Climate and human impacts on key marine fauna of the Mediterranean Sea during the pre-industrial period

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ABSTRACT

Climate changes and human activities have impacted the Mediterranean ecosystem for thousands of years, but the available quantitative evidence is incomplete, hindering a detailed assessment of the marine ecosystem´s baseline state and resources. To disentangle

these impacts, we investigated changes in the distribution, abundance and body size of commercially important species of marine mammals, fishes, and molluscs over the last 130,000 (130 ka) years until the Industrial Revolution (1850) in three Mediterranean sub-regions: Western, Eastern and Adriatic. We identified and integrated quantitative data available from the literature on two marine mammals, thirteen fish and three molluscs, revealing consistent and significant climatic and anthropogenic impacts on three species: the banded-dye murex, the Atlantic bluefin tuna and the gilthead sea bream. Climate change, particularly temperature changes, was the most important factor influencing the past abundance and body size of Atlantic bluefin tuna, while sub-regional differences in the stable isotopic composition of archaeological skeletal remains reflected shifts in the system's productivity. Human activities, particularly overexploitation, impacted the abundance of both banded-dye murex and Atlantic bluefin tuna, as well as the body size of gilthead sea bream and Atlantic bluefin tuna. Our results highlight the significance of studying the relationships between climate, human activities, and marine resources in this large marine ecosystem before the Industrial Revolution and showcases the relevance of integrating past quantitative data with contemporary data to reconstruct ecological baselines and obtain longer and more comprehensive time series of ecosystem change.

1. INTRODUCTION

Marine ecosystems are among the world's most diverse and socio-economically valuable systems, providing invaluable ecosystem services (Millennium Ecosystem Assessment 2005; Halpern *et al.* 2008). The Mediterranean Sea is a marine ecosystem that has provided resources to human populations for millennia (Madariaga 1964; Mehvar *et al.* 2018) and

sheltered significant biodiversity (Coll *et al.* 2010). Evidence shows shellfish exploitation may have already started in Mediterranean coastal areas as early as the Lower Paleolithic (Lotze *et al.* 2006). For example, processed shells of marine molluscs have been recovered from Terra Amata (southern France), dating back to ~300 ka (De Lumley 1966). The exploitation of marine resources expanded over time, eventually evolving into extensive fisheries and trade networks for marine products as early as the Roman period (Lotze, Coll and Dunne 2011; Marzano 2013). Today, the Mediterranean Sea harbours 7.5% of the world's marine diversity, including several emblematic species such as turtles, marine mammals, and fish, among others (Coll *et al.* 2010), and it is considered the second-largest biodiversity hotspot globally (IUCN-MED 2009).

Climate change and human activities significantly impact the Mediterranean Sea, leading to important changes in marine biota (Lotze *et al.* 2006; Coll *et al.* 2010, 2012; Moullec *et al.* 2019). In recent decades, the Mediterranean Sea has experienced warming well exceeding the global average (Salat *et al.* 2019), which has profoundly affected marine ecosystems (Smale *et al.* 2019; Trisos, Merow and Pigot 2020), altering species distributions and abundances (Garrabou *et al.* 2009; Ouled-Cheikh *et al.* 2022). Key human-related threats to marine ecosystems include habitat loss, degradation, and overexploitation of resources (Halpern *et al.* 2008; Coll *et al.* 2010, 2012; Micheli *et al.* 2013), resulting in changes in species productivity, fitness, and distribution (Pauly *et al.* 1998; Howarth *et al.* 2014).

Most ecological research focuses on short-term data from the past century (Jackson 1997; Dayton *et al.* 1998), whereas geological, archaeological, and historical data provide long-term information that is essential for fully understanding how marine ecosystems and species responded to changes over time (Jackson *et al.* 2001; Lotze *et al.* 2006; Fortibuoni et

al. 2010; Agiadi *et al.* 2024). Marine organisms and their remains are used as proxies for reconstructing paleoclimatic and paleoenvironmental conditions (e.g., Richardson 2001; Wanamaker *et al.* 2008; Sisma-Ventura *et al.* 2019) and past human subsistence strategies (e.g., Bosch *et al.* 2018; Branscombe, Bosch and Miracle 2021) in decadal to million-year timescales. Additionally, recent studies have revealed the high potential of geohistorical data for understanding changes in marine ecosystem structure and processes in the past, and how human-induced and environmental changes impacted marine ecosystems over the long term (e.g., Calkin, Wiles and Barclay 2001; Lotze, Coll and Dunne 2011; Agiadi *et al.* 2024).

The present study aims to understand how climatic changes and human activities impacted commercially important species in the Mediterranean Sea over the last 130 ka. We use the information provided by Leal, Agiadi and Bas (2025), who conducted a systematic review of marine mammals, fishes and molluscs in this region. We hypothesise that climatic changes, in particular temperature oscillations associated with warm and cold periods of the Earth's history, affected the targeted marine species across the Mediterranean Sea throughout time. In addition, human activities affected this marine fauna through periods of extensive exploitation across the Mediterranean over the last 130ka. Our ultimate goal is to offer insights to aid in the management and conservation efforts of Mediterranean marine communities and ecosystems, learning from past evidence.

2. MATERIALS AND METHODS

2.1 Study area and species data collection

The Mediterranean Sea is a semi-enclosed basin extending over 3 million km^2 with a maximum depth of approximately 5,300 m (Robinson and Golnaraghi 1994). We divided the

study area into three different sub-regions bounded by the straits of Sicily and Otranto: the Western and Eastern Mediterranean, and the Adriatic Sea (Millot and Taupier-Letage 2005; Rio *et al.* 2007; Robinson *et al.* 2009). The Marmara Sea and the Black Sea were included in the Eastern Mediterranean analyses. We used data on eighteen commercially relevant species of marine mammals, fish and molluscs gathered by Leal, Agiadi and Bas (2025) (Table 1).

Table 1 – Species analysed in this work.

Scientific Name	Common Name	Functional Group
Delphinus delphis Linnaeus, 1758	Common Dolphin	Marine Mammal
Monachus monachus (Hermann, 1779)	Mediterranean monk seal	Marine Mammal
Engraulis encrasicolus (Linnaeus, 1758)	European anchovy	Fish
Sardina pilchardus (Walbaum, 1792)	European pilchard	Fish
Sardinella aurita Valenciennes, 1847	Round sardinella	Fish
Sardinella maderensis (Lowe, 1838)	Madeiran sardinella	Fish
Sparus aurata Linnaeus, 1758	Gilthead sea bream	Fish
Diplodus annularis (Linnaeus, 1758)	Annular sea bream	Fish
Diplodus bellottii (Steindachner, 1882)	Senegal sea bream	Fish
Diplodus cervinus (Lowe, 1838)	Zebra sea bream	Fish
Diplodus levantinus Fricke, Golani & Appelbaum-Golani, 2016	-	Fish
Diplodus puntazzo (Walbaum, 1792)	Sharpsnout sea bream	Fish
Diplodus sargus (Linnaeus, 1758)	White sea bream	Fish
Diplodus vulgaris (Geoffroy Saint-Hilaire, 1817)	Common two-banded sea bream	Fish
Thunnus thynnus (Linnaeus, 1758)	Atlantic bluefin tuna	Fish
Ostrea edulis Linnaeus, 1758	European flat oyster	Mollusc
Hexaplex trunculus (Linnaeus, 1758)	Banded dye-murex	Mollusc
Phorcus turbinatus (Born, 1778)	Turbinate monodont	Mollusc

From the available records, we analysed data on species: 1) presence and abundance, as reflected in Number of Identified Specimens – NISP (Grayson 1984) and Minimum Number of Individuals – MNI (Lyman 1994); 2) catches; 3) body size (as reflected in fish length and molluscs basal diameter), and 4) stable isotopic composition of fish bones (δ^{13}C and δ^{15}N).

The study conducted by Leal, Agiadi and Bas (2025) revealed important available data on Atlantic bluefin tuna catches from Italian tuna traps spanning between 1700 and 1936 (Addis *et al.* 2008; Longo and Clark 2012; Polanco-Martínez *et al.* 2018). Using long-term fluctuations in catches as a proxy for abundance (Ravier 2001), we analysed these data to detect temporal and spatial patterns in Atlantic bluefin tuna abundance in the Mediterranean during the study period. To place these patterns in the paleoclimatic context, we obtained Sea Surface Temperature (SST) data for the same period (Jalali *et al.* 2016). Finally, we investigated the relationships between these catch patterns, major human civilisation events, and advancements in fisheries.

Furthermore, we analysed δ^{13}C and δ^{15}N data extracted from bones of Atlantic bluefin tuna (Andrews *et al.* 2023b, 2023c) and the gilthead sea bream (Fuller *et al.* 2020). No corrections were applied to stable isotope values, as data for each species were produced by the same methodology.

2.2 Data Analyses

Species with the most data over time in each sub-region were selected, and data were categorised into four geological periods: Late Pleistocene (131,949 - 11,650 years BP; Head *et al.* 2021), and Early (11,650 – 8,186 years BP; Stuiver and Reimer 1986)), Middle (8,186 – 4,200 years BP; Stuiver and Reimer 1986)) and Late Holocene (4,200 – 0 years BP; Stuiver

and Reimer 1986)). The temporal coverage of each climatic and cultural event is displayed in Table S1. Normality (Shapiro-Wilk test) and homoscedasticity (Levene's test, *car* package; Fox and Weisberg 2019) were assessed for all variables. For NISP, MNI, body size, and stable isotopic compositions, non-parametric tests (data non-normally distributed) were used: Mann-Whitney *U* for two-group comparisons and Kruskal-Wallis for more than two-group comparisons. The post-hoc pairwise Wilcox test was subsequently used. For the gilthead sea bream (body size and isotopic information) and turbinate monodont's body size, parametric tests (ANOVA or Welch ANOVA) were conducted using the post-hoc Tukey's HSD tests. For catch data, monotonic trends were identified using the Mann-Kendall test (*trend* package; Pohlert 2023). Data were divided into intervals using the Jenks natural breaks classification method (Jenks 1977) (*classInt* package in R; Bivand 2023), and the detected differences between periods were assessed using Kruskal-Wallis and the pairwise Wilcox test. A *p-value* threshold of ≤0.05 was applied when comparing two groups, with the threshold adjusted using the Bonferroni correction. Maps were created using QGIS 3.34.3 (QGIS.org) with bathymetry data from GEBCO (GEBCO Compilation Group 2022). All statistical analyses were performed in R version 4.4.1 (R Core Team 2023).

3. RESULTS

The literature review did not provide results for the Senegal seabream, Zebra seabream, *Diplodus levantinus*, and the Sharpsnout seabream. Most data came from the Western and Eastern Mediterranean, particularly during the Holocene period (11,650-0 years BP; Stuiver and Reimer 1986). In the present work, we presented the statistically significant results of species analyses, for more detailed information, see supplementary material S2 to S6.

3.1 Presence and abundance of targeted species

The NISP data was found for most species, except the annular sea bream, European pilchard, round sardinella, and Madeiran sardinella. Fish presented the most data, followed by molluscs and marine mammals. The data among functional groups were distributed between 100,000–500 years BP, with most samples coming from the Western and Eastern Mediterranean, and few samples from the Adriatic Sea. The analyses performed revealed no significant differences between periods (supplementary material S3).

The MNI data, primarily distributed between 100,000–17,000 years BP, were available for *Diplodus spp.,* banded-dye murex, Mediterranean monk seal, European flat oyster, turbinate monodont and the gilthead sea bream (Figure S3.4). The mollusc turbinate monodont and the banded-dye murex had the most data across periods. Data for the turbinate monodont were available for both the Western and the Eastern Mediterranean, and no significant differences were detected between periods (Figures S3.4.1B and S3.4.2B) in both areas. For the banded-dye murex, significant differences were observed between periods in the Western Mediterranean (H_2 = 15.792; p = 0.0004, Figure 1A), particularly between the Early and Late Holocene (p = 0.0013; Figure 1B, Table S2.1).

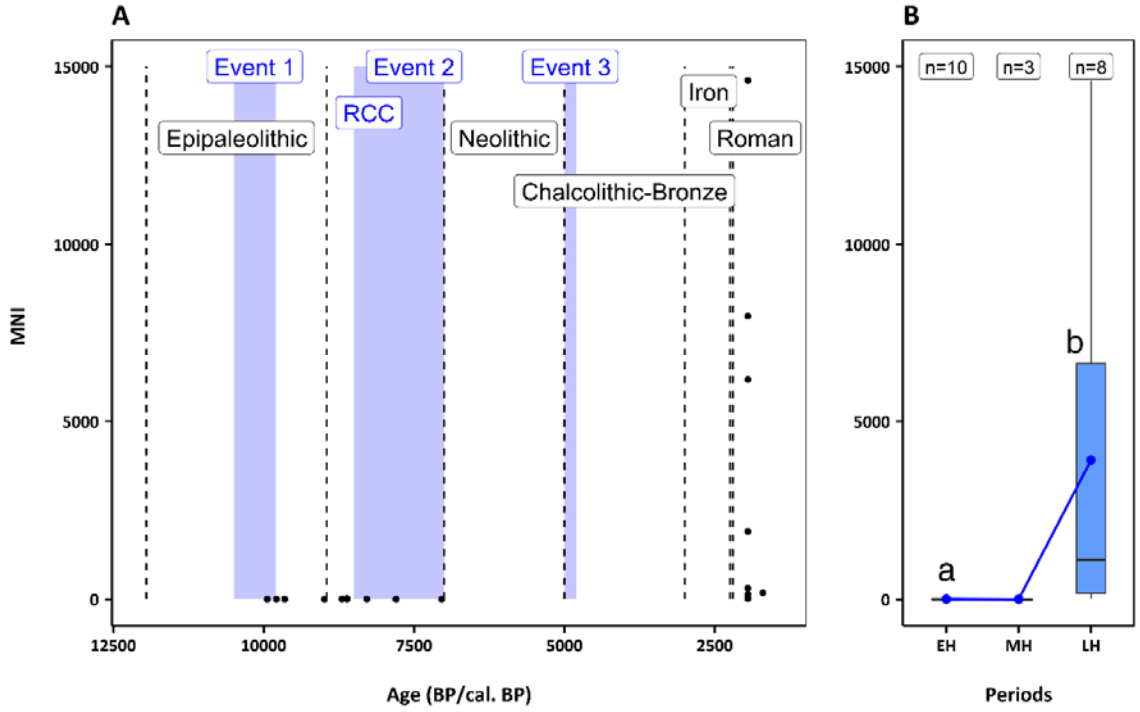


Figure 1 - Distribution of MNI (Minimum Number of Individuals) data for banded-dye murex in the Western Mediterranean. (A) Temporal distribution of records, major climatic events (purple rectangles) and human cultural periods (delimited using black dashed lines); (B) Boxplots of MNI data for each geological period: EH (Early Holocene), MH (Middle Holocene), and LH (Late Holocene). Blue dots represent mean values and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

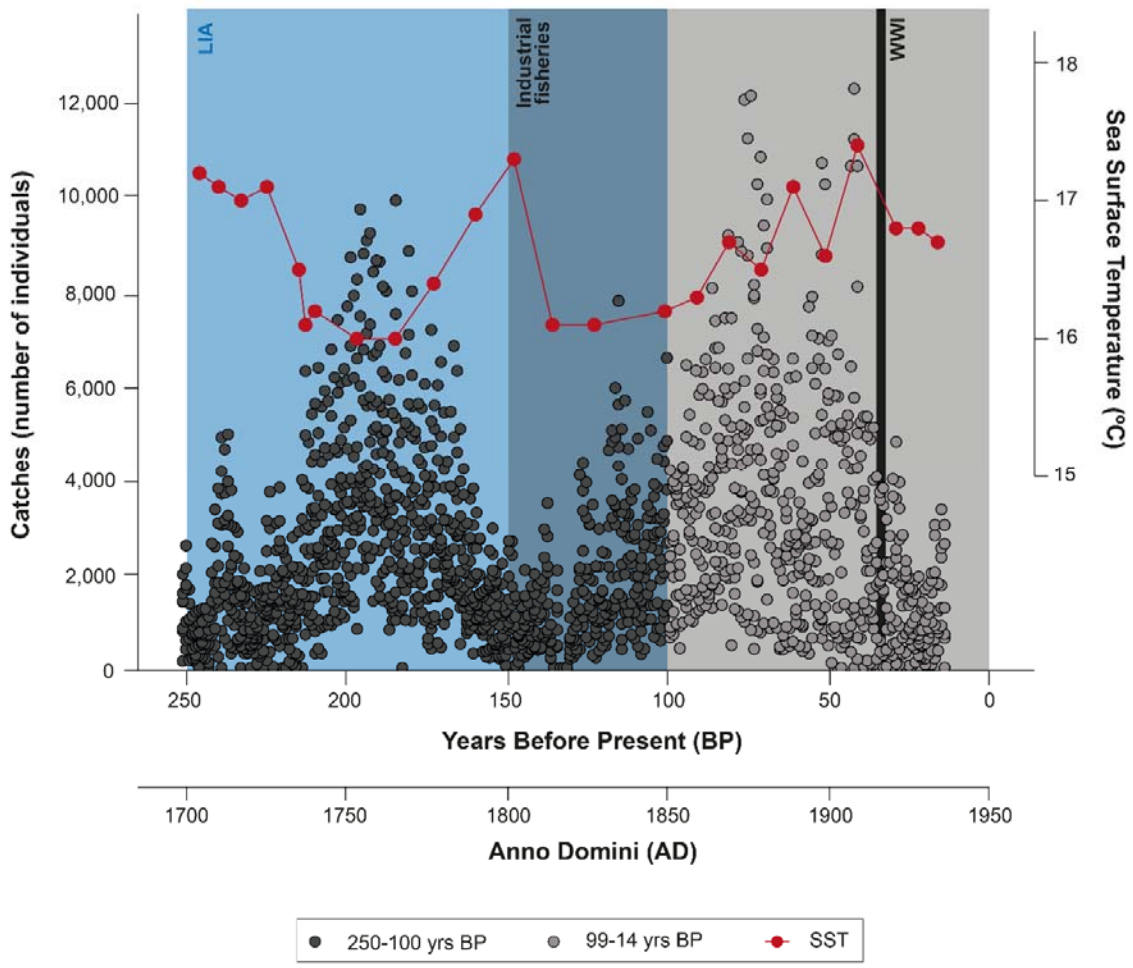
3.2 Catch records

Catch data were available only for the Atlantic bluefin tuna, ranging from zero to approximately 12,500 individuals caught between 250 and 14 years BP (1700-1936 AD; Figure 2). Two peaks were observed: the first (~10,000 individuals) occurred around 200 years BP (~1750 AD) during the Little Ice Age, and the second (~12,000 individuals) between 75–45 years BP (1875–1905 AD), after the onset of industrial fisheries. Declines in catches

175 were evident (S = −3.98 e^{5}; Kendall's tau coefficient = −2.39 e^{-1}; $p < 2.2\ e^{-16}$), with significant

176 differences between some of the periods (H_5 = 407.55; $p < 2.2e^{-16}$; Table S2.2 - S2.2.1, Figure

177 S4).



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179 **Figure 2** – Atlantic Bluefin Tuna catch records between 250 and 14 years BP (1700–1936 AD), from

180 tuna traps in the Western Mediterranean Sea. The black points refer to data collected between 250

181 and 100 years BP (1700–1850 AD), and the light grey points indicate the catch records between 99

182 and 14 years BP (1851–1936 AD). The red points indicate reconstructed SST records from the Gulf of

183 Lions (France) (data from Jalali *et al.* 2016). The light blue rectangle refers to the LIA (Little Ice Age)

184 period and the light grey rectangle refers to the onset of Industrial fisheries, with minor

185 modifications made to tuna traps until the 1960s (Doumenge 1999), including WWI (World War I).

3. 3 Body size measures

We analysed Total Length (TL) data due to the limited availability of Standard Length (SL) measurements (Figures S5.1 and S5.2). The TL data were available for Atlantic bluefin tuna and gilthead sea bream. For the Atlantic bluefin tuna in the Western Mediterranean, we found significant differences between the Medieval Warm Period and the Little Ice Age ($t_{15.141}$ = 2.967; p = 0.01; Figure 3A, Table S2.3 and Figure S5.3). In the Eastern Mediterranean, significant differences in Atlantic bluefin tuna TL were observed between the period before (2,500–1,050 years BP) and during the Medieval Warm Period (1,050–650 years BP; W = 8; p = 0.01035) despite differences in sample sizes (Figure 3B, Table S2.3 and Figure S5.4).

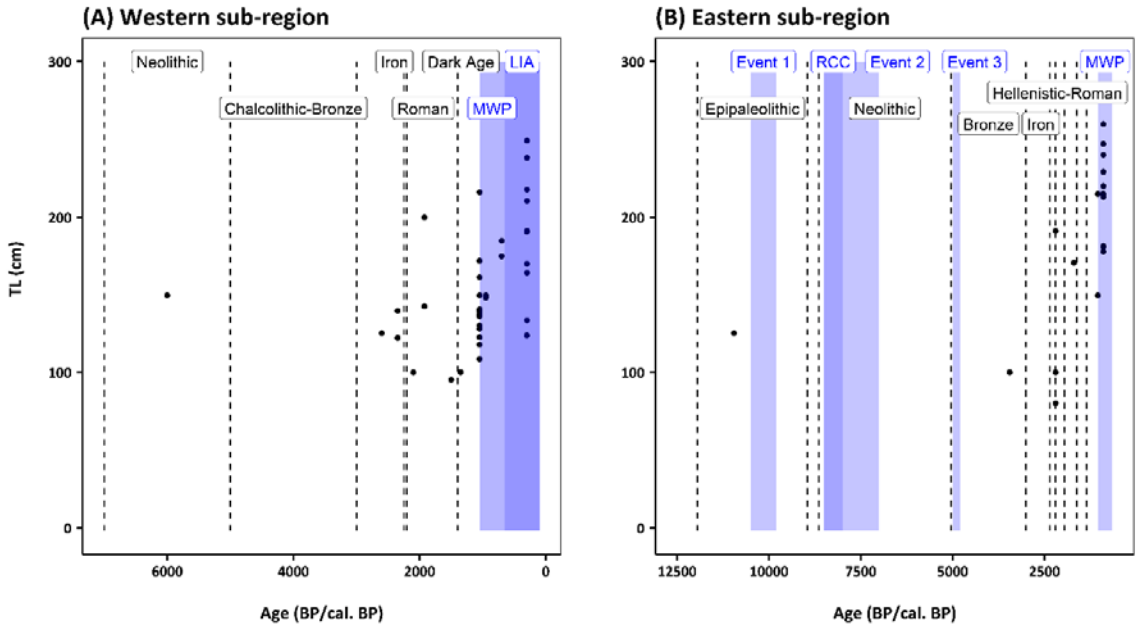

Figure 3 - Distribution of data for the TL (Total Length) of Atlantic bluefin tuna in the Western and Eastern Mediterranean. Temporal distribution of records, including major climatic events (purple

rectangles) and anthropogenic events (black dashed lines); (A) Temporal distribution of records for the Western Mediterranean; (B) Temporal distribution of records for the Eastern Mediterranean.

The TL data for gilthead sea bream were limited to the Eastern Mediterranean (Figure 4). Pairwise comparisons revealed significant differences in sea bream TL between the Early and Late Holocene (p = 0.0061), the Middle and Late Holocene (p = 0.001; Figure 4B), and between the Bronze and Iron Ages and the Byzantine Period (H_2 = 8.501; p = 0.014, Table S2.3 and Figure S5.5).

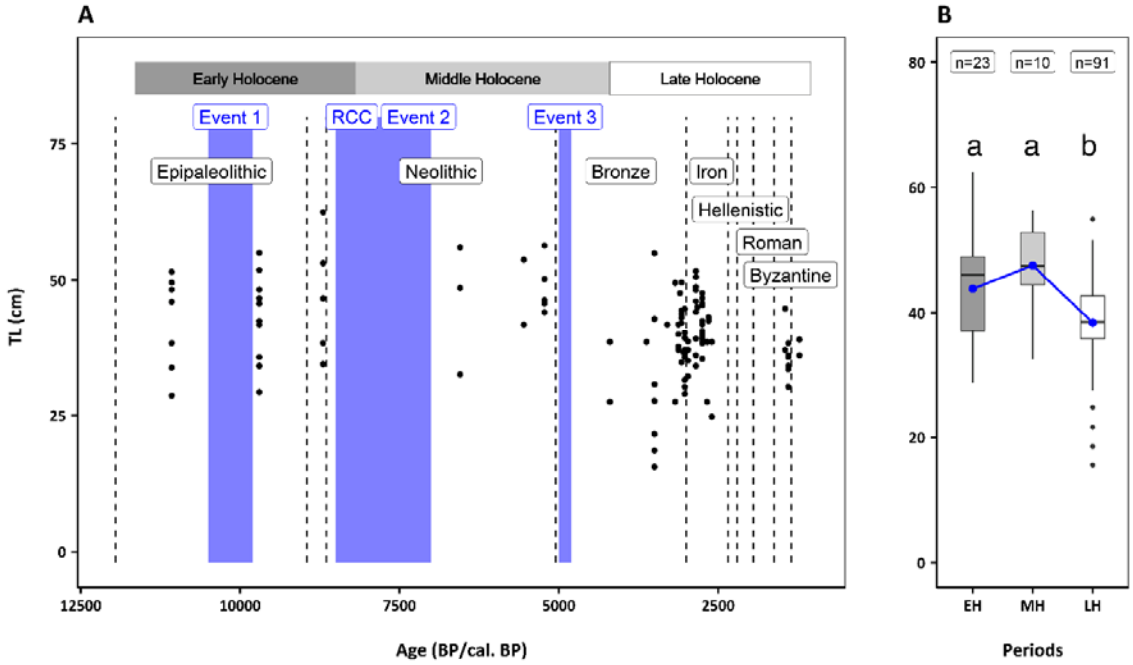

Figure 4 - Distribution of TL (Total Length) data for gilthead sea bream in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of TL data for each geological period: EH (Early Holocene), MH (Middle Holocene), and LH (Late Holocene). Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

The Basal diameter (BD) data for the turbinate monodont were available only for the Eastern Mediterranean, specifically mean and maximum values (Table S2.4 and Figures S5.6 and S5.7). No significant differences were found between periods for both mean and maximum BD (F_{mean} = 2.021; p_{mean} = 0.195; F_{max} = 0.3701; p_{max} = 0.7767; Figures S5.6B and S5.7B, respectively).

3.4 Stable isotopic data

For the Atlantic bluefin tuna significant differences were observed between the Western and Eastern Mediterranean between 1,050-850 years BP (Medieval Warm Period) for both δ^{13}C (W = 1, p = 3.927 e^{-9}; Figure 5A, Table S2.5) and δ^{15}N (W = 16, p = 1.2 e^{-7}; Figure 5B, Table S2.5).

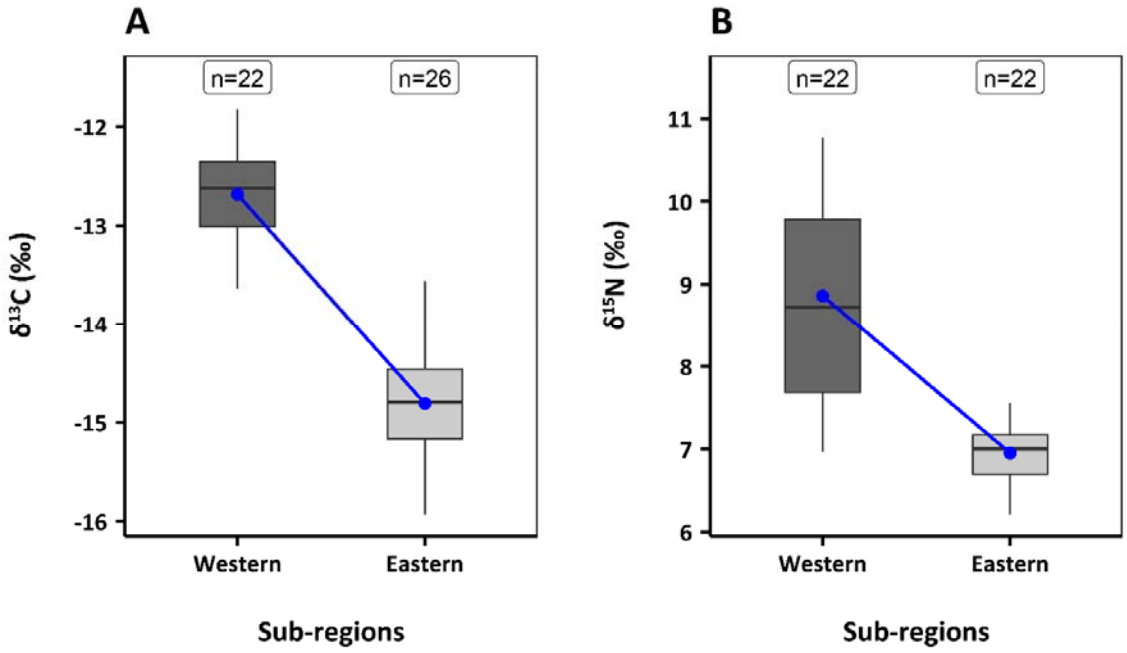

Figure 5 - Distribution of δ^{13}C and δ^{15}N data for Atlantic bluefin tuna in the Eastern and Western Mediterranean for 1,050–850 years BP. (A) Boxplots showing δ^{13}C values for the Eastern and

Western Mediterranean; (B) Boxplots showing $\delta^{15}N$ values for the same sub-regions. Blue dots represent mean values, and bars indicate standard deviation. The number of data samples (n) for each boxplot is shown above. See Figure S6.1 for complete isotopic data dispersion.

For the gilthead sea bream, a few $\delta^{13}C$ and $\delta^{15}N$ records were available covering the Bronze and Iron Ages (Figures S6.2A and S6.3A). Statistical analysis revealed no significant differences between geological periods for either stable isotope ($H_{\delta^{13}C}$ = 0.70028, $p_{\delta^{13}C}$ = 0.705; $F_{\delta^{15}N}$ = 2.344, $p_{\delta^{15}N}$ = 0.177, Table S2.5). However, $\delta^{15}N$ increased sharply from 4,199 to 3,625 years BP, followed by a decrease towards 2,675 years BP (Figure S5.3B).

4. DISCUSSION

Climate change and human activities have significantly impacted the Mediterranean Sea (Lotze *et al.* 2006; Coll *et al.* 2010; Moullec *et al.* 2019), highlighting the need to understand species' responses to these pressures in the past (Jackson *et al.* 2001). In this study, we compiled new information pointing to the importance of studying the impact of pre-industrial climate change and human activities on key marine fauna. Available data was found for banded-dye murex, Atlantic bluefin tuna, and gilthead sea bream, of the Mediterranean Sea. These species have been important for the Mediterranean ecosystem structure and functioning and crucial for sustaining the socioeconomic systems of the peri-Mediterranean countries for thousands of years.

Seawater temperature influences Atlantic bluefin tuna's growth, reproduction, mortality, and migration patterns (Pepin 1991; Graham and Dickson 2004). This highly migratory species moves between cold feeding waters like the North Atlantic Ocean (Mather *et al.*

253 1995; Block *et al.* 2001, 2005) and warm spawning areas such as the Mediterranean Sea
254 (Mather *et al.* 1995; Block *et al.* 2005; Rooker *et al.* 2006). The high number of catches in the
255 Western Mediterranean during the latter stages of the Little Ice Age (650–100 years BP;
256 Briffa 2000) may be linked to a decline in the SST. During this period, there may have been
257 changes in the species' migration patterns due to cooler and unstable meteorological
258 conditions (strong storm activity and cold, windy conditions, etc.), reducing the efficiency of
259 tuna fisheries (Ravier and Fromentin 2004; Ganzedo *et al.* 2016). Temperature also affects
260 plankton production and distribution (e.g., McGowan, Cayan and Dorman 1998; Beaugrand
261 *et al.* 2002) and thus food availability for both juvenile and adult tuna (Mather *et al.* 1995),
262 driving the spatiotemporal dynamics of tuna movements between the spawning and feeding
263 grounds (Ravier and Fromentin 2004).

264 Pleistocene-Holocene climatic variability may have also impacted the body size of tuna, as
265 seen for other species (Agiadi *et al.* 2023; Porz *et al.* 2024). Recent studies suggest stronger
266 consumer-driven control of food webs with warming (Allen, Gillooly and Brown 2005; López-
267 Urrutia *et al.* 2006), which enhances heterotroph abundance, strengthening consumer-
268 resource interactions (O'Connor 2009). This can benefit high trophic-level species (Archibald
269 *et al.* 2022), such as Atlantic bluefin tuna. Species from temperate ecosystems generally
270 have broader niche breadths, making them more adaptive (MacArthur 1972; Olesen and
271 Jordano 2002). The TL increase observed in this study may have been caused by this dietary
272 flexibility, combined with stronger consumer-resource interactions, allowing tuna to thrive
273 during past climatic fluctuations. This hypothesis is consistent with the study by Andrews *et*
274 *al.* (2023a), who observed increased juvenile growth between the 16th and 18th centuries in
275 the Mediterranean Sea, likely linked to warmer sea surface temperature and a positive
276 North Atlantic Oscillation phase.

277 The Mediterranean Sea is broadly oligotrophic with a persistent east-to-west gradient in
278 productivity (Coll *et al.* 2010). Historical data suggest reduced primary productivity in the
279 Eastern Mediterranean (e.g., Kuhnt *et al.* 2008) and higher productivity in the Western
280 Mediterranean (e.g., Incarbona *et al.* 2010). These productivity differences likely explain the
281 δ^{13}C and δ^{15}N variations of Atlantic bluefin tuna's bones from 1,050 to 850 years BP. The
282 δ^{13}C values are good indicators of primary production sources (Hobson, Piatt and Pitocchelli
283 1994; France 1995). Tissues presenting low-δ^{13}C values can be associated with species
284 inhabiting environments dominated by pelagic primary producers or enriched by terrestrial
285 organic matter over benthic carbon sources (Barnes and Jennings, Jon. T. Barry 2009;
286 Magozzi *et al.* 2017). The higher δ^{13}C values in the Western Mediterranean suggest that this
287 species may have used coastal waters in this area, while it might have used offshore areas in
288 the Eastern Mediterranean. This aligns with the use of Western waters for spawning (Oray
289 and Karakulak 2005; Alemany *et al.* 2010) and Eastern waters for offshore foraging,
290 potentially linked to opportunities for deep diving (Wilson and Block 2009; Olafsdottir *et al.*
291 2016) and/or reduced benthic-pelagic coupling (Magozzi *et al.* 2017). Similarly, δ^{15}N values,
292 which are used to estimate the trophic position in the food web (Sigman *et al.* 2009), were
293 higher in the Western Mediterranean, likely reflecting greater secondary productivity.

294 Despite its oligotrophy (Coll *et al.* 2010), Mediterranean coastal areas experience nutrient
295 enrichment through local factors such as wind conditions, currents, and fluvial discharges
296 (Zavatarelli *et al.* 1998; Bosc, Bricaud and Antoine 2004). These localised nutrient inputs,
297 combined with the generalist feeding strategy of Atlantic bluefin tuna (MacArthur 1972;
298 Olesen and Jordano 2002), may have facilitated its success in the West, while in the East the
299 more oligotrophic conditions may have led to more specialised diets. Nevertheless, a
300 previous study using long-term records from eastern Atlantic, Mediterranean and Black Sea

locations found no significant shifts in the trophic position of this species over the past millennia despite extensive modifications in marine ecosystems (Andrews *et al.* 2023c).

This study also highlights the impact of sustained exploitation on the abundance and body sizes of different species. The banded-dye murex was extensively harvested during the Late Holocene (4,200 years BP to the present day; Stuiver and Reimer 1986), particularly in the Roman Period (2,249-1,400 years BP; Roberts *et al.* 2011). This gastropod inhabits the intertidal zone (Bonanno *et al.* 2016), making it accessible to hunter-gatherers (e.g., Fernández-López De Pablo and Gabriel 2016) and later to civilisations that harvested it at an industrial scale (Michel and McGovern 1987; Oliver 2015). The Romans used this species, along with *Bolinus brandaris* and *Stramonita haemastoma* to produce Purple Dye, highlighting its economic significance (Oliver 2015).

The Atlantic bluefin tuna abundance seems to have also been influenced by industrial fisheries (Polanco-Martínez *et al.* 2018; this study). The most common method of capture was tuna traps (*tonnare* in Italian), which caught the fish near the shore where they spawned (Longo 2012), making it a sustainable fishery (De la Serna *et al.* 2012). With industrial fishing, *tonnare* were slowly modified with more robust materials (e.g., iron anchors, steel cables, etc.; Lentini 2001) and later replaced by modernised fishing gears, like purse-seiners and longlines (Joseph 2003). The 19th century, which roughly coincides with the increasing use of modernised gears, was marked by the starting decades of intense exploitation of tuna (Andrews *et al.* 2022). The high number of catches after the 19th century might reflect this slow transformation from a low-scale, sustainable fishery into a large-scale, unsustainable fishery. Generally, removing top predators may lead to changes in the food web structure through top-down control (Pauly *et al.* 1998; Scheffer, Carpenter and Young

2005), although the ecosystem impacts of these removals remain understudied. Similar processes are documented for sea otters, heavily hunted by Aboriginal Aleuts 2,500 years ago, that led to their population decline and an increase in the sea urchin population, resulting in deep changes to kelp forest ecosystems (Simenstad, Estes and Kenyon 1978; Jackson *et al.* 2001).

Our findings indicate that the overexploitation of Atlantic bluefin tuna and gilthead sea bream may have resulted in body size changes. Historical records show tuna catch declined in Spain between mid-16th and 18th centuries (Sarmiento 1757). Overexploitation in previous centuries of juveniles and seabed disturbances near tuna traps likely contributed to changes in tuna migration routes (García 2016). Andrews *et al.* (2023a) proposed that the increased growth in juveniles between the 16th and 21st centuries in the Mediterranean Sea was linked to fisheries-induced evolution. This process selects species traits (early maturation, increased reproductive output, and reduced growth post-maturation) that favour faster life histories through enhanced survival and the number of offspring of species subjugated to intensive fishing (Law 2000; Enberg *et al.* 2012). In contrast, the gilthead sea bream experienced overexploitation in the Late Holocene in the Eastern Mediterranean with a body size decrease (Guy *et al.* 2018; this study). This pattern of body size reduction also occurred with *Archosargus probatocephalus* due to long-term fishing activities (Guiry *et al.* 2021). These size reductions, driven by overfishing and size-selective gear, can have profound effects on trophic interactions within marine ecosystems (Shackell *et al.* 2010; Garcia *et al.* 2012).

It is necessary to be cautious when analysing our results due to some assumptions. The study is constrained towards economically relevant species, potentially overlooking other

key species. The lack of comprehensive data for the Adriatic Sea suggests gaps in earlier studies or unpublished data. Variations in data quality and standardisation (dating systems and body size measures) presented challenges in analysing data. The resolution needed to reconstruct past population sizes limited the assessment of the magnitude of change. Despite these limitations, our study provides important insights into how past environmental and human impacts have shaped species abundance, body size, and trophic ecology of key species in the Mediterranean Sea.

Conclusions

This work underscores the importance of studying the impact of pre-industrial climate change and human activities on Mediterranean species, focusing on abundance, body size, and trophic ecology. We show that the Atlantic bluefin tuna was likely affected by both factors, while the banded-dye murex and gilthead sea bream were mainly impacted by human exploitation. Understanding the history of marine ecosystems and species-specific responses to environmental and anthropogenic disturbances is essential to ensure the development of effective present and future environmental management strategies while supporting the implementation of targeted adaptive conservation measures.

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AUTHOR CONTRIBUTIONS

Daniela Leal: Conceptualisation, Data Curation, Methodology, Formal analysis, Writing - original draft, Funding acquisition. **Konstantina Agiadi:** Conceptualisation, Methodology, Writing - Review & Editing, Supervision. **Marta Coll:** Writing - Review & Editing. **Maria Bas:** Conceptualisation, Methodology, Writing - Review & Editing, Supervision.

DECLARATION OF INTERESTS

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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DATA AVAILABILITY

All data produced for this work have been made available within the main manuscript and in the supplementary material.

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Supplementary material

S1. List of climatic and cultural events

Table S1 – List of climatic and cultural events, with corresponding names, time intervals and references.

Type of Event	Name	Interval (years BP)	Reference
Climatic	Last Glacial Maximum (LGM)	32,000 - 21,000	Lionello *et al.* (2023)
	Younger Dryas	14,749 - 13,646	Benjamin *et al.* (2017)
	Holocene 1st cooling event (Event 1)	10,500 - 9,800	Lionello *et al.* (2023)
	Rapid Climate Change (RCC)	8,499 - 7,999	Krauß *et al.* (2018)
	Holocene 2nd cooling event (Event 2)	8,000 - 7,000	Lionello *et al.* (2023)
	Holocene 3rd cooling event (Event 3)	5,000 - 4,800	Lionello *et al.* (2023)
	Medieval Warm Period (MWP)	1,050 - 650	Briffa (2000)
	Little Ice Age (LIA)	650 - 100	Briffa (2000)
Cultural	Late Paleolithic	51,949 - 21,949	Stiner and Kuhn (2006)
	Mesolithic	21,949 - 11,949	Stiner and Kuhn (2006)
	Epipaleolithic	11,949 - 8,949	Tortosa (1995); Sánchez (2007)
	Neolithic (Eastern Mediterranean)	8,649 - 5,049	Andreou *et al.* (1996)
	Neolithic (Western Mediterranean)	7,000 - 5,000	Stuiver and Reimer (1986)
	Bronze Age (Eastern Mediterranean)	5,049 - 2,999	Andreou *et al.* (1996)
	Chalcolithic-Bronze (Western Mediterranean)	5,000 - 3,000	Stuiver and Reimer (1986)

Iron Age	3,000 - 2,200	Stuiver and Reimer (1986)
Hellenistic Period	2,349 - 1,950	Morand (2020)
Roman Period (Western Mediterranean)	2,249 - 1,400	Roberts *et al.* (2011)
Roman Period (Eastern Mediterranean)	1,950 - 1,350	Morand (2020)
Byzantine Period	1,626 - 497	Athanassopoulos (2004)
Dark Age	1,400 - 1,090	Roberts *et al.* (2011)

S2. Results from statistical analyses

Table S2.1 – Results from the statistical analyses performed regarding MNI data for the banded-dye murex for the Western Mediterranean. Numbers in bold represent statistical differences.

Species/Tests	Shapiro-Wilk test	Levene's test	Kruskal-Wallis test	Pairwise Wilcox test
Banded-dye murex	$W = 0.480$ $p = 1.349e^{-7}$	$F = 4.270$ $p = 0.03$	$H_2 = 15.792$ **$p = 0.0004$**	**$p = 0.0013$**

Table S2.2 – Results from the statistical analyses performed regarding catch data for the Atlantic bluefin tuna for the Western Mediterranean, for periods divided using the Jenks natural breaks classification method (*classInt* package; Bivand 2023).

Tests	Shapiro-Wilk test	Levene's test	Kruskal-Wallis test
Atlantic bluefin tuna	$W = 0.91514$ $p = 3.12e^{-12}$	$F = 33.624$ $p < 2.2e^{-16}$	$H_5 = 407.55$ **$p < 2.2e^{-16}$**

Table S2.2.1 – Results from the pairwise comparisons between periods for the Atlantic bluefin tuna, adjusted by the Bonferroni correction method. Numbers in bold represent the periods that differ significantly from each other.

	[14,95]	(54, 95]	(95,136]	(136,175]	(175,212]
(54, 95]	**$< 2e^{-16}$**				
(95,136]	1	**$< 2e^{-16}$**			
(136,175]	1	**$< 2e^{-16}$**	1		
(175,212]	**$< 2e^{-16}$**	1	**$< 2e^{-16}$**	**$< 2e^{-16}$**	
(212,250]	**$6e^{-04}$**	**$< 2e^{-16}$**	**$3e^{-04}$**	**$1.1e^{-05}$**	**$< 2e^{-16}$**

Table S2.3 – Results from the statistical analyses performed regarding total length (TL) data for the Atlantic bluefin tuna and the gilthead sea bream by subregions of the Mediterranean Sea.

Tests	Shapiro-Wilk test		Levene's test		Two samples t-test	Mann-Whitney *U* test	one-way ANOVA
Species/ Subregion	Western	Eastern	Western	Eastern	Western	Eastern	Eastern
Atlantic bluefin tuna	$W = 0.9593$ $p = 0.1686$	$W = 0.9091$ $p = 0.0163$	$F = 2.103$ $p = 0.1554$	$F = 0.9167$ $p = 0.3468$	$t = 2.967$ **$p = 0.01$**	W = 8 p = **0.01035**	
Gilthead sea bream		$W = 0.9898$ $p = 0.4921$		$F = 1.5013$ $p = 0.227$			$F = 10.28$ **$p = 7.54e^{-05}$**

Table S2.4 – Results from the statistical analyses performed regarding basal diameter (BD) data (mean and maximum values) for the Turbinate monodont for the Eastern Mediterranean.

Tests	**Shapiro-Wilk test**		**Levene's test**		**one-way ANOVA**	**Welch ANOVA**
Variable/ Subregion	Mean	Maximum	Mean	Maximum	Mean	Maximum
Turbinate monodont	$W = 0.9102$ $p = 0.245$	$W = 0.9794$ $p = 0.4367$	$F = 1.2519$ $p = 0.3364$	$F = 4.4836$ $p = 0.0071$	*$F = 2.021$ $p = 0.195$*	*$F = 0.3701$ $p = 0.7767$*

Table S2.5 – Results from the statistical analyses performed regarding stable isotopic data ($\delta^{13}C$ and $\delta^{15}N$ values) for the Atlantic bluefin tuna between the Western and Eastern Mediterranean and the gilthead sea bream for the Eastern Mediterranean.

Tests	**Shapiro-Wilk test**		**Levene's test**		**Mann-Whitney *U* test**		**Kruskal-Wallis**	**one-way ANOVA**
Species/ Stable Isotopes	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Atlantic bluefin tuna	$W = 0.9335$ $p = 0.0091$	$W = 0.8727$ $p = 0.0002$	$F = 1.141$ $p = 0.291$	$F = 41.743$ $p = 8.626e^{-8}$	W = 1 **$p = 3.927e^{-9}$**	W = 16 **$p = 1.2e^{-7}$**		
Gilthead sea bream	$W = 08855$ $p = 0.1794$	$W = 0.9172$ $p = 0.3695$	$F = 45.719$ $p = 0.0002$	$F = 3.7329$ $p = 0.0885$			$H = 0.70028$ $p = 0.7046$	*$F = 2.344$ $p = 0.177$*

S3. Presence and abundance of the targeted species

The temporal distribution of data varies across these groups: fish data are concentrated between 100,000–12,500 years BP, mollusc data between 100,000–50,000 years BP, and marine mammal data between 9,000–500 years BP (Figures S3.1, S3.2, and S3.3). Geographically, the majority of data samples are from the Western (n = 194) and Eastern (n = 326) Mediterranean, with only a few data samples from the Adriatic Sea (n = 11). Among marine mammals, the monk seal shows a peak in NISP (~70) around 12,500 years BP in the Western Mediterranean. Within the Western and Eastern Mediterranean, the gilthead sea bream, Atlantic bluefin tuna, and turbinate monodont have the highest amounts of data. For fish, data for the gilthead sea bream and Atlantic bluefin tuna span the entire time interval. However, comparisons between periods for these two species within each region yielded no significant differences (Figures S3.1.1B–S3.1.4B). Regarding molluscs, the turbinate monodont is the only species with sufficient data to analyse differences between periods across the Mediterranean. This species shows two distinct NISP peaks: one between 45,000–30,000 years BP in the Eastern Mediterranean and another between 15,000–10,000 years BP, primarily in the Western Mediterranean. Despite these patterns, comparisons across periods revealed no significant outcomes (Figures S3.2.1B and S3.2.2B).

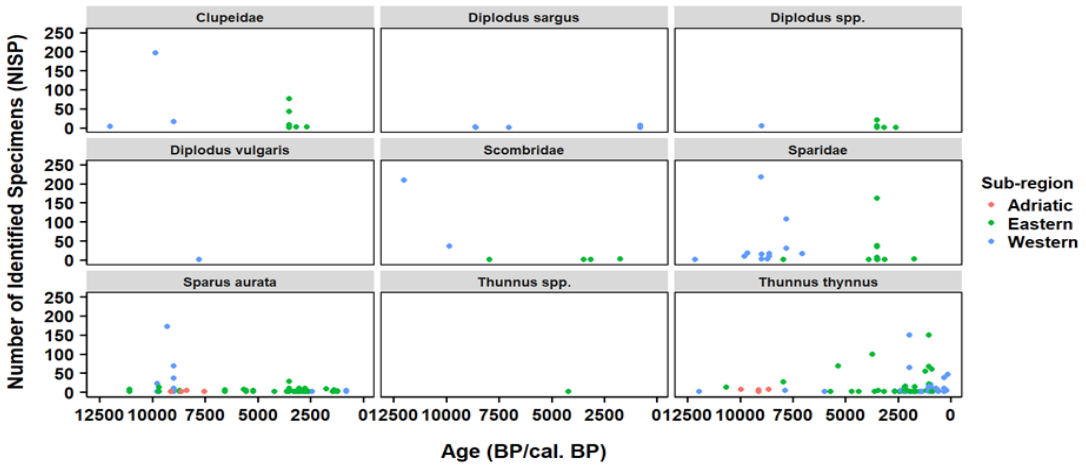


Figure S3.1 - Distribution of data for NISP for fishes. Colours separate the data for each Mediterranean of the Mediterranean Sea.

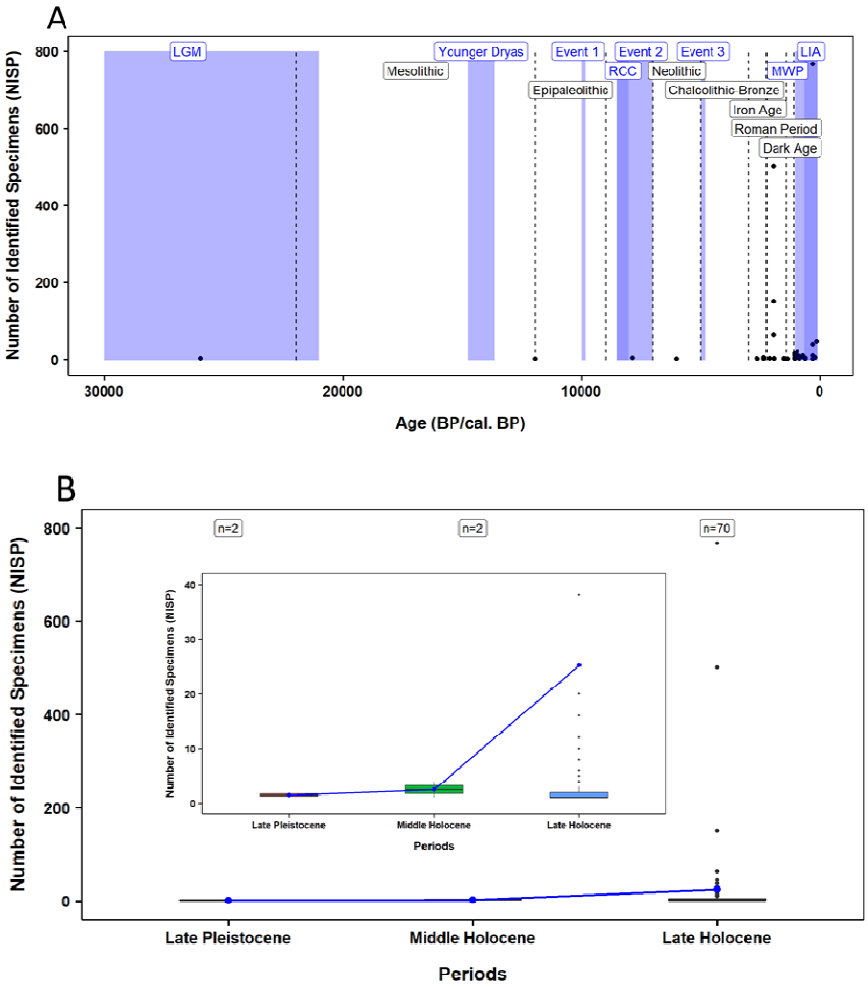


Figure S3.1.1 - Distribution of data for NISP on the Atlantic bluefin tuna in the Western Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of NISP data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above. The plot inside the second figure is a zoom-in of the data, for better visualisation of the increase in NISP values towards the Late Holocene (no outliers were excluded).

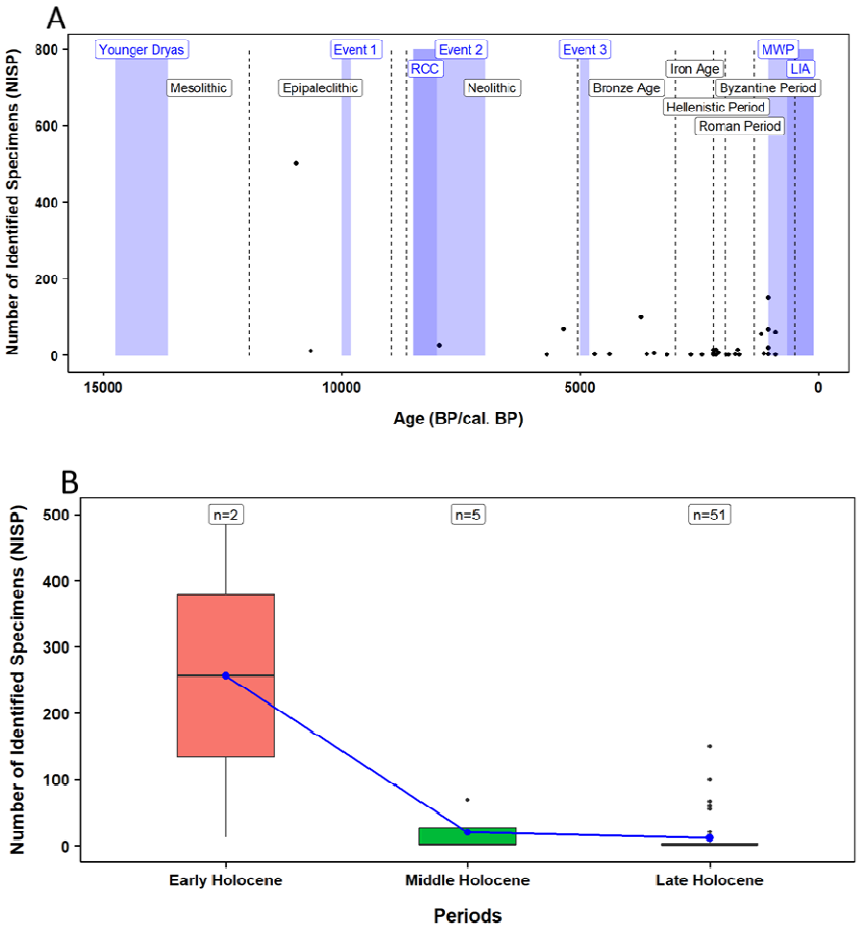


Figure S3.1.2 - Distribution of data for NISP on the Atlantic bluefin tuna in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of NISP data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

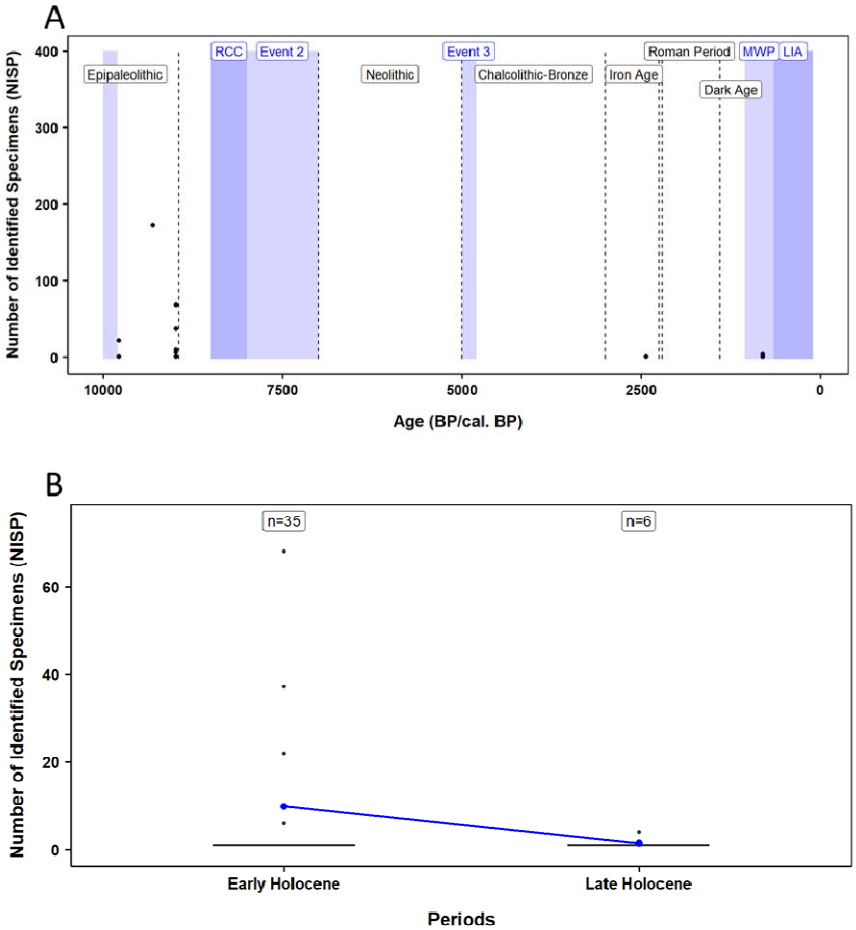
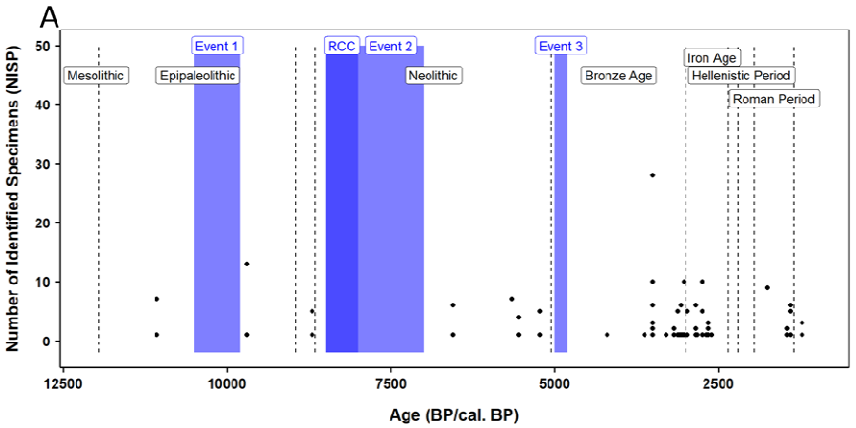


Figure S3.1.3 - Distribution of data for NISP on the gilthead sea bream in the Western Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of NISP data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.



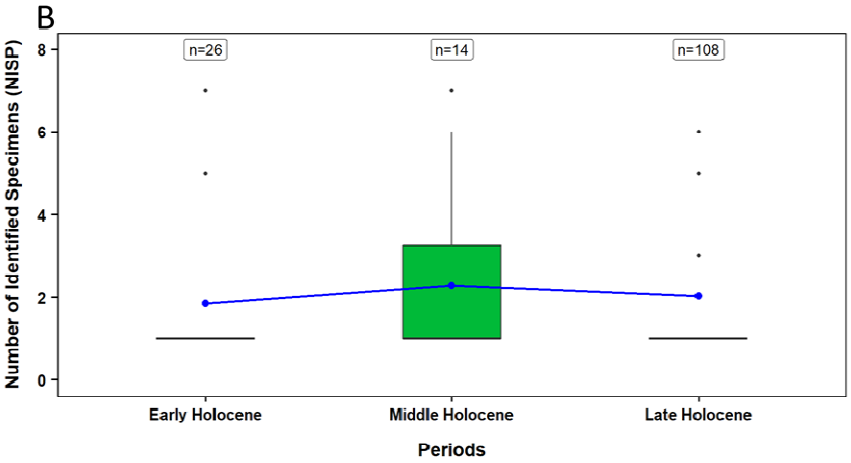


Figure S3.1.4 - Distribution of data for NISP on the gilthead sea bream in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of NISP data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

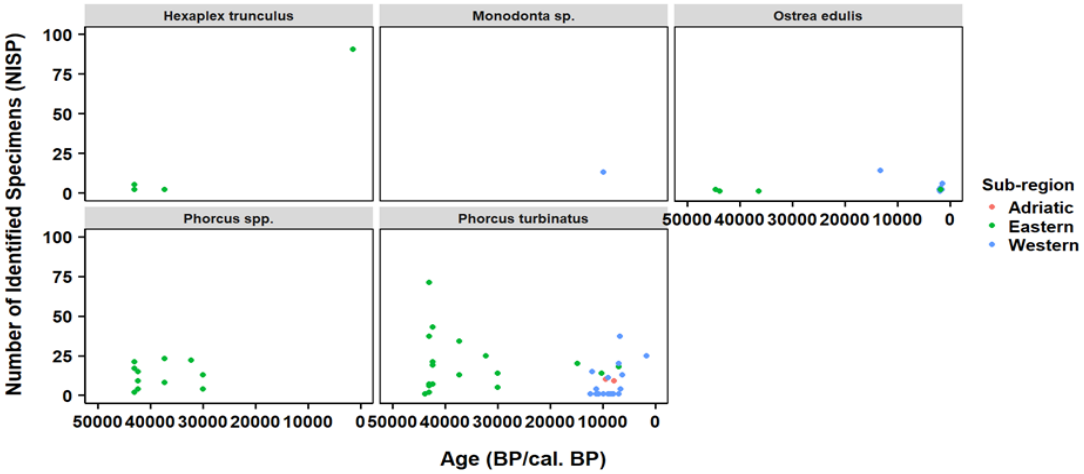


Figure S3.2 - Distribution of data for NISP for molluscs. Colours separate the data for each Mediterranean of the Mediterranean Sea.

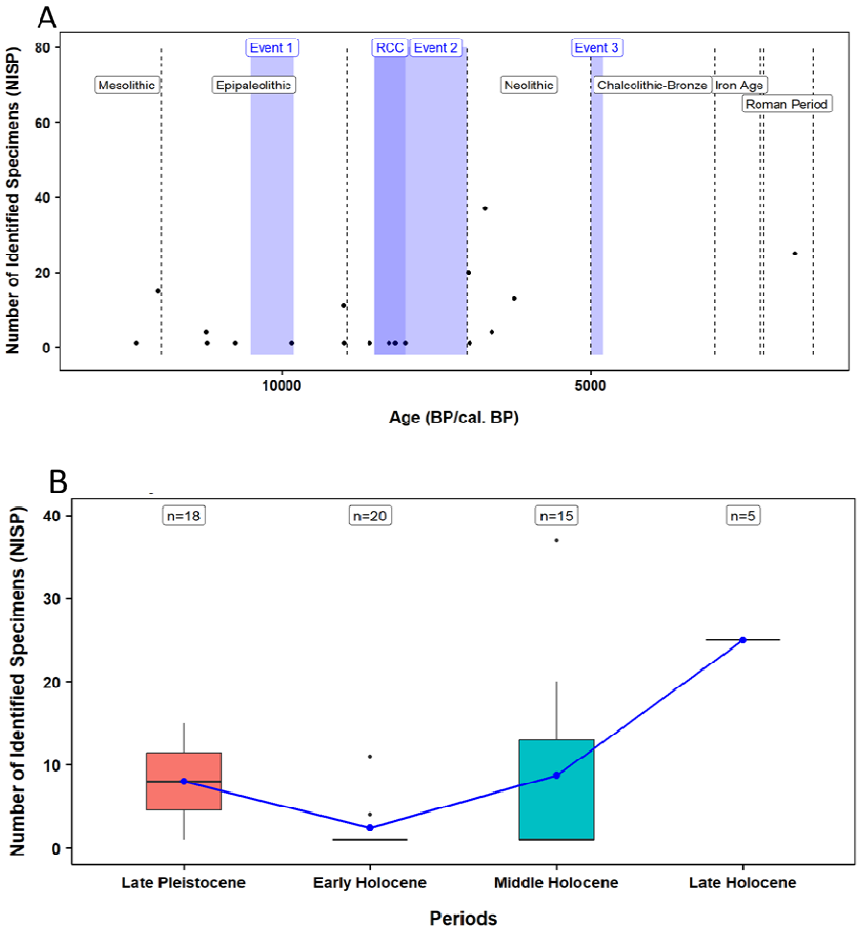
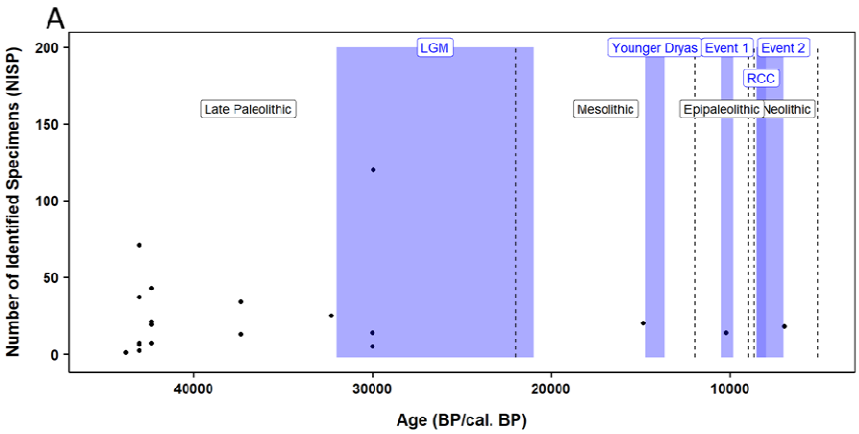


Figure S3.2.1 - Distribution of data for NISP on the turbinate monodont in the Western Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of NISP data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.



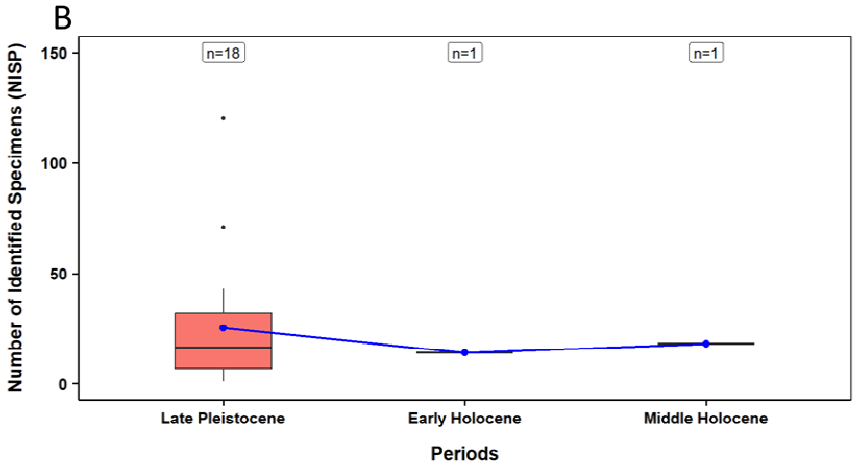


Figure S3.2.2 - Distribution of data for NISP on the turbinate monodont in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of NISP data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

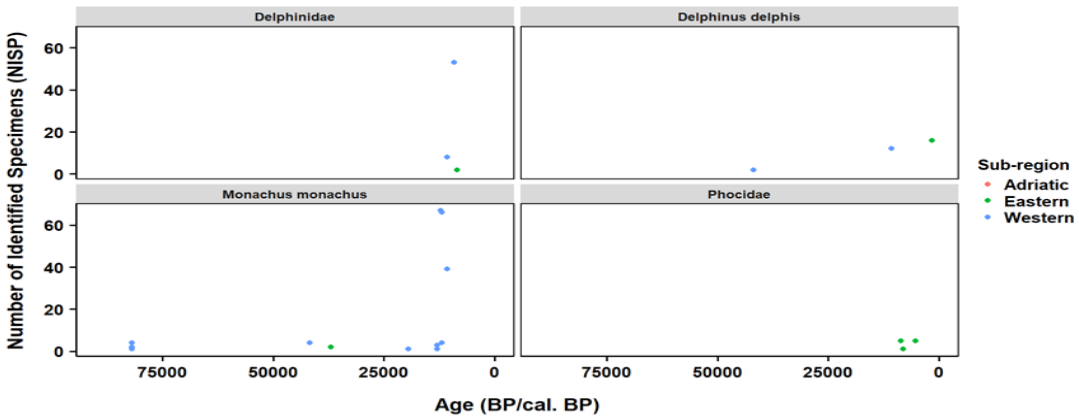


Figure S3.3 - Distribution of data for NISP for marine mammals. Colours separate the data for each Mediterranean of the Mediterranean Sea.

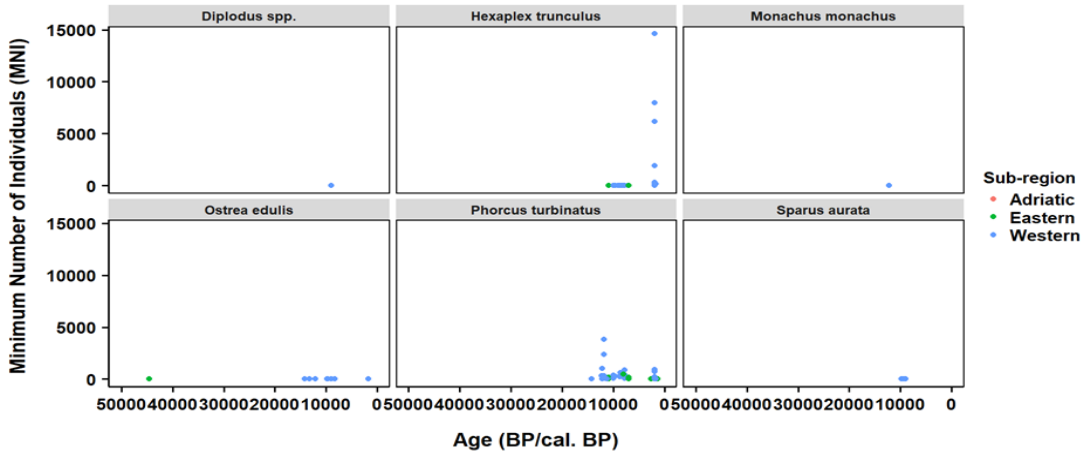


Figure S3.4 – MNI species distribution data. Colours separate the data for each Mediterranean of the Mediterranean Sea.

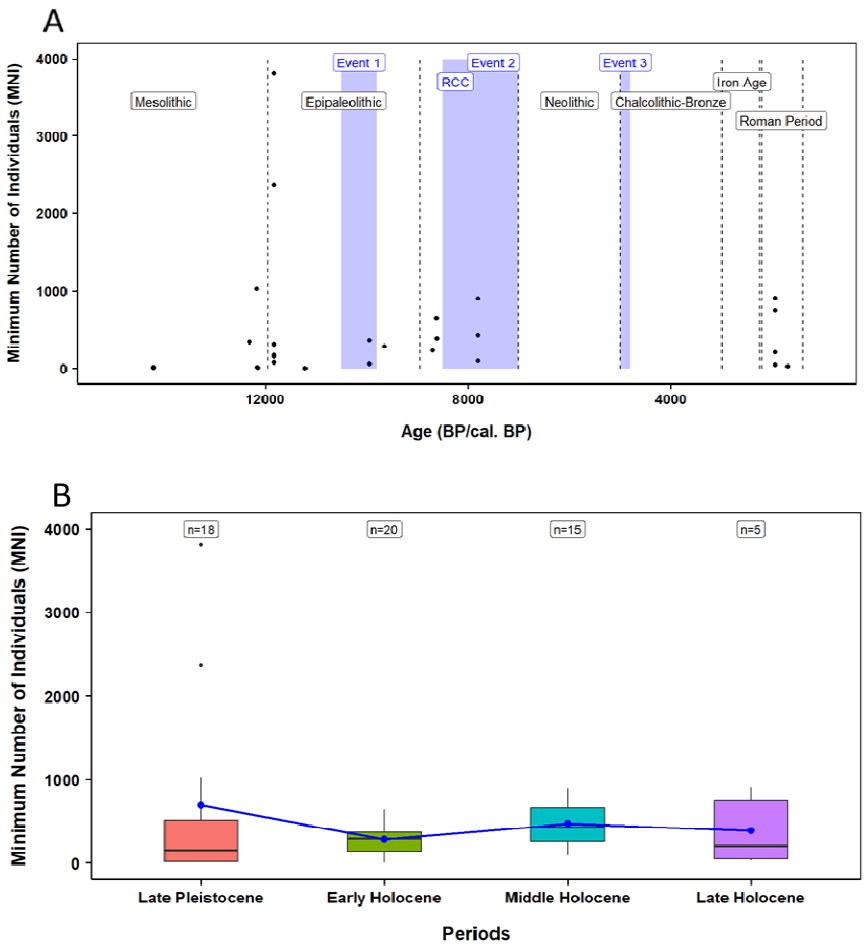


Figure S3.4.1 - Distribution of data for MNI on the turbinate monodont in the Western Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of MNI data for each

geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

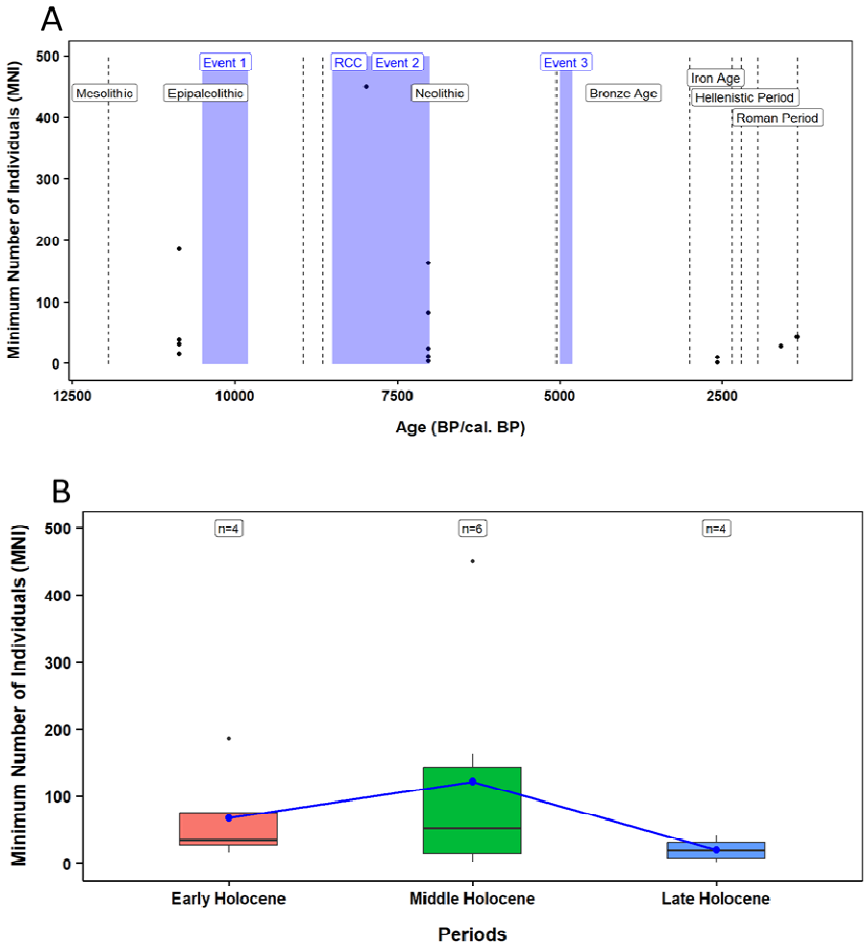


Figure S3.4.2 - Distribution of data for MNI on the turbinate monodont in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of MNI data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

S4. Catch records

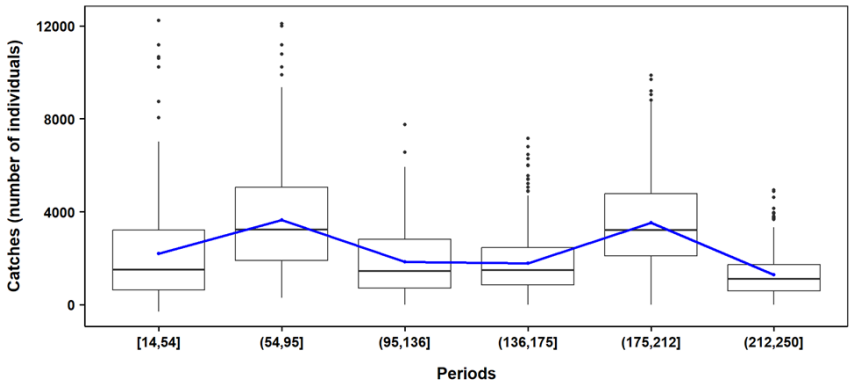


Figure S4 – Catches records of the Atlantic bluefin tuna divided into six periods, using the Jenks Natural Breaks Method, between 250–14 years BP. The blue dots, connected by the blue line, are the mean values for each period. The number of samples (n) included in each box plot is indicated above. The black dots are outliers.

S5. Body size measures

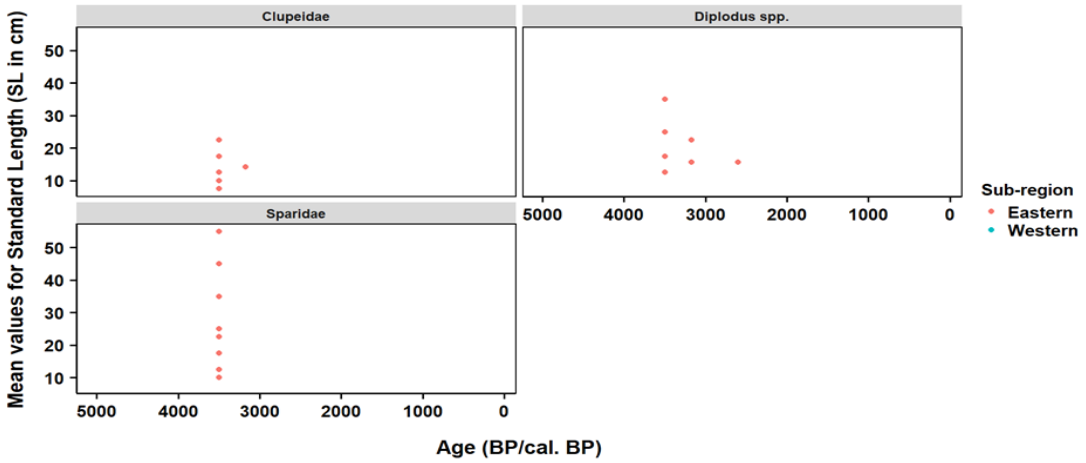


Figure S5.1 – Fishes distribution of data for Standard Length (SL). The colour indicates that the data comes from the Eastern Mediterranean Sea.

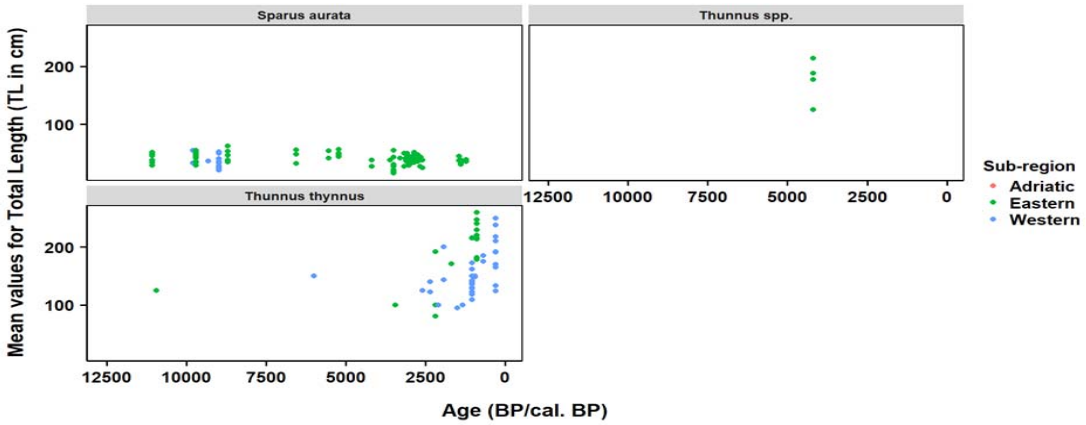
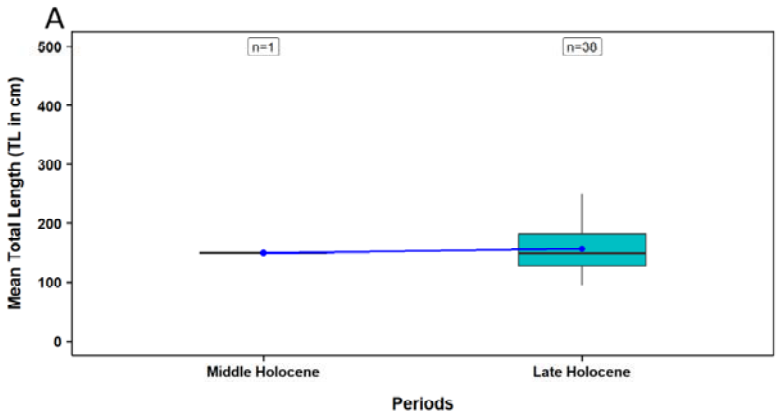


Figure S5.2 – Fishes distribution of data for Total Length (TL). The colour indicates from which sub-basin of the Mediterranean Sea the data comes.



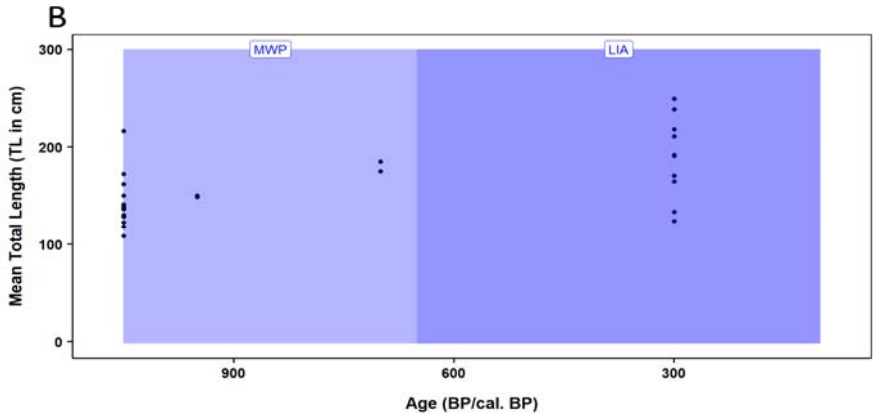
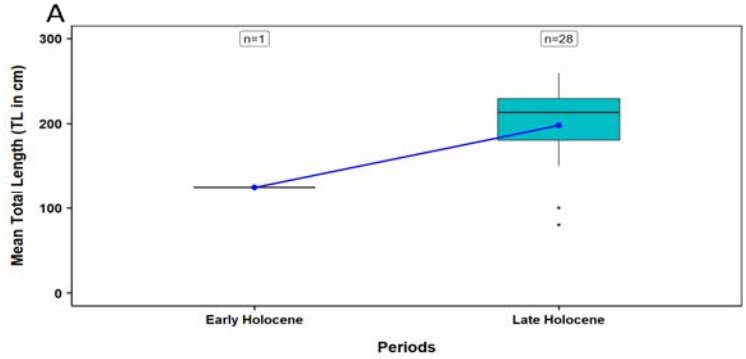


Figure S5.3 – Distribution of data for TL on the Atlantic bluefin tuna in the Western Mediterranean. (A) Boxplots of TL data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above. (B) Total length differences between the MWP (Medieval Warm Period) and LIA (Little Ice Age).



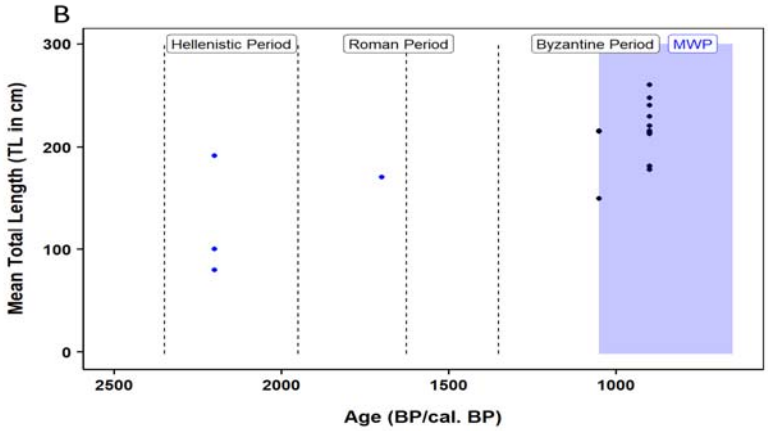


Figure S5.4 – Distribution of data for TL on the Atlantic bluefin tuna in the Eastern Mediterranean. (A) Boxplots of TL data for each geological period. Blue dots represent mean

values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above. (B) differences between the before and during the MWP (Medieval Warm Period).

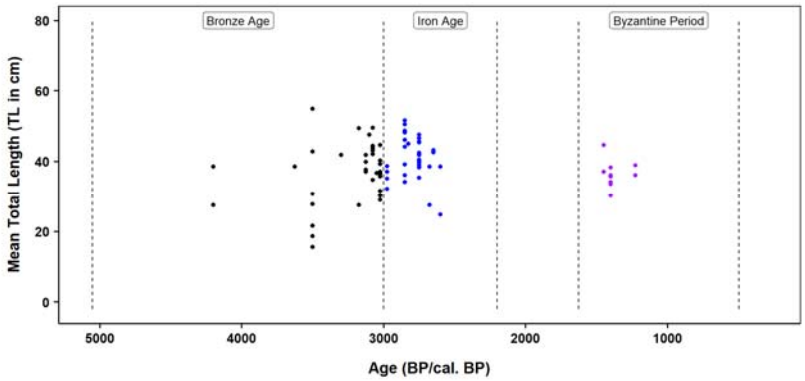


Figure S5.5 – Distribution of data for the TL on the Gilthead sea bream in the Eastern Mediterranean. Differences between the Bronze and Iron Ages and the Byzantine period.

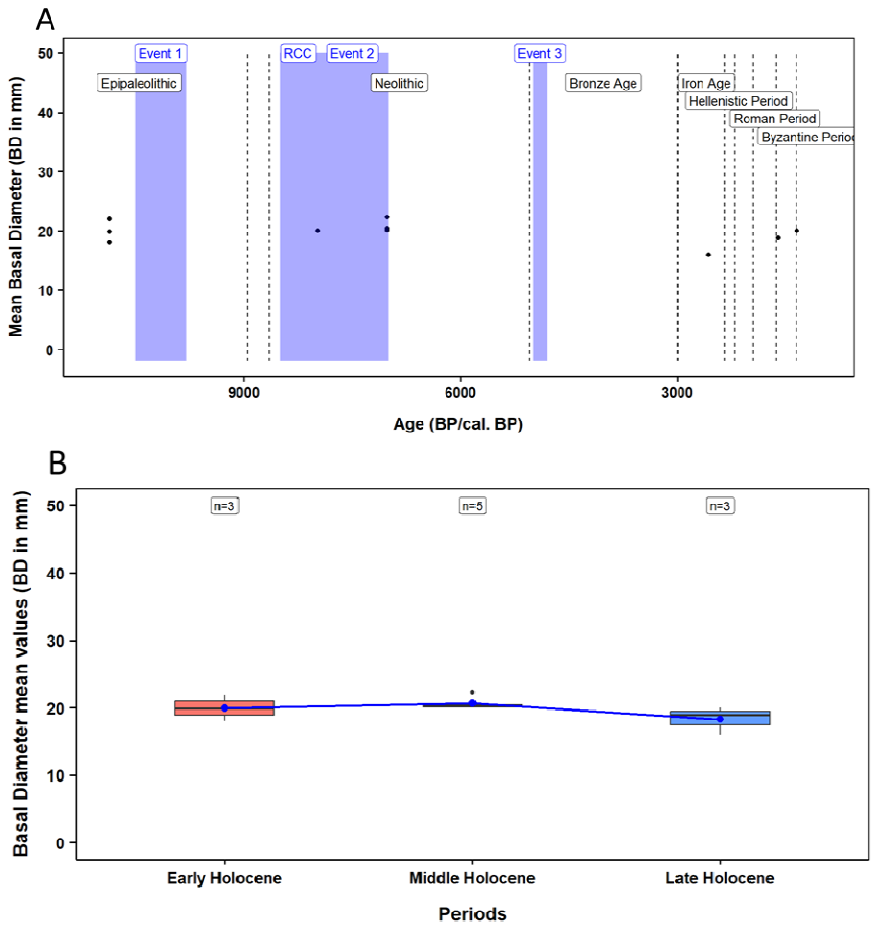


Figure S5.6 - Distribution of data for mean BD on the turbinate monodont in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of BD data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

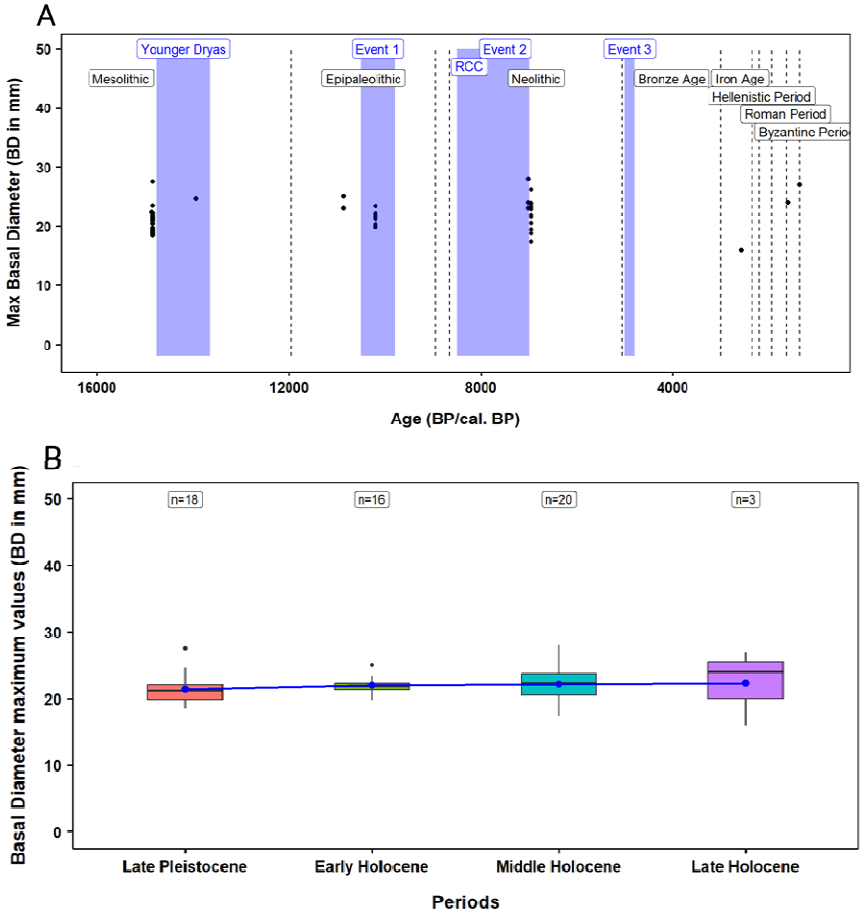


Figure S5.7 - Distribution of data for maximum values of BD on the turbinate monodont in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (purple rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of BD data for each geological period. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

S6. Stable isotopic data

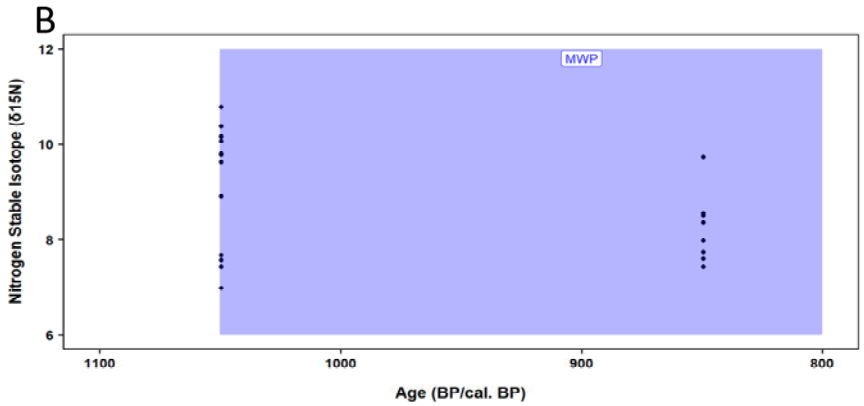
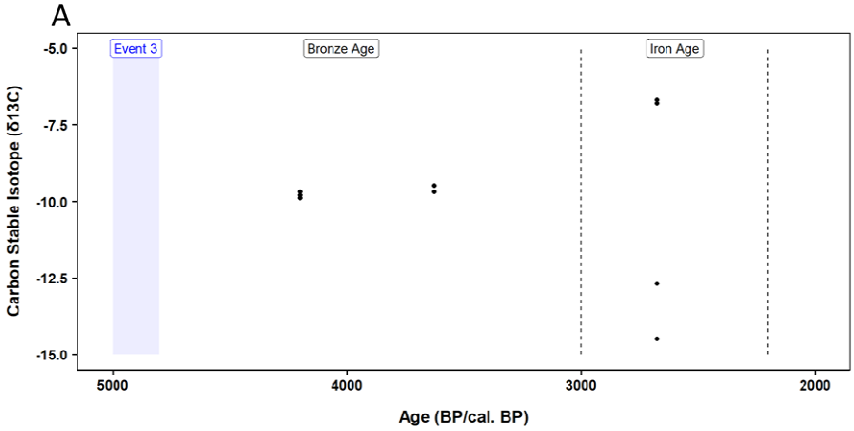


Figure S6.1 – Distribution of data for the δ^{13}C and δ^{15}N of the Atlantic bluefin tuna from the Western and Eastern Mediterranean. (A) The δ^{13}C values fall within the Medieval Warm Period (MWP); (B) The δ^{15}N values fall within the Medieval Warm Period (MWP).



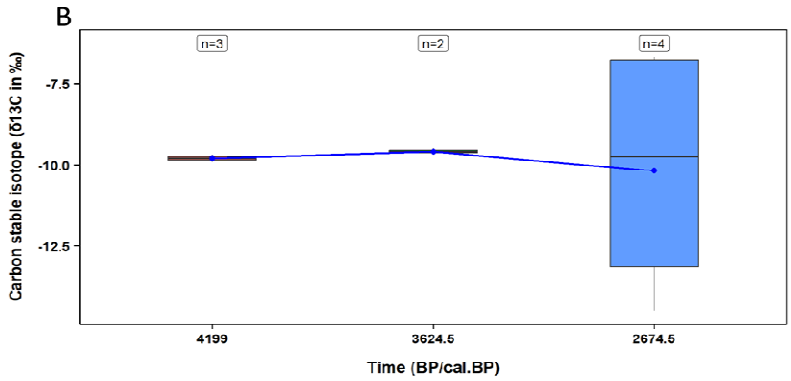


Figure S6.2 – Distribution of data for the δ^{13}C of the gilthead sea bream from the Eastern Mediterranean. (A) The δ^{13}C values fall between the Bronze and Iron Ages; (B) Boxplots of the differences between data with three mean ages. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

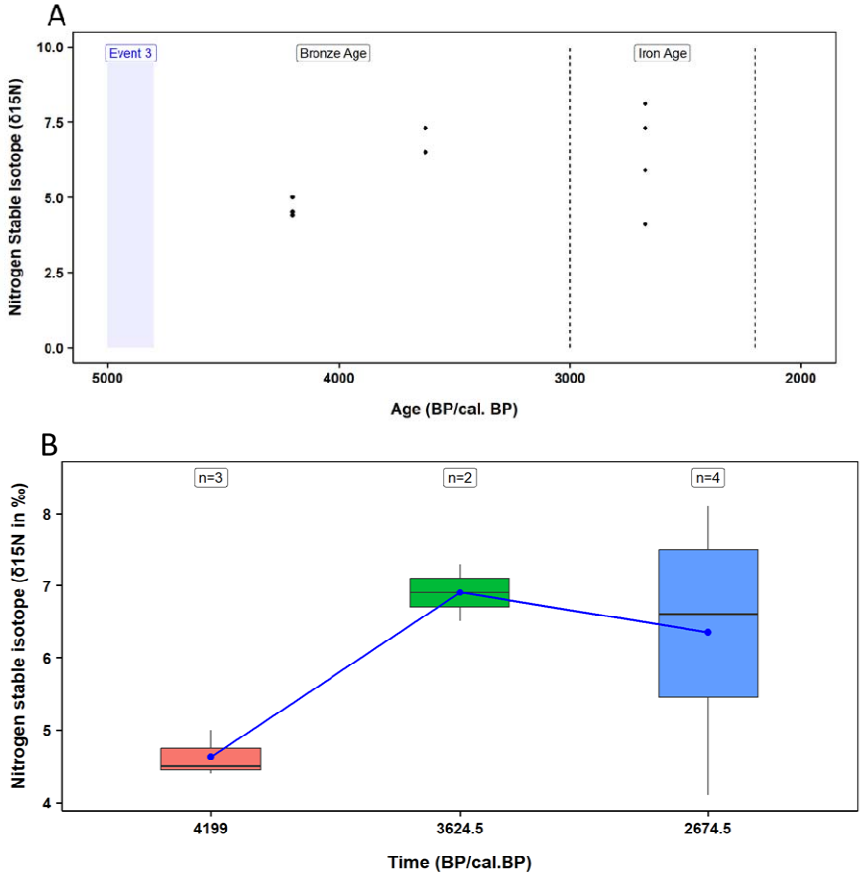


Figure S6.3 – Distribution of data for the δ^{15}N of the gilthead sea bream from the Eastern Mediterranean. (A) The δ^{15}N values fall between the Bronze and Iron Ages; (B) Boxplots of

the differences between data with three mean ages. Blue dots represent mean values, and bars indicate standard deviation. Letters denote statistically significant differences between periods. The number of data samples (n) for each boxplot is shown above.

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