





RESEARCH ARTICLE

Length estimation of Atlantic bluefin tuna (*Thunnus thynnus*) using vertebrae

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Funding information

H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 813383

Abstract

Atlantic bluefin tuna (*Thunnus thynnus*; BFT) is a large (up to 3.3 m in length) pelagic predator which has been exploited throughout the eastern Atlantic and Mediterranean since prehistoric times, as attested by its archeological remains. One key insight derivable from these remains is body size, which can indicate past fishing abilities, the impact of fishing, and past migration behavior. Despite this, there exists no reliable method to estimate the size of BFT found in archeological sites. Here, 13 modern *Thunnus* spp. skeletons were studied to provide power regression equations that estimate body length from vertebra dimensions. In modern specimens, the majority of BFT vertebrae can be differentiated by their morphological features, and thus, individual regression equations can be applied for each rank (position in vertebral column). In an archeological context, poor preservation may limit one's ability to identify rank; hence, "types" of vertebrae were defined, which enable length estimates when rank cannot be determined. At least one vertebra dimension, height, width, or length correlated highly with body length when vertebrae were ranked ($R^2 > 0.97$) or identified to types ($R^2 > 0.98$). Whether using rank or type, length estimates appear accurate to approximately $\pm 10\%$. Finally, the method was applied to a sample of Roman-era BFT vertebrae to demonstrate its potential. It is acknowledged that further studies with larger sample sizes would provide more precision in BFT length estimates.

KEYWORDS

Atlantic bluefin tuna, osteometry, size estimation, vertebrae, zooarcheology

1 | INTRODUCTION

Archeological fish remains are vital when investigating the role that fish have played in cultural developments and, conversely, how such developments have impacted fish populations themselves (Colley, 1990; Erlandson & Rick, 2010; Orton, 2016). Studies on fish

remains typically utilize a number of methodologies to do this, for example, recording the location, identity, and number of remains recovered (Colley, 1990; Hoffmann, 2005); analysis of their taphonomy and archeological context (Çakırlar et al., 2016; Prieto, 2021; van Neer et al., 2004); their morphological identification, provenance, and genetics inferred by applications of biomolecular tools (Andrews et al.,

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2021, 2022; Orton, 2016; Richter et al., 2011; Winter et al., 2021); and the estimation of fish size from measurements on fish remains (Casteel, 1976; Desse et al., 1989; Wheeler & Jones, 1989).

Methods to estimate size are particularly useful to identify which fishing methods were used in the past, since different techniques target different sizes of fish (Gabriel et al., 2012; Greenspan, 1998; Owen & Merrick, 1994). It is used to investigate how size classes were distributed spatially (Sanchez, 2020) and to assess exploitation impacts, since a symptom of overfishing is the truncation of size classes (Barrett, 2019; Morales-Muniz & Roselló-Izquierdo, 2007; Plank et al., 2018). Size information can also be useful in biomolecular studies since biochemical compounds, for example, stable isotopes, vary with body size (see Barrett et al., 2011, and references therein). Moreover, size information can be used as an additional species identification criterion and to assess the minimum number of individuals (MNI) recovered in excavations (Orchard, 2005). The need for archeological size metrics to inform present-day sustainability is particularly important for one key species, Atlantic bluefin tuna (*Thunnus thynnus*, hereafter BFT), since it appears to have had a long and intense history of exploitation yet the impact on the population is unknown (Andrews et al., 2022). Despite much interest in BFT archeology (Felici, 2018; García Vargas et al., 2018; Mylona, 2021; Nielsen & Persson, 2020), there are currently no reliable methods to estimate BFT size from archeological remains. Here, a method is developed to estimate BFT straight fork length (hereafter FL) from measurements of isolated (and sometimes poorly preserved) vertebrae recovered in archeological excavations.

Size estimations on archeological fish bones are achieved by comparing their measurements to those of reference specimens of known lengths or weights (Casteel, 1976; Desse et al., 1989; Wheeler & Jones, 1989). Cranial elements are sometimes used as the reference of choice because these are readily identified and produce good estimations of body size (Desse & Desse-Berset, 1996; Jiménez-Cano & Masson, 2016; Thieren & van Neer, 2016). Given the rarity with which BFT cranial elements are recovered in archeological contexts (Andrews et al., 2022), vertebrae—a robust and well-preserved element—were chosen as an alternative. Size estimations have been seldom applied to BFT, namely, by Rose (1994), who developed a coarse method of estimating length from a single vertebra (also applied by Mylona, 2018, and Morales-Muniz & Roselló-Izquierdo, 2007, who developed a precursor to the current study). Development of a reliable BFT size estimation tool in these studies has been precluded by a difficulty in obtaining numerous modern reference specimens of known lengths or weights because large adult BFT are expensive and challenging to process. Studies of this type, on any fish species, face two further challenges: (a) how to identify isolated vertebrae found in archeological excavations and assign them to rank (i.e., position in the vertebral column) and (b) how to select the best statistical model of estimation suited to fish growth and account for variation observed within this model.

Taphonomic damage sometimes makes it difficult to establish vertebra rank in archeological specimens (Lambrides & Weisler, 2015; Sinha et al., 2019). Due to size variation throughout the vertebral column in fishes, length estimates will be less accurate if rank cannot be

determined. As an alternative, it is possible estimate length using sections of similar vertebrae, herein called types. One way to discover types is to study which vertebrae are morphologically similar and assess whether these similarities would hold true in an archeological context. Another is to apply the Global Rachidian Profiles (GRP) method (sensu Desse et al., 1989) that identifies which sections of the vertebral column contain vertebrae that do not differ greatly in size (Lambrides & Weisler, 2015; Lidour et al., 2018; Thieren et al., 2012). Regardless of the method used, it is necessary to measure the variation between vertebrae within each type, as this is sometimes too large for meaningful estimates (Jelu et al., 2021). In addition, there is a need to attempt rank or type identification from as much of the vertebral column as possible; otherwise, estimations may be hindered if particular vertebrae are required and not recovered in excavations.

When dealing with vertebrae rank or type, the use of power regression equations has become common in estimating body length, where model fit is often assessed by the coefficient of determination (R^2) and standard error values (Gabriel et al., 2012; Jelu et al., 2021; Marrast & Béarez, 2019; Martínez-Polanco & Béarez, 2020; Rurua et al., 2020). Because fish growth is considered allometric, that is, the relationship between body length and vertebrae dimensions is not linear, power regression models are optimal because they account for this (Reitz et al., 1987).

The accuracy of size estimates also needs to be taken into account, because for all fishes, but especially BFT and other tuna (*Thunnus* spp.), intraspecific variation exists in, for example, body length, vertebral length, size-at-age, and in length-weight relationships (Cort, 1989; Perçin & Akyol, 2009; Rodriguez-Marin et al., 2015; Rodriguez-Roda, 1964; Santamaria et al., 2009) because individuals experience varied life histories within a single population or generation (Mather et al., 1995). Therefore, size estimates can be expected to deviate from true values, and this error must be measured and considered when interpreting estimated values.

This study aimed to (1) identify which BFT vertebrae can be identified to rank if found isolated and which “types” of BFT vertebrae exist that can be used to group potentially poorly preserved archeological vertebrae if rank identification is too challenging; (2) develop power regression equations to estimate FL from vertebra measurements and concurrently identify which vertebra dimensions should be selected for estimations; and (3) assess method's accuracy. As an illustration, a case study is presented, where the method is applied to 59 BFT vertebrae recovered from a second century BCE refuse site Punta Camarinal (near the Roman city of Baelo Claudia, Andalusia, Spain). A guide to identify BFT vertebrae to rank or type was developed to aid length estimations (Appendix S2). An online calculator was also established at <https://tunaarchaeology.org/lengthestimations>, allowing researchers to retrieve length estimates for each vertebra measurement.

2 | MATERIALS AND METHODS

Nine BFT vertebral columns were collected from specimens fished or stranded throughout the eastern Atlantic, Mediterranean, and Sea of

Marmara between 1987 and 2020 (Table 1). These were complemented with vertebral columns of two albacore tuna (*Thunnus alalunga*, hereafter ALB) and two bigeye tuna (*Thunnus obesus*, hereafter BET) to better represent intra- and inter-specific variation, as the current study dealt with relatively few reference specimens. BFT specimens comprised a range of growth stages from juveniles to large adults, between 26.5 and 220 cm FL. The ALB and BET fall into this size range with a FL between 45 and 190 cm FL (Table 1).

Morphological features unique to each vertebra were inspected to determine which vertebrae could be identified to rank if found disarticulated. Subsequently, vertebrae that would likely be indistinguishable from each other if damaged due to taphonomic processes were grouped into vertebra types. These identification criteria were illustrated using photographs of vertebrae from one reference specimen and constitute a guide to identify rank and type in BFT which can be found in Appendix S2.

FL was chosen as the preferred measurement of fish size for BFT because it is the most accurate and frequently used length measure in tuna fisheries, more readily enabling comparisons between lengths estimated from archeological remains and modern fishery data. Conversion factors to standard length (SL) and total length (TL) are supplied following published equations (Table S1). A conversion factor for weight is supplied (Table S1), but it is not estimated here because it is highly seasonally variable and estimates would be subject to wide error margins (Cort, 1989; Rodriguez-Marin et al., 2015). Caution should generally be taken when applying length–weight relationships for archeological specimens because fattening rates vary spatially (Cort & Estruch, 2016) and are unknown for the ancient past.

Using digital calipers, the posterior height, posterior width, and length of all 39 vertebrae centra were measured to the nearest 0.01 mm (Figure 1). Exceptions were the first vertebra (V1), where length was not measured since it is fused to the skull in adults, and

the last vertebra (urostyle; V39), where only anterior height and width could be measured. Measurements were sometimes missing hampered by butchery marks. For simplicity, vertebrae are referred to by their rank (i.e., V1 to V39). For the main analysis, the greatest length measurement (comparing left and right side) for each vertebra centrum was used; however, length was recorded on both sides of vertebrae in specimen V8 to assess its variation. Anterior height and width were also measured in specimen V8 to assess variation compared with the posterior dimensions.

When deciding on a regression model to use, linear and logarithmic models were considered (see Lernau & Ben-Horin, 2016, but these did not provide satisfactory fits (data not shown). Since BFT length relationships appear to follow allometric growth patterns (Santamaria et al., 2009), the power regression approach was adopted herein, which provided more appreciable results. Power regression equations for each vertebrae rank and type were defined using measurements from all 13 *Thunnus* spp. specimens and the core function (lm [formula = $\log(\text{response variable}) \sim \log(\text{predictor variable})$]) in R (Team RC, 2013), applied to each dimension separately. Standard deviation (SD) observed in height, width, and length across vertebrae within each type was assessed by calculating the standard deviation between vertebrae of each specimen before averaging across specimens. The best model fit for each vertebral rank and type was judged according to the vertebral measurement with the highest coefficient of determination (R^2) and lowest residual standard error (RSE) values. Where SD between vertebrae measurements was high for the model of best fit identified using R^2 and RSE, the dimension with the highest R^2 value and lowest SD combination was selected as the best model.

There was a need to understand the error associated with estimates produced by our method, because this would give some indication of how reliable inferences might be based on them. Therefore, prediction accuracy for each of the best scoring models was tested by

TABLE 1 Modern reference specimens of Atlantic bluefin tuna (*Thunnus thynnus*; BFT), albacore tuna (*Thunnus alalunga*; ALB), and bigeye tuna (*Thunnus obesus*; BET) used to produce length estimate equations

	Species	Catch date	Origin	Sex	FL (cm)	TL (cm)	Weight (kg)
1	BFT	1987	Torreveja, Spain	-	26.5	32.5	-
2	ALB	1988	Gijon, Spain	-	54	59	-
3	ALB	2006	Gijon, Spain	M	85	91	-
4	BFT	2010	Istanbul, Turkey	-	113	-	-
5	BFT	2015	Istanbul, Turkey	-	120	-	-
6	BET	2020	Barbate, Spain	-	122	135	38
7	BFT	1988	Huelva, Spain	-	124	130	-
8	BFT	2020	Fano, Italy	-	130	137	-
9	BFT	2015	Istanbul, Turkey	-	170	-	90
10	BET	2001	Gijon, Spain	M	190	-	138
11	BFT	2015	Barbate, Spain	M	200	208	190
12	BFT	2012	Chryssi Island, Crete, Greece	-	212	-	-
13	BFT	1993	Southern Crete, Greece	F	220	232	200

Note: Origin refers to the location each specimen was landed or stranded (in the case of specimen 12). Abbreviations: F, female; FL, straight fork length; M, male; TL, total length; -, not available.

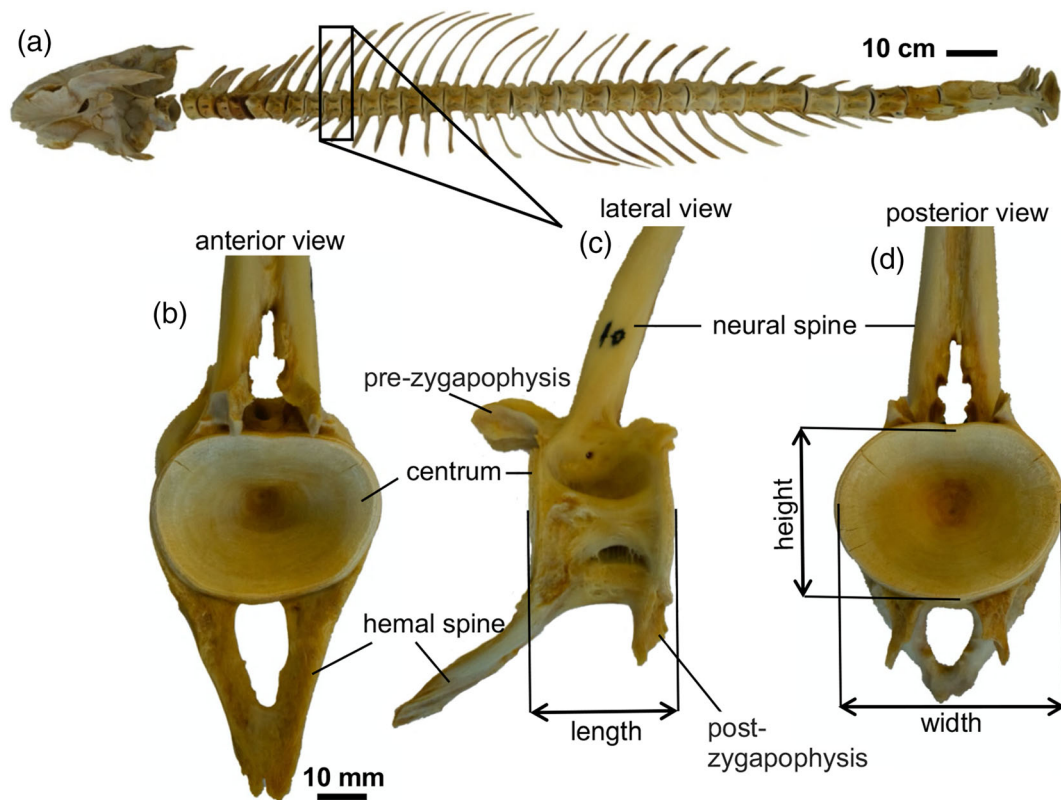


FIGURE 1 (a) Lateral view of a complete 200 cm straight fork length (FL) Atlantic bluefin tuna (*Thunnus thynnus*) skull and vertebral column showing all 39 vertebrae. V10 is shown as an example to illustrate anatomical features and measurements in (b) anterior view, (c) lateral view, and (d) posterior view. The scales (black bars) are approximations only [Colour figure can be viewed at wileyonlinelibrary.com]

comparing predicted values to reference values for each specimen using the statistical model with the greatest R^2 for each vertebrae rank and type. For each type, measurements were taken at random from one of the vertebrae, for each specimen.

Interspecific variation was inspected visually within types by projecting ALB and BET measurements onto a BFT power regression line fit for the vertebrae measurement with the greatest R^2 within each type by using `stat_smooth` (`method = nls`, `formula = y ~ a*x^b`) in the `ggplot2` package (Wickham, 2011) in R. Independent t tests were performed in R to test for differences between the left- versus right-sided centrum length measurements and anterior versus posterior centrum height and width measurements.

3 | RESULTS

All except 4 or 5 (V19–22/23) of 39 BFT reference vertebrae could be distinguished by their morphological features (Appendix S2). The discrepancy at V19–V22/23 was caused by a transverse foramen on V23 not being consistently present among all specimens. Nonetheless, our observations suggest that when spines are excessively damaged by taphonomic processes, it will be too challenging to identify vertebral rank in most BFT vertebrae, except V1 and V36–39, which are especially unique (Appendix S2). We described six vertebral types

which can be differentiated from each other by morphological features (Appendix S1, Table S3). Note that V23, V30, and V31 are present in multiple types because they sometimes exhibit a transverse foramen (see Appendix S2 details on which to select). Differences in standard deviation were found between measurements on vertebrae grouped into types. This should influence decisions on which measurement should be selected for size reconstructions so that error can be minimized when using types. Variation between vertebral measurements within types was generally acceptable at $\leq 5\%$ but was higher in the vertebrae type V33–35 (Table S3). Though, it is likely researchers can identify rank for V33–35 in most cases due to their distinctive morphological features (Appendix S2).

Power regression models for vertebrae identifiable to rank and each of the types reliably described the data where R^2 values >0.98 and >0.97 were reported, respectively (Tables S2 and S3). RSE correlated with R^2 values in all cases. Variations in model fit for each vertebrae rank or type were evident between vertebrae dimensions, though for each vertebral rank or type at least one high scoring model (>0.97) was identified (Tables S2 and S3).

Estimated FL values calculated using the reference dataset deviated from their true reference FL value at a mean range between -9.6% and 6.8% across ranked vertebrae in reference specimens >30 cm. Estimations on the single BFT reference specimen <30 cm deviated to a greater extent (range 2.3% to 21.4%). A

similar pattern was observed for types across all individuals >30 cm (mean range -7.0% to 3.2%) and for the <30 cm BFT (range -10.5% to 18.8%) (Figure 2). There was no correlation between deviation and vertebra type nor notable difference in deviation between reference and predicted values for each *Thunnus* species (Table 1; Figure 2).

Vertebral measurements of BET and ALB fit the BFT power regression line well for each type, falling within the variation observed between BFT reference specimens (Figure S1). Differences between posterior and anterior height were not significant ($p = 0.676$, $t[65] = 0.421$), but percentage differences were greater in some vertebrae than others (V6–32: mean 0.9% , range -0.1% to 3.7% , V2–3 and V33–36: range -14.3% to 0.1%). No significant differences were observed between posterior and anterior width ($p = 0.799$, $t[65] = 0.256$), but again, percentage differences were greater in some vertebrae than others (V6–32: mean 0.4% , range -4.8% to 4.1% , V2–3 and V33–36: range -11.1% to 11.0%). No significant differences were found between length measurements on the left and right side

of vertebrae centra ($p = 0.859$, $t[66] = 0.179$), and percentage differences were small (mean 0.88% , range 0.2% to 3.6%).

4 | DISCUSSION

In theory, all except four or five (i.e., V19–22/23) BFT vertebrae can be identified to rank. However, our observations suggest that in an archeological context, poor preservation will hinder rank identification. Poorly preserved vertebrae could, however, be identified to type, and in some cases, for example, V1 and V36–39, types should not be needed when vertebrae are especially unique (Appendix S2). It is important for researchers to be able to utilize all vertebrae for BFT size estimations since recoveries of BFT vertebrae are usually few, articulated vertebrae are rare, and recovered BFT vertebrae often vary significantly in rank depending upon their archeological context (Andrews et al., 2022). Seldom can all vertebrae be used for archeological size estimations of fishes. One good example is another large

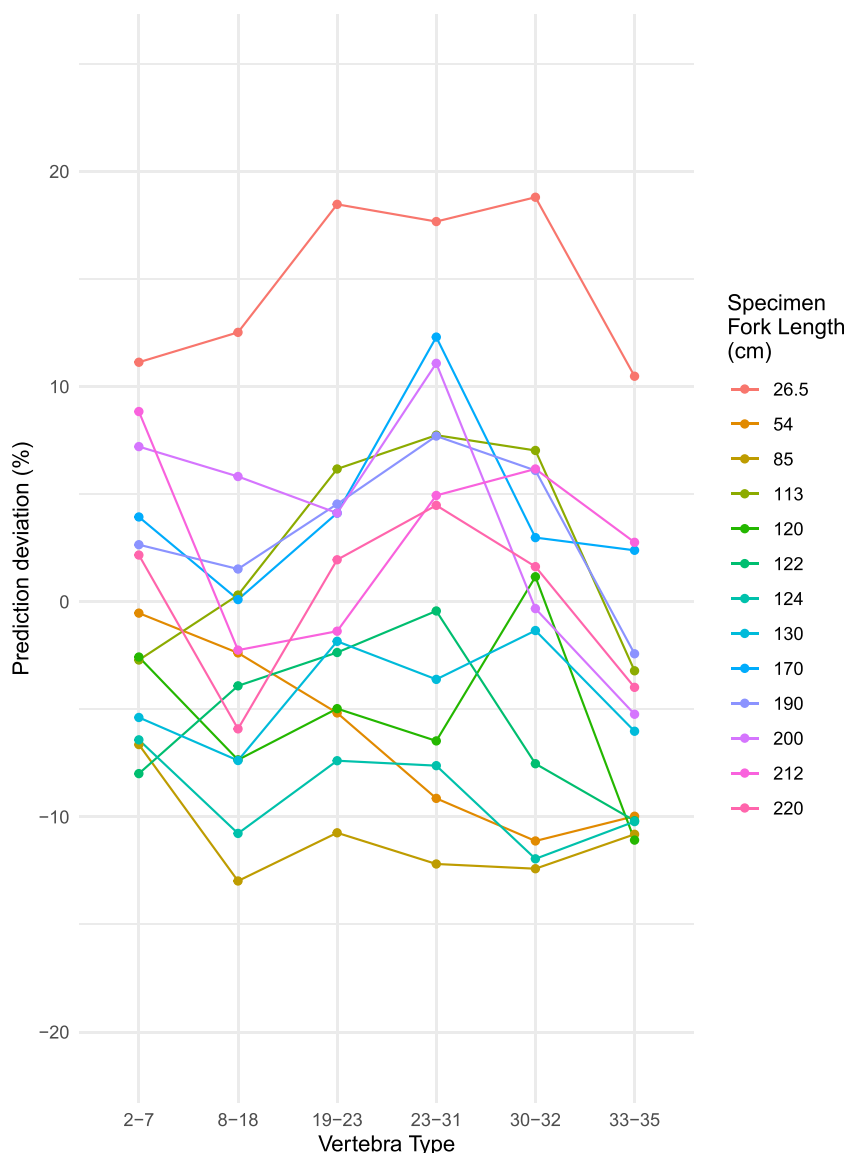


FIGURE 2 Deviation between the estimated and true reference straight fork length (cm) values for each reference specimen, using types. The best performing model was applied to each type as judged from Table S2 [Colour figure can be viewed at wileyonlinelibrary.com]

species, meager (*Argyrosomus regius*; Gabriel et al., 2012). Studies on the majority of other fishes must necessarily use particular vertebrae or sections of vertebral columns (Jelu et al., 2021; Marrast & Béarez, 2019; Martínez-Polanco & Béarez, 2020; Rurua et al., 2020). Clearly, the extent to which researchers will be able to identify rank or type in BFT will depend on the preservation of vertebrae. Despite obvious challenges, our methods account for the degree of taphonomic damage expected in the majority of archeological BFT recovered (as summarized in Andrews et al., 2022). Moreover, if vertebrae cannot be identified into one of the types described here, their size ought not to be estimated since vertebrae centra are thus likely too damaged for accurate measurements.

To understand how reliable our method is, and thus how readily interpretations can be drawn from these size estimations, it would be useful to compare the accuracy of our equations with those published. Since the majority of studies have not reported prediction error, that is, difference between actual and predicted values (sometimes called back-calculations), it is challenging to do this. Some studies (e.g., Desse & Desse-Berset, 1996; Jelu et al., 2021; Lidour et al., 2018) have only reported R^2 values, to which our R^2 values of >0.97 and >0.98 compare favorably. Others (Gabriel et al., 2012; Marrast & Béarez, 2019; Martínez-Polanco & Béarez, 2020; Rurua et al., 2020; Thieren et al., 2012) report standard error of estimate (SEE) values without defining how they are calculated, which limits comparisons with our RSE values. In any case, R^2 and standard error values are prone to be skewed if sampling is uneven across a given size range and if error is not normally distributed.

Similar to the current study, Thieren et al. (2012) calculated prediction error, reporting that the majority of their best-fitting equations for each element estimated fish length to an error of $\leq 10\%$ for $\sim 80\%$ of reference specimens, which is congruent with our findings for BFT. Such levels of variation are expected in BFT. Even early biological studies (e.g., Rodríguez-Roda, 1964) noted this when comparing V35 radius with FL. Our estimates showed that no one element, dimension, or section of the vertebral column is free from this potential source of bias. Moreover, as Lernau (2016) states, archeological size estimations are approximations only, and error margins of at least 10% can be expected. This degree of error will limit some studies interested in detecting fine-scale differences, but assuming this is a component of all archeological estimation methods, it has not limited studies in estimating gear types and target sizes (Blevis et al., 2021; Gabriel et al., 2012; Greenspan, 1998; Lernau, 2016; Owen & Merrick, 1994), how size cohorts were distributed spatially (Sanchez, 2020), or potential shifts in size structure over time (Barrett, 2019; Maschner et al., 2008; Plank et al., 2018). Our results suggest that interspecific variation (differences between *Thunnus* species) in vertebra-FL relationships is small. It might therefore be possible for future studies to apply our methods to suspected BET and ALB, which is useful since their distributions overlap with BFT (Pérez Bielsa et al., 2021), and morphologically, their vertebrae are indistinguishable.

It is acknowledged that using such few reference specimens (compared to usually around 20–70 individuals in other species; Jelu

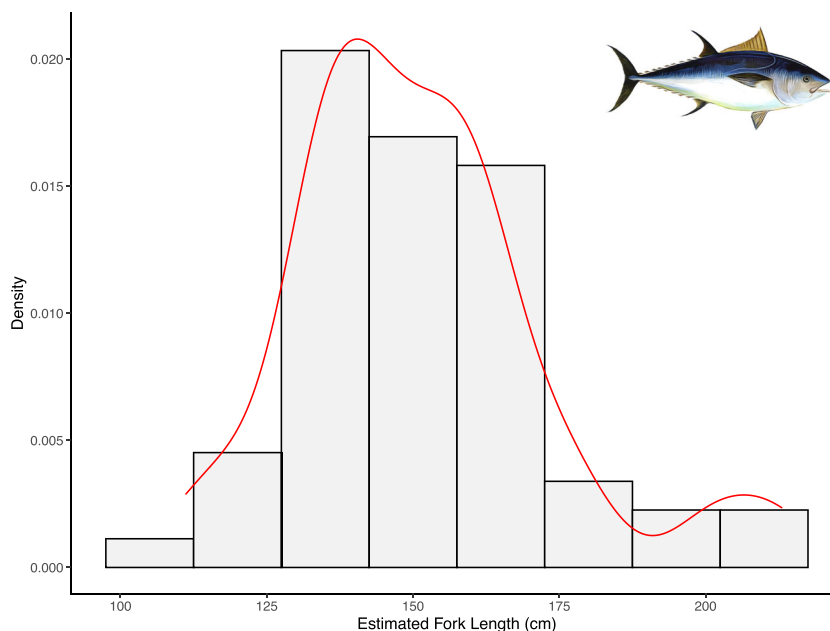
et al., 2021; Marrast & Béarez, 2019; Thieren et al., 2012) may underestimate error in the current study. It is possible that the full extent of intraspecific variation might not have been observed and, therefore, caution should be taken in that the prediction error observed herein should be interpreted as an absolute minimum upon which further studies with greater sample sizes should elaborate on. However, because our reference specimens originated from different locations and years, including a range of sizes, and sister-species, a good degree of intraspecific variation is probably present in our reference dataset (see Gabriel et al., 2012). The need to extrapolate from the BFT regression models might be an issue (Lernau & Ben-Horin, 2016), despite that reference specimens covered a wide size range (26.5–220 cm FL), large BFT reference specimens were missing. BFT of ~ 300 cm might be occasionally recovered in archeological assemblages, and these would fall outside of the regression, which may affect the accuracy of estimations on very large specimens. In any case, a 10% error margin should be applied for all estimations >50 cm FL produced using these equations. Applying this error to very large specimens especially may provide more confidence in extrapolated estimates. According to our prediction accuracy, this error margin should be increased to 20% for BFT estimated <50 cm FL using our methods. Nonetheless, the proportion of this juvenile size class is expected to be small since BFT are ~ 50 cm FL at age 2 (Santamaria et al., 2009), and historical fishing was likely to have targeted spawning migrations (García Vargas & Florido del Corral, 2010).

It is cautioned that despite not being significant, if the anterior surface (instead of posterior) vertebral measurements, or the shorter side (instead of the longer side) of vertebral length measurements are used, estimation accuracy is expected to decrease. This applies also if one of the poorer scoring models for each vertebrae rank or type is used. This error is notwithstanding user error and biases from using archeological bones that, even in the best cases of preservation, will be damaged and likely affect the accuracy of measurements.

5 | APPLICATION OF THE METHOD IN THE FIELD: A CASE STUDY

Fifty-nine BFT vertebrae recovered from a second century BCE layer at Punta Camarinal, Andalusia, Spain, were studied to estimate length. Punta Camarinal is a refuse dump (midden) site at the rear of a beach adjacent to the Roman-era city and salting factories of Baelo Claudia (González et al., 2006; Morales-Muniz & Roselló-Izquierdo, 2007). This site is unique in being one of the few BFT midden sites located to date. This is important because large BFT are seldom recovered in settlements and salting factories where most excavations have focused on, probably because processing was more practical at the shore (Andrews et al., 2022). Midden sites might therefore provide a more representative sample of BFT fishing in any given region or period. Punta Camarinal is one of many sites in the key location of the Strait of Gibraltar where the spawning (and return) migrations of BFT can be intercepted annually between April and October. At this location and period, fishing for BFT is theorized to have been conducted

FIGURE 3 Density curve and histogram of estimated FL (cm) for 59 archeological BFT vertebrae recovered from a second century BCE layer at Punta Camarinal, Baelo Claudia (Andalusia, Spain). Each histogram size class is 15 cm wide [Colour figure can be viewed at wileyonlinelibrary.com]



by nets, specifically the *Almadra de tiro* (beach seine tuna trap) method (García Vargas & Florido del Corral, 2010).

Morphological features were studied for each of the vertebrae following Appendix S2. Vertebrae were measured as depicted in Section 2 and Figure 1. The vertebrae recovered from the second century BCE context of Punta Camarinal were estimated to represent BFT between 111 and 213 cm FL, with most specimens at ~150 cm FL (Table S4; Figure 3). Vertebrae were well preserved and could be identified to rank in 55 out of 59 cases. In four cases, types were required to perform the estimations. Preservation was also sufficient that the vertebral dimension with the best power model fit could be applied to all but two of the vertebrae.

The length estimates suggest that Roman-era fisheries at Punta Camarinal would have mainly targeted mature (age ~4+) BFT migrating to and from Mediterranean spawning sites. As is the case with other schooling fishes, BFT associate with fish of equal size when migrating (Mather et al., 1995). Those recorded here reflect several cohorts, which evidence fishing in several different episodes. This might suggest that fixed *Almadras* (weighted to the seabed) were used to capture the various cohorts, as is suspected but not currently shown for the Roman era (Andrews et al., 2022; García Vargas & Florido del Corral, 2010). This hints at a more complex fishing scenario than hitherto postulated, an issue in need of further exploration (Morales-Muniz & Roselló-Izquierdo, 2007).

6 | CONCLUSION

BFT historical size data have utility to inform on a variety of ecological and anthropological research questions. Archeological BFT vertebrae can be readily identified to type, but rank identifications might prove challenging. In any case, regression equations were

defined for each BFT type and rank. The regression models appear to estimate fork length within error ranges of approximately $\pm 10\%$, in line with expectations for archeological size estimations. This method can be readily applied by researchers with little experience, according to its simplicity, which is aided by the supporting information (Appendix S2) and online calculator. It is acknowledged that in cases where vertebrae are excessively damaged, even type identifications might not be achieved and that the reliability of the methods might be improved by further studies with larger reference sample sizes.

ACKNOWLEDGMENTS

Antonio Di Natale is thanked for his advice on modern length-weight metrics, as is Corrado Piccinetti for the acquisition of one of the reference specimens. We are grateful for the comments of three anonymous reviewers, which improved the quality of this manuscript. This work is a contribution to the MSCA SeaChanges ITN and was funded by EU Horizon 2020 (H2020 Marie Skłodowska-Curie Actions, Grant Number: 813383).

CONFLICT OF INTEREST

No conflict of interest exists related the funding of this work.

DATA AVAILABILITY STATEMENT

Raw reference measurement data are uploaded as supporting information.

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How to cite this article: Andrews, A. J., Mylona, D., Rivera-Charún, L., Winter, R., Onar, V., Siddiq, A. B., Tinti, F., & Morales-Muniz, A. (2022). Length estimation of Atlantic bluefin tuna (*Thunnus thynnus*) using vertebrae. *International Journal of Osteoarchaeology*, 1–9. <https://doi.org/10.1002/oa.3092>