	30.693	0.8452	0.9705	31	Opercle M3	10.435	0.9728	0.974	32
Premaxilla M3	66.229	0.812	0.8706	31	Opercle M4	15.956	1.0039	0.982	32

Premaxilla M4	19.785	0.9123	0.9784	31	Preopercle M1	145.66	0.6982	0.8592	32
Maxilla M1	52.631	0.8866	0.9649	31	Preopercle M2	16.098	1.0366	0.9754	32
Maxilla M2	64.582	0.9095	0.9595	31	Preopercle M3	6.3709	0.988	0.9871	32
Maxilla M3	18.073	0.9195	0.9758	31	Post-temporal M1	19.837	1.0139	0.9744	32
Dentary M1	62.18	0.8751	0.9501	32	Post-temporal M2	35.784	0.9252	0.9618	32
Dentary M2	112.33	0.7932	0.9239	32	Urohyal M1	93.073	0.853	0.9393	32
Dentary M3	30.742	0.8725	0.9498	32	Urohyal M2	16.936	0.9427	0.9575	32
Dentary M4	14.333	0.9488	0.9802	32	Urohyal M3	14.793	0.9966	0.9809	32
Anguloarticular M1	61.607	0.7871	0.8831	32	First vertebra M1	53.395	0.8453	0.9828	32
Anguloarticular M2	86.36	0.8957	0.9385	32	First vertebra M2	49.444	0.8527	0.9717	32
Anguloarticular M3	87.527	0.8785	0.9556	32	First vertebra M3	71.781	0.7934	0.9139	32
Anguloarticular M4	15.719	0.9781	0.9655	32	First vertebra M4	87.231	0.7948	0.9386	32
Quadrate M1	87.4	0.8487	0.9494	32	First vertebra M5	49.772	0.8416	0.98	32
Quadrate M2	25.347	0.9171	0.9778	32	Vertebra praecaudalis 2 M1	66.176	0.7851	0.9681	32
Quadrate M3	17.668	1.0391	0.9672	32	Vertebra praecaudalis 2 M2	79.239	0.7344	0.9445	32
Cleithrum M1	148.31	0.7013	0.7732	32	Vertebra praecaudalis 2 M3	78.261	0.8713	0.9705	32
Cleithrum M2	5.5208	0.9895	0.9915	32	Urostyle M1	82.572	0.872	0.9625	32
Scapula M1	131.21	0.812	0.9057	32	Urostyle M2	89.286	0.836	0.9758	32
Scapula M2	60.292	1.0431	0.9669	32	Sagitta M1	15.432	1.3749	0.9201	31
Scapula M3	35.893	0.9284	0.9624	32	Sagitta M2	26.3	1.3824	0.9216	31
Palatine M1	15.73	0.8913	0.9844	31	Sagitta Weight	846.93	0.44	0.8957	31
Palatine M2	26.017	0.8592	0.983	31					
Palatine M3	79.191	0.8158	0.9604	31					

Table 2. Regression formulae parameters for estimating the total length of spangled emperors (*Lethrinus nebulosus*) from bone measurements (in mm)

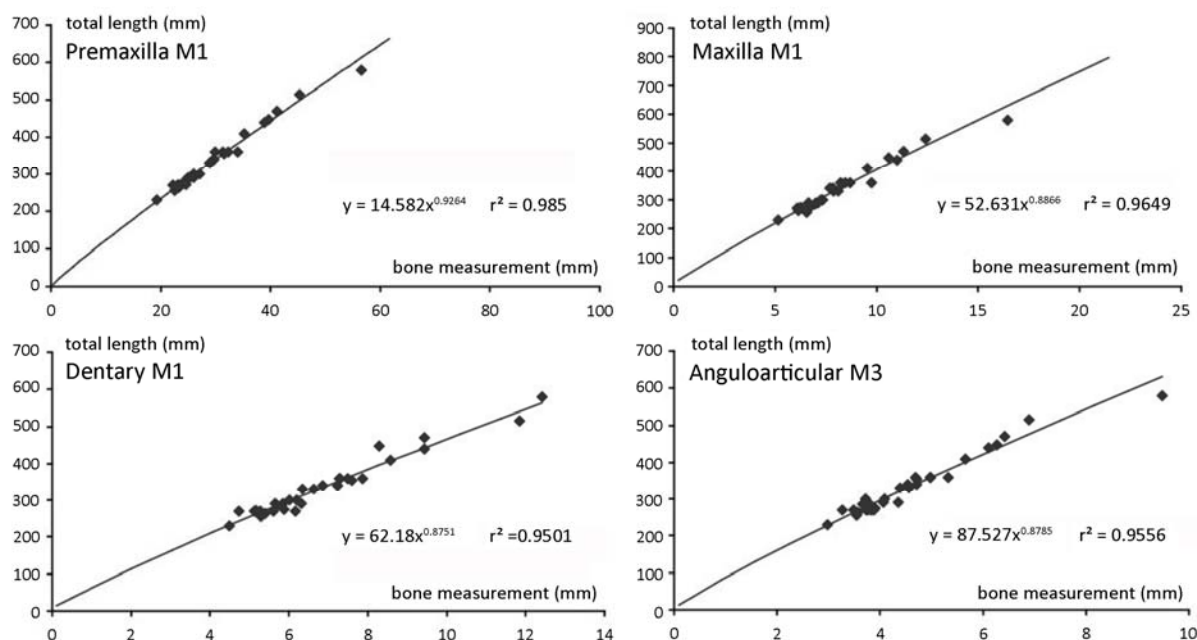


Figure 5. Examples of the graphs modelling the regression formulae obtained, giving the parameters shown in Table 3. Note that all measurements are in millimetres

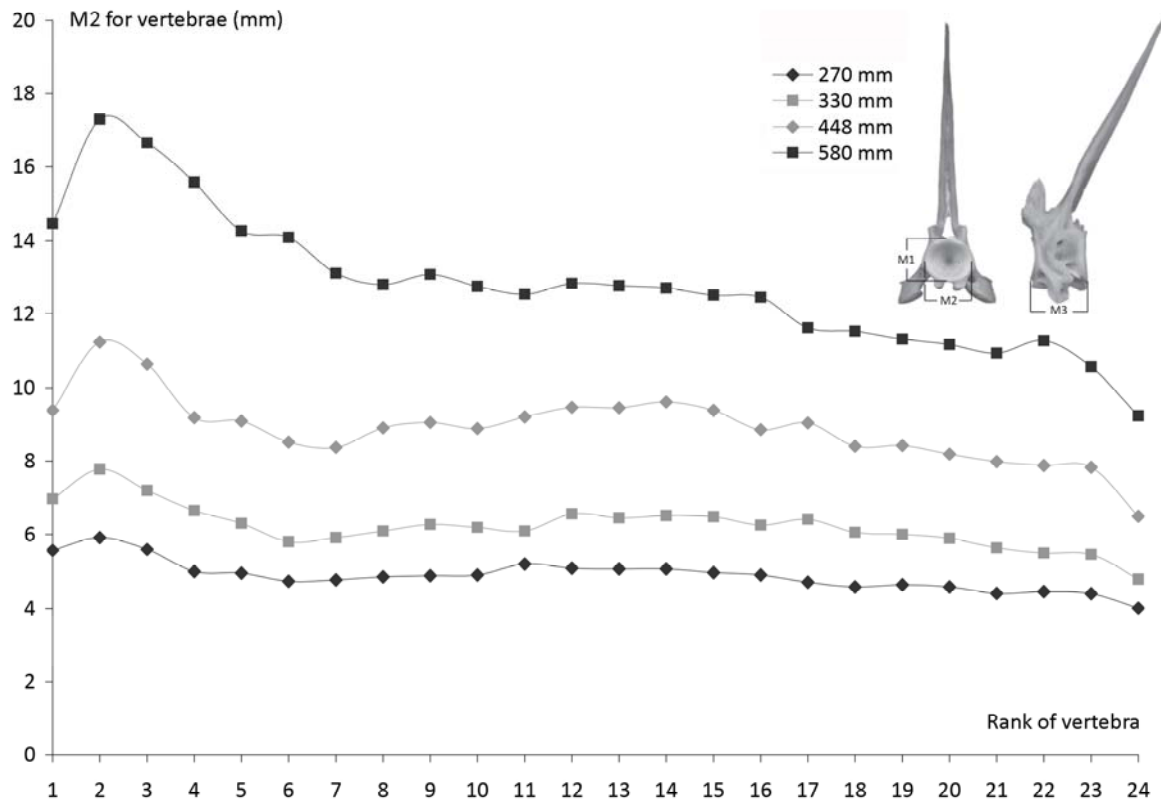


Figure 5. Global Rachidian Profiles obtained for four different specimens of spangled emperors, ranging from 270 to 580 mm (total length)

Suitability of a generic model

The generic model obtained for the length-weight correlation is quite good. It was calculated by combining data from *Lethrinus* specimens (N = 72) from the MNHN-ICOS and Desse collections. It could be applied with only a relatively low error rate (the coefficient of determination was 0.97 for the TL and 0.94 for the SL) as previously suggested (Vorenger, 2017: 117, graph 24-25). In very few cases measurements were useful to reconstruct life-size at a generic level, even accepting a 5% error. Here, we can see the importance of working at the specific level. We suggest the elaboration and publication of more identification keys for fish osteological studies in future, especially for *Lethrinus* species, occurring in Eastern Arabia or elsewhere, in order to extend the potential application of this study. Some of the emperor bones from the Akab site have been well assigned to spangled emperors, which has enabled the first application of our model using archaeological material.

Noting the overlapped curves of the GRP for several species of the genus *Lethrinus* (Vorenger, 2017: 122-123, graph 1), the profile constructed for *Lethrinus nebulosus*, in this study, could be applied as a generic GRP and provide a relatively good order of magnitude to size estimations. However, it is difficult to differentiate the majority of emperor vertebrae from those of other Perciformes, especially caudals from other sparoids like seabreams (Sparidae) and threadfin breams (Nemipteridae). Precaudals are easier to identify, although

they are morphologically close to those of grunts (Haemulidae). Hence, species identification is potentially more reliable when referring to spangled emperor precaudals.

Archaeo-ichthyological application

Over a total of 702 lethrinid bones, 158 could be attributed to *Lethrinus nebulosus*, 100 of which could be and exploited for the application of the present osteometric model.

Measurements associated with low rates of determination (< 0.95) were not used (e.g. Vomer M2 and Cleithrum M1); therefore, for each bone we preferred to use the measurement with the highest rate of determination. An MNI calculation was not performed for this study, because of important bias caused by both taphonomic processes and sampling methods (Grayson, 1984; Morales-Muñiz, 1984). Measurements were mostly carried out on palatines (28%), maxillae (25%), quadrates (14%) and anguloarticulars (12%), followed by dentaries, premaxillae, hyomandibulars, scapulae and basioccipitals.

The minimal reconstructed length was 20 cm (TL) and the maximum was 53.8 cm (TL), which gave a mean of 37.6 cm (TL) and a median of 35.7 cm (TL). The main size class represented was 30-35 cm (N = 26; 26% of the total population).

5. Discussion

Figure 7b gives the structure of the archaeological population in size classes, and Figure 7a gives the natural structure of the modern population of spangled emperor (N = 781, Grandcourt *et al.*, 2010). The latter shows a distinctive normal pattern which could be interpreted as a survivorship curve (truncated distribution), with an underrepresentation of young individuals because of the selectivity of modern fisheries.

Constructing a size distribution histogram

The archaeological histogram seems to depict a normal distribution with a distinct deficit of the 35-45 cm (TL) size classes. If this drop is not considered as an 'artefact', we can argue that the distribution could be bimodal. It is possible that fishes ranging from 25 to 35 cm (TL) and those ranging from 35 to 60 cm (TL) could have been caught with distinct techniques or gears, like nets and lines of different meshes and sizes. At Akab, several net sinkers and shell fish hooks were found (Méry *et al.*, 2008). We applied a modified von Bertalanffy size-to-age equation to model the age distribution (data from Grandcourt *et al.*, 2006), and discovered that all the fish year classes are represented in the Akab fishery, while 6-year-old fish are less numerous. This confirms that bimodality does not result in two cohorts of distinct ages. However, the annual pattern of increment formation on otoliths (sagittae) remains to be strongly validated. Indeed, important differences in the size of equal-age specimens were observed by Grandcourt *et al.* (2006: fig. 4) – a phenomenon also reported for other hermaphroditic species. Several explanations could be suggested, such as an irregular higher mortality within this cohort or the selectivity of fishing both smaller and bigger specimens.

The normal distribution of sizes was thus tested according to the Shapiro-Wilk (W), Anderson-Darling (A) and Jarque-Bera (JB) methods (Shapiro & Wilk, 1965; Anderson & Darling, 1952; Jarque & Bera, 1980). Because of the low probabilities obtained, respectively $W = 0.9698$ $p_{normality} = 1.923 \cdot 10^{-3}$; $A = 1.582$ $p_{normality} = 1.582 \cdot 10^{-5}$; $JB = 4.307$ $p_{normality} = 1.161 \cdot 10^{-1}$, the normality pattern was unvalidated. A normal probability plot was also applied (Figure 7c). The line of dark spots (measured population) shows two undulations through the red line, graphically evidencing bimodality. A bimodal distribution was first suggested when applying a kernel smoothing curve to the bar chart (Figure 7b). This method is useful to estimate a real-valued function if no parametric model is known. The mixture analysis permits the determination of the multimodal distribution parameters on a pooled univariate sample. In this case, the method could be used to study differences between the two groups of individuals when no independent information is available (Figure 7d). The bimodal distribution seems, therefore, to be validated and could originate from two distinct fishing techniques.

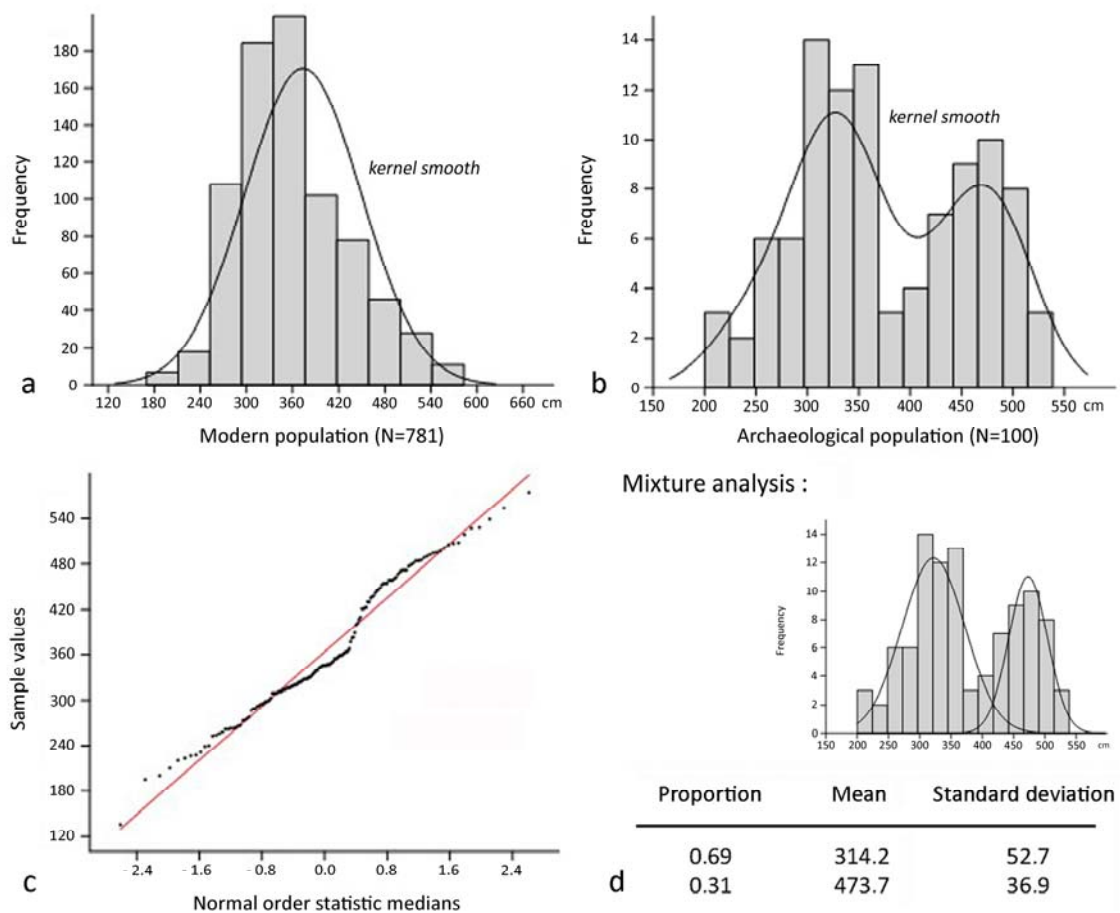


Figure 7. (a) Sizes (total length) of modern spangled emperors obtained from annual landings in Abu Dhabi, UAE—N = 781 (Grandcourt et al., 2006); (b) estimated lengths (total length) of spangled emperors caught at Akab during the Neolithic—N = 100 (present study); (c) normality plot applied to the spangled emperors sizes from Akab; (d) mixture analysis, with Gaussian curves and parameters

Fishing strategies

Because otoliths are not well preserved and not easily identified and collected by many archaeologists and field workers unless they are specifically trained, the presence of certain fish has probably been underestimated at several sites. This is certainly the case at Akab where there is an obvious disproportion of emperors with the neighbouring site of Umm al-Quwain 2 (Mashkour *et al.*, 2016), and where similar fishing techniques were probably carried out inside the lagoon, such as beach seines and traps built with stones, palm leaves or even net stakes (local *haddrah* and *sakkar* types). These low selective techniques are well adapted to catch the wide diversity of fishes identified at Akab (in particular small seabreams, needlefish and barracudas) along with a significant amount of brackish and soft-bottom dwellers (e.g. mullets, catfishes, flatheads and even tripod fishes). Only a few small, well-preserved bones could be identified as very young emperors, although not down to the species level, and it is very likely that spangled emperors could be found among them.

According to ecologic data of the spangled emperor, there is no reason that the techniques used to catch medium-size and large individuals did not also permit the catching of juvenile spangled emperors, which also mainly occur in lagoons and over grass beds. If we accept that immature spangled emperors are probably underrepresented at Akab, assuming that this is not due to sampling bias, we can argue that emperor fishing was also carried out inside the lagoon. According to their effective maturity, which is estimated at about 26.7 cm (FL) or 29 cm (TL) by Grandcourt *et al.* (2010), 14% (N = 14) of the spangled emperors caught at Akab are theoretically considered as immature, assuming that this data has not changed since the Neolithic.

On the other hand, it demonstrates that the larger spangled emperors are also well represented in the assemblage. Nowadays, in the Umm al-Quwain area, as in Kalba (Fujairah Emirate, UAE), mature spangled emperors are mostly caught during the spawning season which occurs close to lagoons in March and April (Figure 2). It is therefore likely that at Akab, the fishermen also benefitted from the spawning season to catch larger emperors. The possible use of shell fish hooks as lures to catch kawakawa tunas during surface bust-ups in open water and the trapping of trevallies on the falling tide, across or close to the lagoon inlet, would also demonstrate that Neolithic fishing already involved a wide range of strategies to maintain and improve the food supply. These express an attentive observation of natural phenomena and fish behaviour.

Seasonality evidence

As previously mentioned, it was initially suggested that Neolithic societies followed a similar mobility schema as traditional Bedouin tribes from Eastern Arabia, alternating between summer and winter settlements (Tosi, 1986). However this theory is now more nuanced (Biagi & Nisbet, 2006; Zazzo *et al.*, 2014) and our data also confirms that certain Neolithic sites could have been inhabited all year round. Indeed, if Neolithic fishermen took advantage of the spawning aggregation of spangled emperors, which occurs during the spring, that would suggest that Akab was inhabited not only during the winter, the current kawakawa tuna fishing season, but also during the spring. However, the application of actualist data to ancient times raises some difficulties because of the evolution of climate and environments.

It could be possible, in the future, to address this issue on the basis of interlinked palaeoenvironmental and schlerochronological studies.

Impact of ancient fisheries on fish populations

A comparison between data on modern (Grandcourt *et al.*, 2010) and archaeological sizes do not show any relevant differences which could reveal a reduction in fish sizes due to fishing. Nevertheless, the archaeological population is more diversified in size than the modern one. This is certainly due to fishery restrictions regarding both the size limit (22 cm, TL) and the prohibition of fishing inside some areas of Abu Dhabi waters, as is the case for the UAQ lagoon.

If the fishermen of Umm al-Quwain have been exploiting the spawning phenomenon of spangled emperors over 6 500 years, from the Neolithic to the present day, it is surprising to not observe a reduction in fish sizes. However, it is difficult to compare the modern and archaeological populations because their population structures are not natural, since both originate from human selectivity through fishing. To clarify this trend it would be necessary to investigate fisheries from other periods. Al-Taboor (2004) explains that ancient fishermen have maintained the traditional knowledge and experience of the marine environment, including fish behaviour. In particular, they are careful about spawning periods, locally called *al-manakif*, in order to protect the fishing grounds. He also said:

“They also avoid catching smaller fishes by using the right fishing gear and methods, as well as abiding strictly to rules and regulations, which they inherited generation after generation. This unfortunately does not apply to our fishermen today, who care very little about protecting the marine environment [...]” (Al-Taboor, 2004).

It is possible, therefore, that since the Neolithic, fishermen have been careful to maintain fish populations, in order to secure the fish landings and a continuous food supply. It is also possible that, as the demographic pressure remained low in the area over several millennia, the subsistence did not require large fisheries, which would have impacted fish populations. Moreover, considering that Neolithic fishermen probably had not yet developed fish preservation techniques, fisheries remained diversified throughout the year for other taxa such as trevallies, seabreams, mullets and kawakawa tunas.

Conclusion

The principal aim of this paper was to build an osteometric model for archaeo-ichthyologists working on Indo-Pacific sites, in particular Eastern Arabia, where emperors may have been caught and consumed. It has demonstrated that an osteological model is quite limited at the generic level, because only few bones provided an acceptable correlation. However, the length-weight equation and the GRP (Figure 6) were suitable, and have the potential to be two very useful tools for archaeo-ichthyologists. We also showed the value of working at the species level despite identification difficulties, which will involve creating and publishing identification keys on bones. Indeed, this ecological data can be exploited to discuss fishing

grounds, techniques, seasonality and even overexploitation of evidence, or not, through time.

The exploitation of the spangled emperors' spawning aggregation, which occurs in the vicinity of lagoon inlets, was documented at Akab and questions the seasonal mobility initially suggested by ethnographic studies. Thus, Akab was probably inhabited from winter to spring, at least, according to the fishing activities now highlighted.

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