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

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ABSTRACT

Climate and human impacts have impacted the Mediterranean ecosystem for thousands of years. Still, their evidence has been incomplete, hindering a proper assessment of the marine ecosystem's baseline state and resources. In an attempt to disentangle these impacts, we conducted a study focused on commercially important species of marine mammals, fishes, and molluscs over the last 130,000 (130 ka) years until the Industrial Revolution (the year 1850). To assess differences within the basin, we subdivided the Mediterranean Sea into three subregions - Western, Eastern and Adriatic. Our work revealed 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, influenced the abundance and body size of Atlantic bluefin tuna, while subregional differences in the stable isotopic composition of archaeological skeletal material reflected shifts in the system's primary 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. These results highlight the significance of studying the relationships between climate, human activities, and marine resources in this large marine ecosystem. As well as integrating past data with contemporary data to reconstruct ecological baselines and obtain longer and more comprehensive time series of ecosystem change. 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 conservation measures.

1. INTRODUCTION

Marine ecosystems are among the world's most diverse and socio-economically valuable systems (Millennium Ecosystem Assessment, 2005; Halpern et al., 2008). They provide several important ecosystem services, including regulation, protection, and food provision, among others (Doney et al., 2012; Liquete et al., 2013). 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). There is evidence that shellfish exploitation may have started already in the Lower Paleolithic in Mediterranean coastal areas. 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 (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; Moullec et al., 2019). In recent decades, the Mediterranean basin has experienced a temperature increase exceeding the global average, mainly due to greenhouse gas emissions (Lionello & Scarascia, 2018; Pastor et al., 2020; IPCC, 2023). Global warming has profoundly affected marine ecosystems (Smale et al., 2019; Trisos et al., 2020), altering species distributions and abundances (Garrabou et al., 2009). Key human-related threats to marine ecosystems include habitat loss and degradation, overexploitation of resources, pollution, and invasions by non-indigenous species (Halpern et al., 2008; Coll et al., 2010). These pressures have resulted in changes in species phenology, ultimately impacting 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 marine ecosystem history and how species respond to changes over time (Jackson et al., 2001; Agiadi et al., 2024). Marine organisms and the isotopic compositions of their skeletal material are invaluable 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 et al., 2020) in decadal to million-year timescales. Additionally, recent studies have revealed the great potential of geohistorical data for

understanding changes in marine ecosystem structure and processes in the past, and how human-induced and natural perturbations impacted marine ecosystems over the long term (e.g., Calkin et al., 2001; Lotze et al., 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 et al. (2025), who conducted a systematic review of marine mammals, fishes and molluscs. We hypothesise that climatic changes and human activities affected the targeted marine species from different functional groups, focusing on particular drivers, namely temperature oscillations and overexploitation. Our goal is to offer insights to aid in the management and conservation efforts of Mediterranean marine communities and ecosystems. Understanding the past responses of marine functional groups will allow for better identification of both current and future climate and human impacts and facilitate more effective conservation and management strategies.

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 & Golnaraghi, 1994). We have divided the study area into three different subregions bounded by the straits of Sicily and Otranto: the Western and Eastern Mediterranean and the Adriatic Sea (Millot & Taupier-Letage, 2005; Rio et al., 2007; Robinson et al., 2009). We used data on seventeen commercially relevant species of marine mammals, fish and molluscs gathered by Leal et al. (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

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 body length and molluscs basal diameter), and 4) stable isotopic composition of fish bones ($\delta^{13}C$ and $\delta^{15}N$). In our analysis, the Marmara Sea and the Black Sea were included in the Eastern Mediterranean.

Leal et al. (2025) revealed important, available data on Atlantic bluefin tuna catches from Italian tuna traps spanning between 1700 and 1936 (Addis et al., 2008; Longo & Clark, 2012; Polanco-Martínez et al., 2018). Using long-term fluctuations in catches as a proxy for abundance (Ravier & Fromentin, 2001), we analysed these data to detect temporal and spatial patterns in Atlantic bluefin tuna abundance in the Mediterranean over this 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 relationships between these patterns in catches and major human civilisation events and advancements in fisheries.

Furthermore, we analysed $\delta^{13}C$ and $\delta^{15}N$ data extracted from the bones (mainly vertebrae) of Atlantic bluefin tuna (Andrews et al., 2023b,c) and bones of gilthead sea bream (Fuller et al., 2020). No baseline corrections were applied to the carbon and nitrogen isotope values, as data for each species had been produced with the same methodologies.

2.2 Data Analyses

Outliers were excluded from each variable before analysis. Species with the most data over time in each subregion were selected, and data were categorised into four geological periods: Late Pleistocene, and Early, Middle and Late Holocene. 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 & Weisberg, 2019) were assessed for all variables. For NISP, MNI, body size, and stable isotopic compositions, non-parametric tests were used: Mann-Whitney *U* for two-group comparisons and Kruskal-Wallis for multiple groups, with the Bonferroni correction. When there were significant differences, the post-hoc pairwise Wilcox test was posteriorly used. For some species' 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; Bivand, 2023), and the detected differences between periods

were assessed using Kruskal-Wallis with Bonferroni correction and pairwise Wilcox tests. A *p-value* threshold of ≤0.05 was applied. 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

See supplementary material S2 to S6 regarding explicit results from the statistical analyses on each variable.

3.1 Presence and abundance of targeted species

NISP data were available for most of the targeted species. However, their analyses revealed no significant outcomes (for more information see S3).

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 (Supplementary Material S2.4). The 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). For the banded-dye murex, significant differences were observed between periods in the Western Mediterranean (H_2 = 15.792; p = 0.0004), particularly between the Early and Late Holocene (p = 0.0013; Figure 1B, Table S2.1).

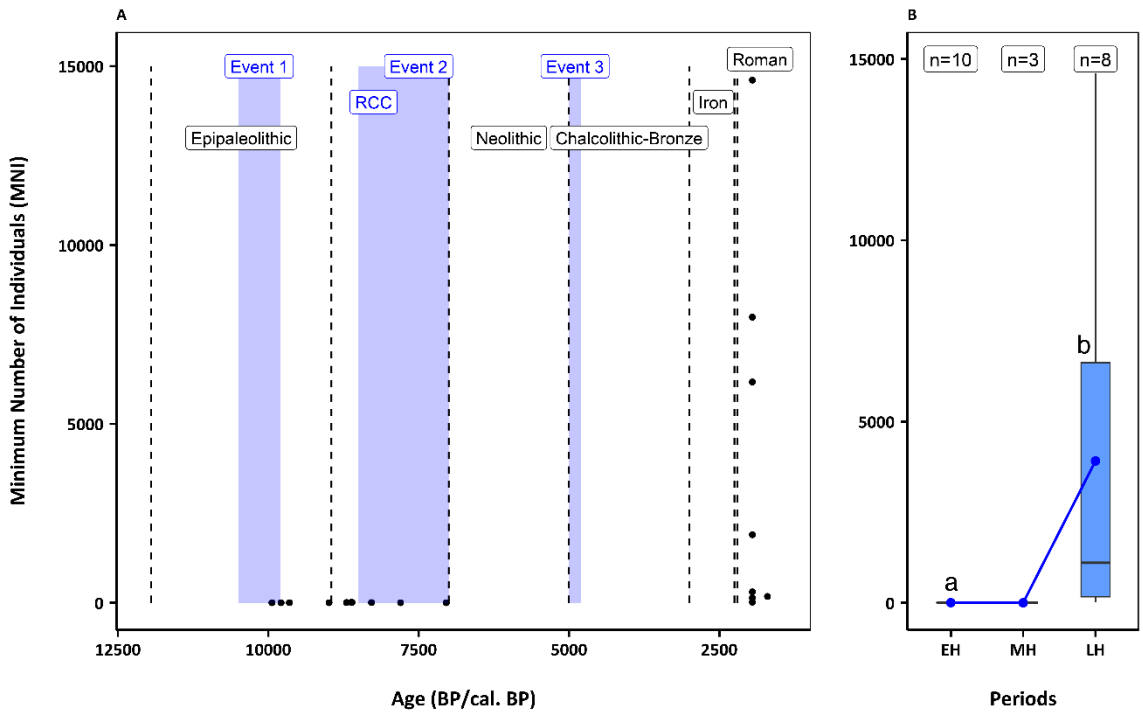

Figure 1 - Distribution of MNI data for banded-dye murex in the Western Mediterranean. (A) Temporal distribution of records, major climatic events (blue rectangles) and human cultural periods (delimited using black dashed lines); (B) Boxplots of MNI data for each geological period: EH (Early Holocene), 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 from 250 to 14 years BP (1700-1936 years; Figure 2). Two peaks were observed: the first (~10,000 individuals) occurred around 200 years BP (~1750) during the Little Ice Age, and the second (~12,000 individuals) between 75–45 years BP (1875–1905), after the onset of industrial fisheries. Declines in catches were evident (S = −3.98 e^{5}; Kendall's tau coefficient = −2.39 e^{-1}; p < 2.2 e^{-16}), with significant differences between some of the periods (H_5 = 407.55; p < 2.2e^{-16}; Table S2.2 - S2.2.1, Figure S4).

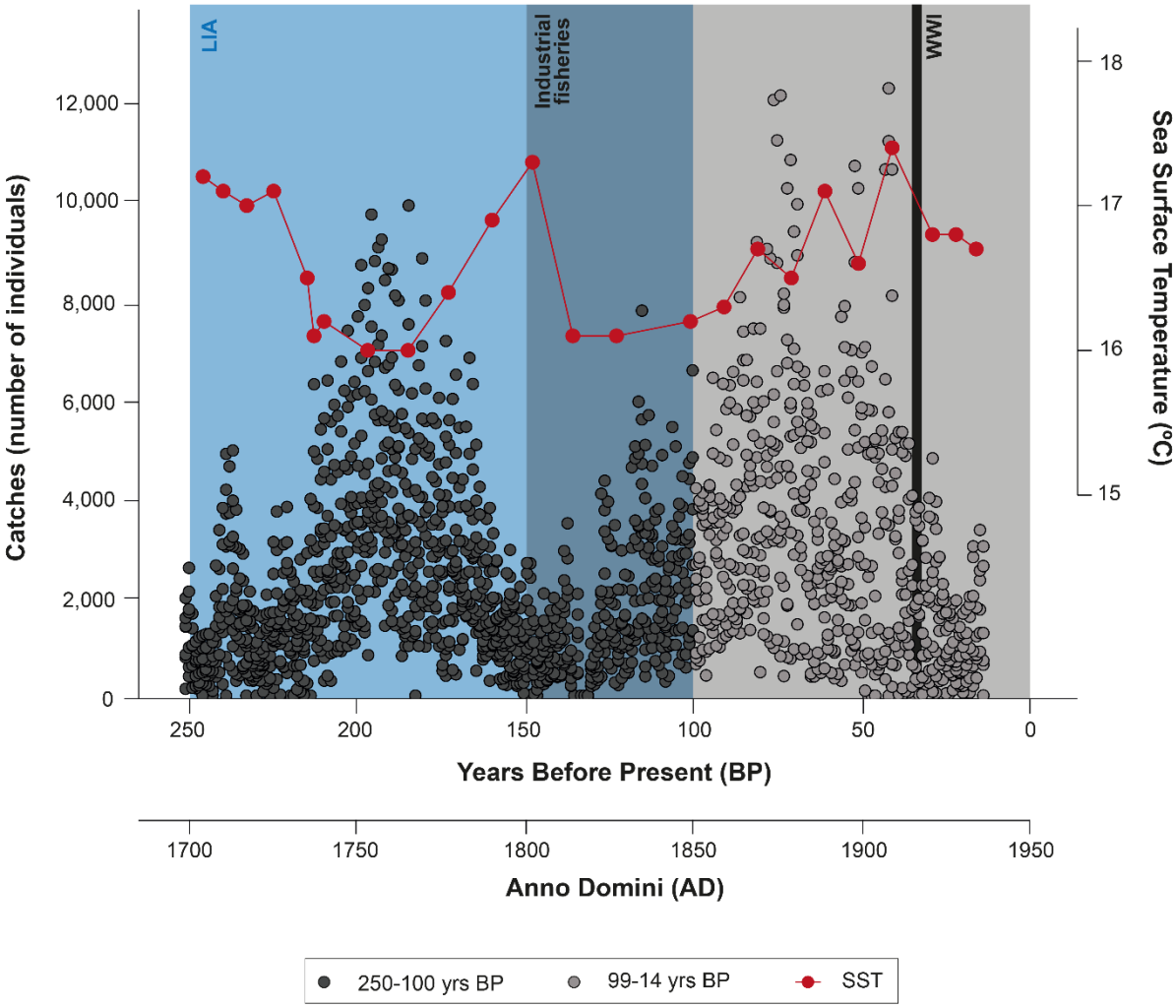

Figure 2 – Atlantic Bluefin Tuna catch records between 250 and 14 years BP (1700–1936), from tuna-traps in the Western Mediterranean Sea. The black points refer to data collected between 250 and 100 years BP (1700–1850), and the light grey points indicate the catch records between 99 and 14 years BP (1851–1936). The red points indicate reconstructed SST records from the Gulf of Lions (France) (data from Jalali et al., 2016). LIA: Little Ice Age; Industrial fisheries: minor modifications were made to tuna traps until the 1960s (Doumenge, 1999); 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). TL data were available for Atlantic bluefin tuna and gilthead sea bream. 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 tuna body size 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).

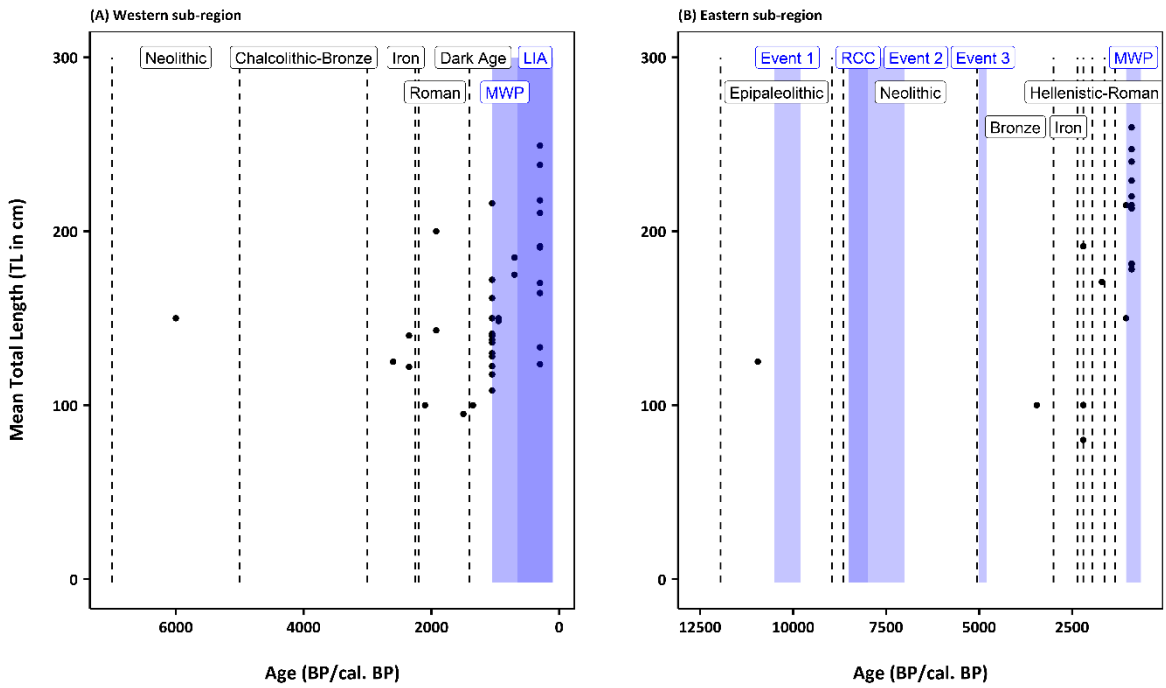

Figure 3 - Distribution of data for the TL of Atlantic bluefin tuna in the Western and Eastern Mediterranean. Temporal distribution of records, including major climatic events (blue rectangles) and anthropogenic events (black dashed lines); (A) Temporal distribution of records for the Western Mediterranean; (B) Temporal distribution of records for the Eastern Mediterranean.

Total length data for gilthead sea bream were limited to the Eastern Mediterranean (Figure 4). Pairwise comparisons revealed significant differences in sea bream body size 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).

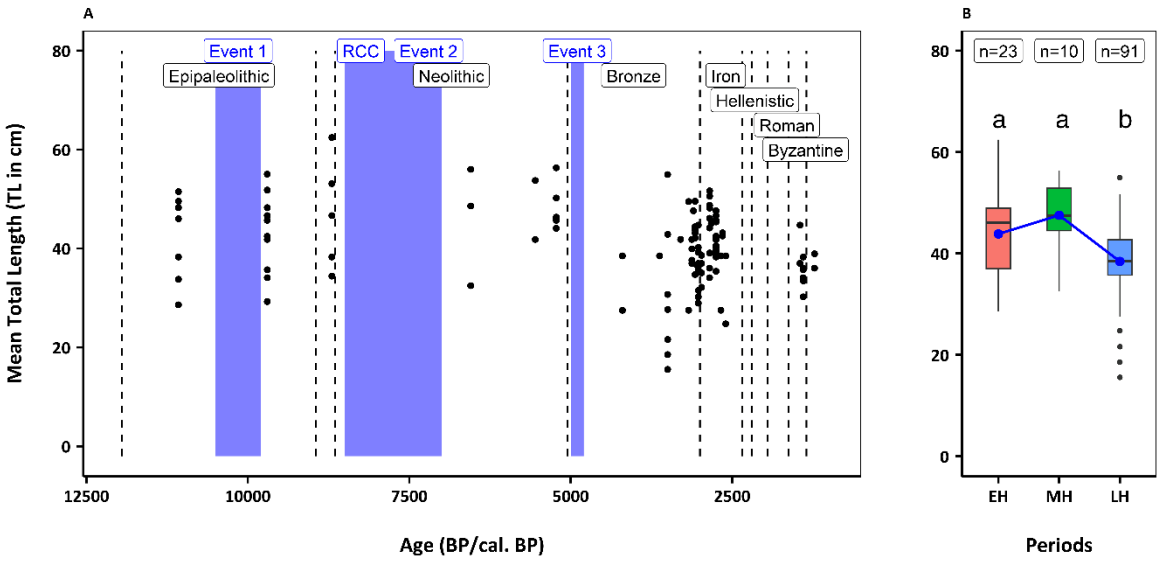

Figure 4 - Distribution of TL data for gilthead sea bream in the Eastern Mediterranean. (A) Temporal distribution of records, including major climatic events (blue rectangles) and anthropogenic events (black dashed lines); (B) Boxplots of TL data for each geological period: EH (Early Holocene), MH (Middle 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.

Body size data for the turbinate monodont were available only for the Eastern Mediterranean, specifically mean and maximum basal diameter (BD) 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

All stable isotope data for Atlantic bluefin tuna fell within the Medieval Warm Period (Figure S6.1). Statistical analysis revealed significant differences between the Western and Eastern Mediterranean between 1,050-850 years BP 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).

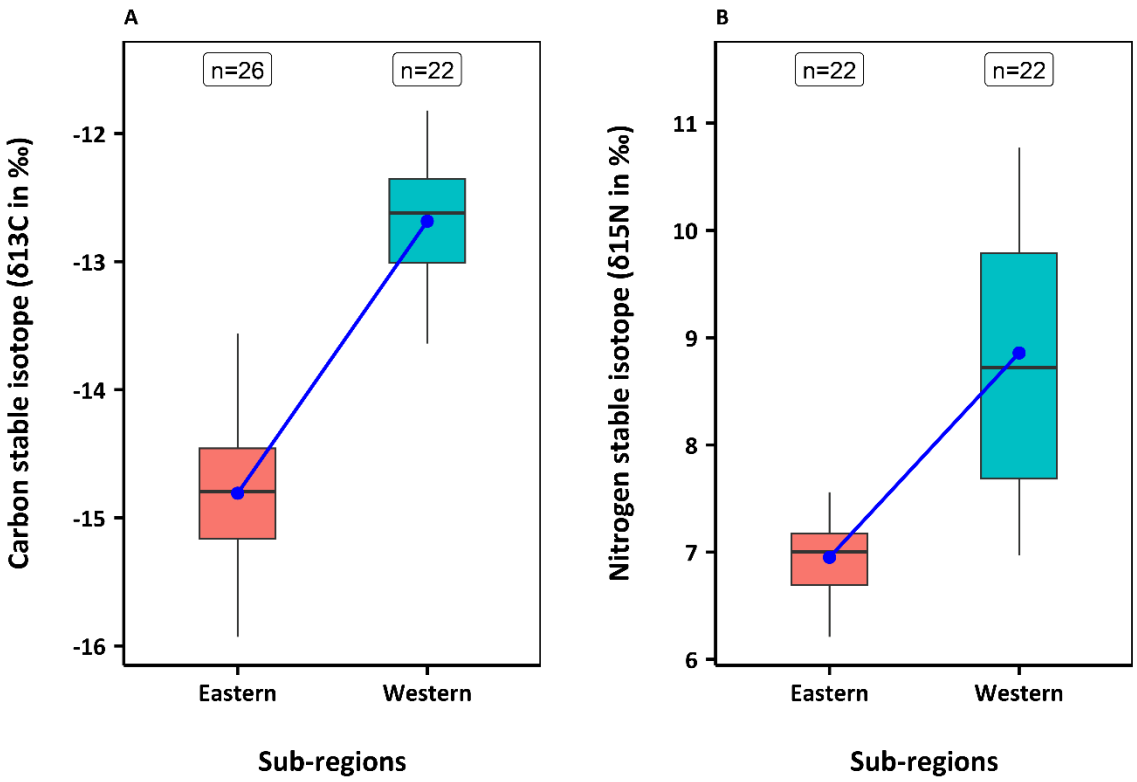

Figure 5 - Distribution of δ^{13}C and δ^{15}N data for Atlantic bluefin tuna in the Eastern and Western Mediterranean for 1,050–850 years BP. (A) Boxplots showing δ^{13}C values for the Eastern and Western Mediterranean; (B) Boxplots showing δ^{15}N values for the same subregions. Blue dots represent mean values, and bars indicate standard deviation. The number of data samples (n) for each boxplot is shown above.

For the gilthead sea bream, few δ^{13}C and δ^{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, δ^{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 infer the impacts of pre-industrial climate and human activities on banded-dye murex, Atlantic bluefin tuna, and gilthead sea bream. 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 & Dickson, 2004). This highly migratory species moves between cold feeding waters like the North Atlantic Ocean (Mather et al., 1995; Block et al., 2001, 2005) and warm spawning areas like the Mediterranean Sea (Mather et al., 1995; Block et al., 2005; Rooker et al., 2006). The high number of catches observed in the Western Mediterranean during the latter stages of the Little Ice Age (650–100 years BP; Briffa, 2000) may be linked to a decline in seawater temperature. During this period, there may have been changes in the species' migration patterns due to cooler and unstable meteorological conditions (strong storm activity and cold windy conditions, etc.), reducing the efficiency of tuna fisheries (Ravier & Fromentin, 2004; Ganzedo et al., 2016). Temperature also affects plankton production and distribution (e.g., McGowan et al., 1998; Beaugrand et al., 2002) and thus food availability for both juvenile and adult tuna (Mather et al., 1995), driving the spatiotemporal dynamics of tuna movements between the spawning and feeding grounds (Ravier & Fromentin, 2004).

Pleistocene–Holocene natural climatic variability may have also impacted the body size of tuna in the past as they have done for other species (Agiadi et al., 2023; Porz et al., 2024). Recent studies have suggested stronger consumer-driven control of food webs with warming (Allen et al., 2005; López-Urrutia et al., 2006). Warming enhances heterotroph abundance, strengthening consumer-resource interactions (O'Connor, 2009), which benefits high trophic-level species (Archibald et al., 2022) such as Atlantic bluefin tuna. Temperate consumers, like tuna, generally have broader niche breadths, making them more adaptive (MacArthur, 1972; Olesen & Jordano, 2002). The TL increase observed through the present analyses may have been caused by this dietary flexibility, combined with stronger consumer-resource interactions, allowing tuna to thrive during past climatic fluctuations. This hypothesis is consistent with the study by Andrews et al. (2023a), who documented an increase in juvenile growth between the 16th and 18th centuries in the Mediterranean Sea, likely linked to warmer sea surface temperatures and a positive North Atlantic Oscillation phase.

The Mediterranean Sea is broadly oligotrophic with a persistent east-to-west gradient in productivity (Coll et al., 2010). Historical data suggest reduced primary productivity in the Eastern Mediterranean (e.g., Kuhnt et al., 2008) and higher productivity in the Western Mediterranean (e.g., Incarbona et al., 2010). This productivity difference likely explains the δ^{13}C and δ^{15}N variations from 1,050 to 850 years BP. δ^{13}C values are good indicators of primary production sources (Hobson et al., 1994; France, 1995), with lower values typically associated with coastal waters that are enriched in terrestrial-derived carbon (low-δ^{13}C), and lower concentrations of remineralised carbon from benthic sources (high-δ^{13}C; Barnes et al., 2009; Magozzi et al., 2017). The higher δ^{13}C values in the Western Mediterranean suggest that Atlantic bluefin tuna may have used coastal waters in this area, while in the Eastern Mediterranean, it might have used offshore areas. This aligns with the use of Western waters for spawning (Oray & Karakulak, 2005; Alemany et al., 2010) and Eastern waters for

offshore foraging, potentially linked to opportunities for deep diving (Wilson & Block, 2009; Olafsdottir et al., 2016) and/or reduced benthic-pelagic coupling (Magozzi et al., 2017). Similarly, δ^{15}N values, which are used to estimate the trophic position in the food web (Sigman et al., 2009), were higher in the Western Mediterranean, likely reflecting greater nutrient availability. Despite its oligotrophy (Coll et al., 2010) Mediterranean coastal areas experience nutrient enrichment through local factors such as fluctuating wind conditions, currents, and fluvial discharges (Bosc et al., 2004; Zavatarelli et al., 1998). These localised nutrient inputs, combined with the generalist feeding strategy of Atlantic bluefin tuna (MacArthur, 1972; Olesen & Jordano, 2002) may have facilitated its success in the Western Mediterranean, while the more oligotrophic conditions in the Eastern Mediterranean may have led to a more specialised diet. Nevertheless, Andrews et al. (2023c), 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.

Our results evidence the impact of sustained exploitation on the abundances and body sizes of species from different marine groups. The banded-dye murex was extensively harvested during the Late Holocene (4,200 years BP to present days; Stuiver & Reimer, 1986), particularly during 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., De Pablo & Gabriel, 2016) and later to civilisations that harvested it at an industrial scale (Michel & McGovern, 1987; Oliver, 2015). The Romans used this species, along with related ones like *Bolinus brandaris* and *Stramonita haemastoma*, to produce Purple Dye, highlighting its economic significance (Oliver, 2015).

The Atlantic bluefin tuna abundance seems to also have been influenced by industrial fisheries (Polanco-Martínez et al., 2018; this study). The most common method of capture of this species 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, such as purse-seiners and longlines (Joseph, 2003). The 19th century, which is roughly coincident with the increasing use of industrial fisheries, was marked by the starting decades of extensive exploitation of tuna (Andrews et al., 2022). The high number of catches after the onset of industrial fishing might reflect this slow transformation from a low-scale, sustainable fishery into a large-scale, unsustainable fishery of Atlantic bluefin tuna. In general, removing top predators, such as tuna, may lead to changes in the food web structure through top-down control (Pauly et al., 1998; Scheffer et al., 2005). Similar impacts are documented for sea otters, heavily hunted by Aboriginal Aleuts 2,500 years ago led to their population decline and an increase in the sea urchin population resulting in deep changes to kelp forest ecosystems (Simenstad et al., 1978; Jackson et al., 2001).

Our results highlight that the intensive exploitation of Atlantic bluefin tuna and gilthead sea bream could have led to body size changes. Historical records show tuna catch declined in Spain during the mid-16th to 18th centuries (Sarmiento, 1757). Overexploitation in previous centuries of juvenile stages and disturbances of the seabed 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 artificial 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 intense fishing pressure in the Late Holocene in the Eastern Mediterranean with a decrease in its body size (Guy et al., 2018; this study). This reduced body size pattern also occurred in other regions, such as the steady decrease in body size of *Archosargus probatocephalus* due to long-term fishing activities (Guiry et al., 2021). These size reductions, driven by overfishing and size-selective gear, have profound effects on trophic interactions within marine ecosystems (Shackell et al., 2009; Garcia et al., 2012). Such changes highlight the cascading impacts that targeted harvesting can have on marine communities.

It is necessary to be cautious when analysing these results due to some previous assumptions. The study is constrained towards economically important 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 (e.g., dating systems, and body size measurements) presented challenges in compiling and analysing information. Additionally, the resolution needed to reconstruct past population sizes limited the assessment of impact magnitude. Despite these limitations, our study provides important insights into how past climate changes and human activities have shaped species abundance, body size, and trophic ecology in the Mediterranean Sea.

Conclusions

This work highlights the significance of studying the impact of pre-industrial climate change and human activities on Mediterranean species, particularly regarding abundance, body size, and trophic ecology. We demonstrate that the Atlantic bluefin tuna was likely influenced by both climate change and human activities, while the banded-dye murex and gilthead sea bream were probably impacted by human exploitation. Having a historical perspective, by integrating past data with current data, can inform current and future conservation and management strategies by understanding species-specific responses to disturbances and how contemporary trends fit within multi-temporal analyses. Furthermore, addressing the limitations of integrating past data remains an important area for future research.

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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 sub-region)	8,649 - 5,049	Andreou et al. (1996)
	Neolithic (Western sub-region)	7,000 - 5,000	Stuiver and Reimer (1986)
	Bronze Age (Eastern sub-region)	5,049 - 2,999	Andreou et al. (1996)
	Chalcolithic-Bronze (Western sub-region)	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 sub-region)	2,249 - 1,400	Roberts et al. (2011)
	Roman Period (Eastern sub-region)	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 (δ^{13}C and δ^{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	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{13}C
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 database included data for most of the searched species, except the annular sea bream, European pilchard, round sardinella, and Madeiran sardinella. The functional groups with the most data were fish, followed by molluscs and marine mammals. 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 (see supplementary material S3.1, S3.2, and S3.3). Geographically, the majority of data samples are from the Western (n = 194) and Eastern (n = 326) sub-regions, 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 sub-region. Within the Western and Eastern sub-regions, 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 (see supplementary material S3.1.1B–S3.1.4B). Regarding molluscs, the turbinate monodont is the only species with sufficient data to analyse differences between periods across sub-regions. This species shows two distinct NISP peaks: one between 45,000–30,000 years BP in the Eastern sub-region and another between 15,000–10,000 years BP, primarily in the Western sub-region. Despite these patterns, comparisons across periods revealed no significant outcomes (see supplementary material S3.2.1B and S3.2.2B).

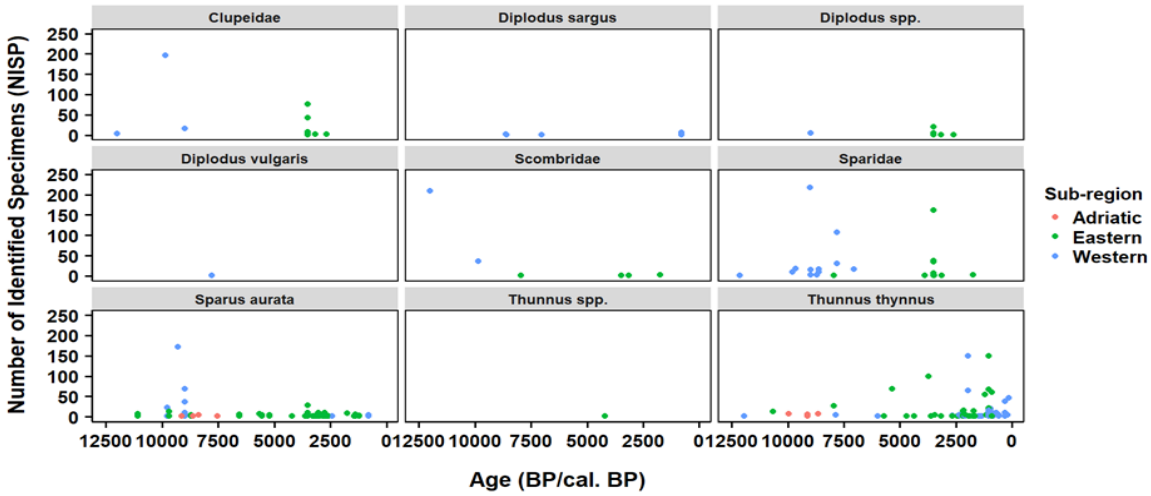


Figure S3.1 - Distribution of data for NISP for fishes. Colours separate the data for each sub-region of the Mediterranean Sea.

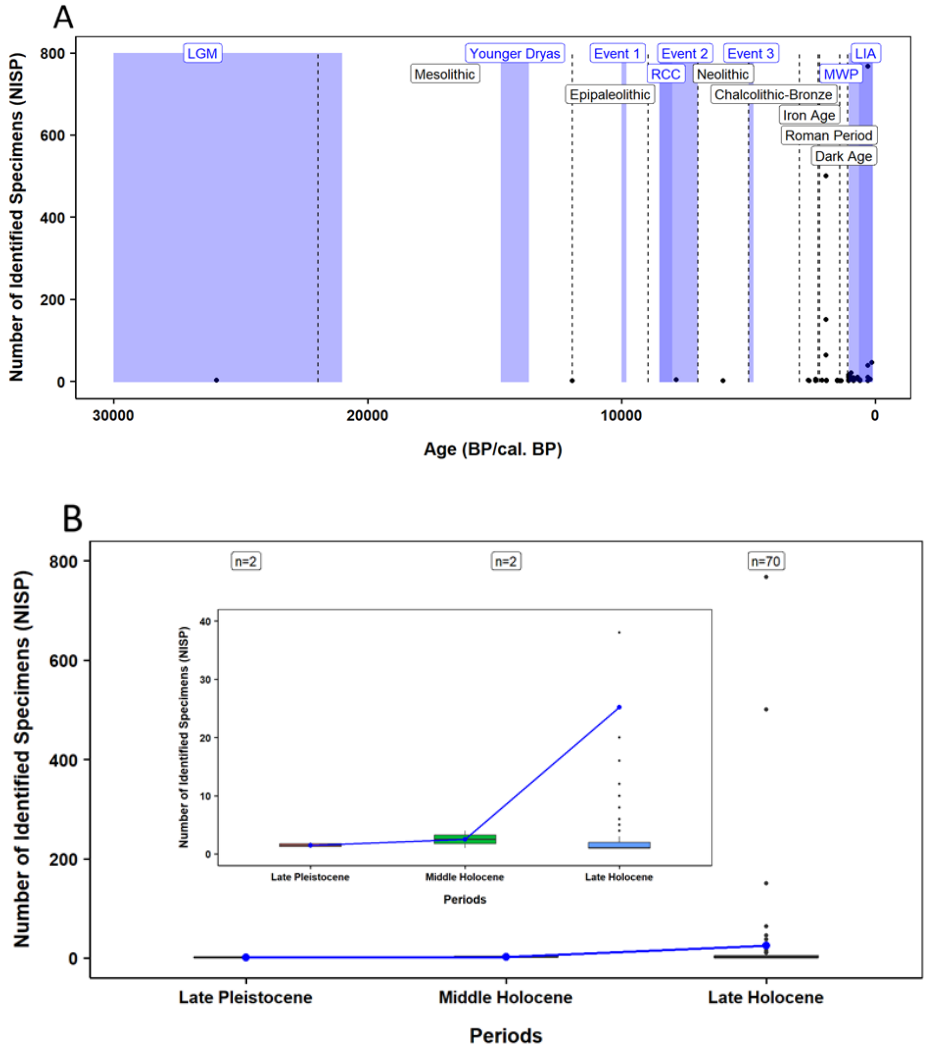


Figure S3.1.1 - Distribution of data for NISP on the Atlantic bluefin tuna in the Western sub-region. (A Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated 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).

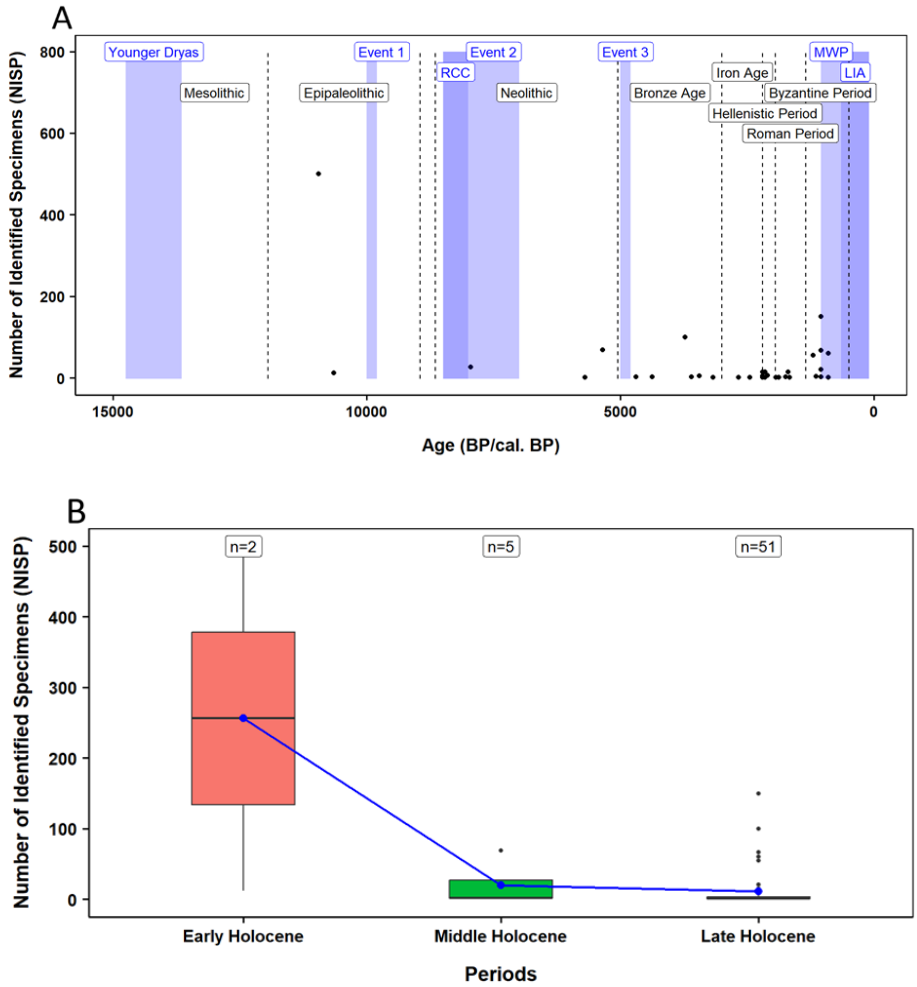
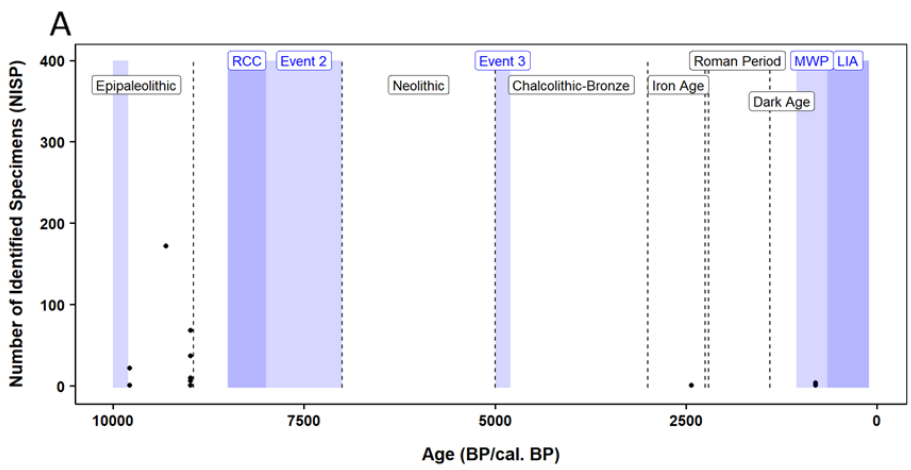


Figure S3.1.2 - Distribution of data for NISP on the Atlantic bluefin tuna in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.



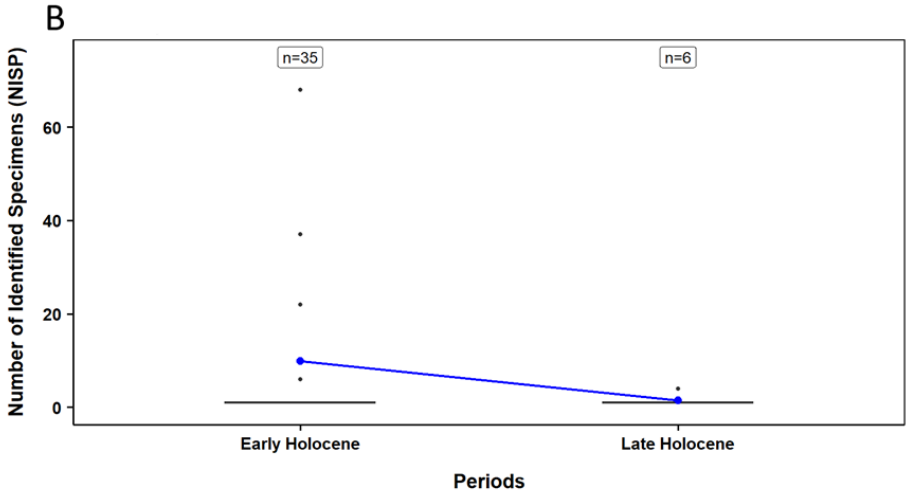


Figure S3.1.3 - Distribution of data for NISP on the gilthead sea bream in the Western sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

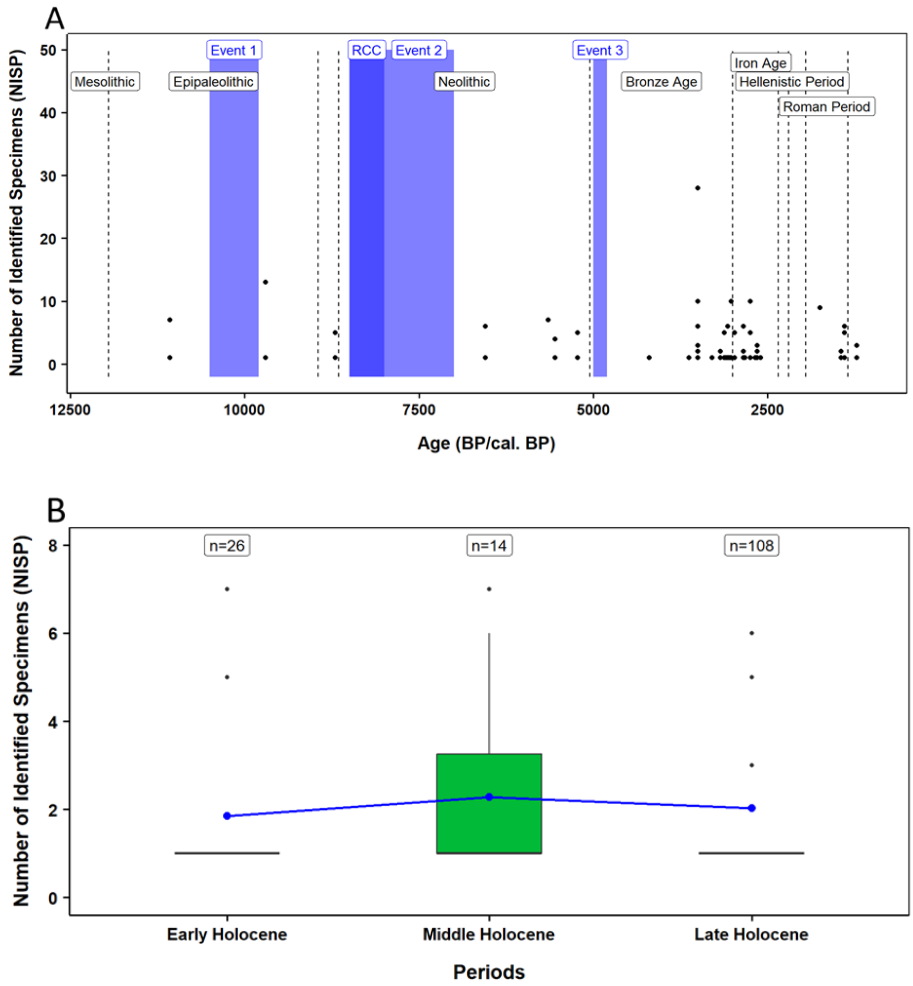


Figure S3.1.4 - Distribution of data for NISP on the gilthead sea bream in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

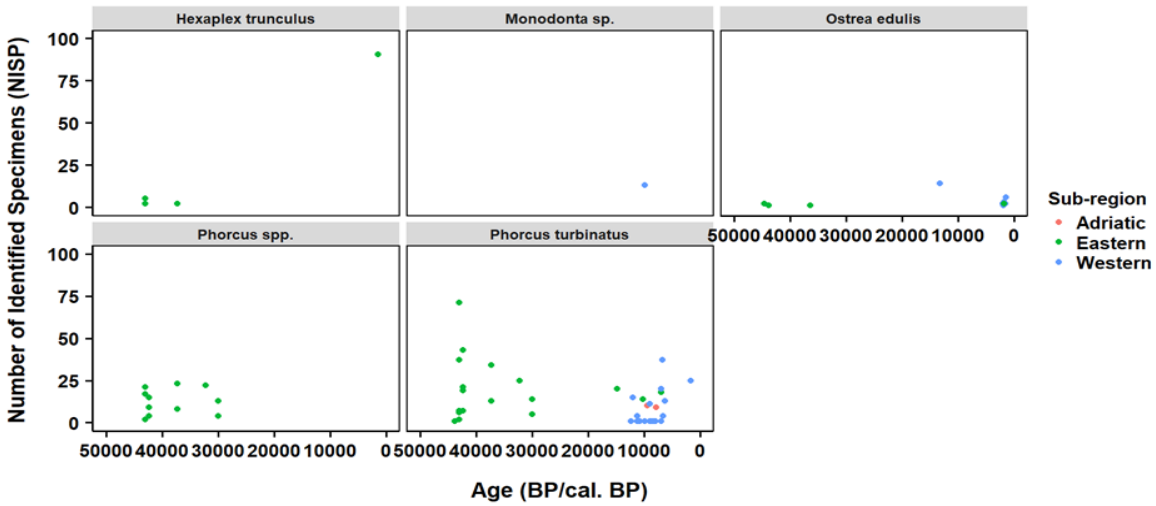
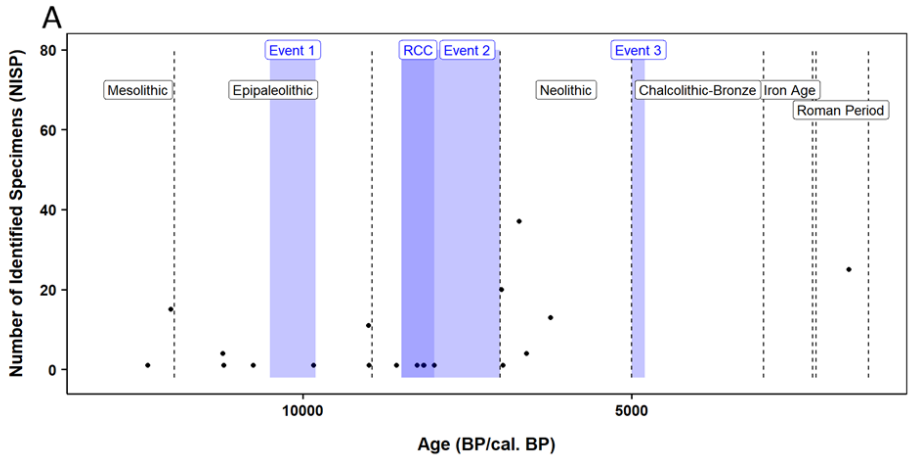


Figure S3.2 - Distribution of data for NISP for molluscs. Colours separate the data for each sub-region of the Mediterranean Sea.



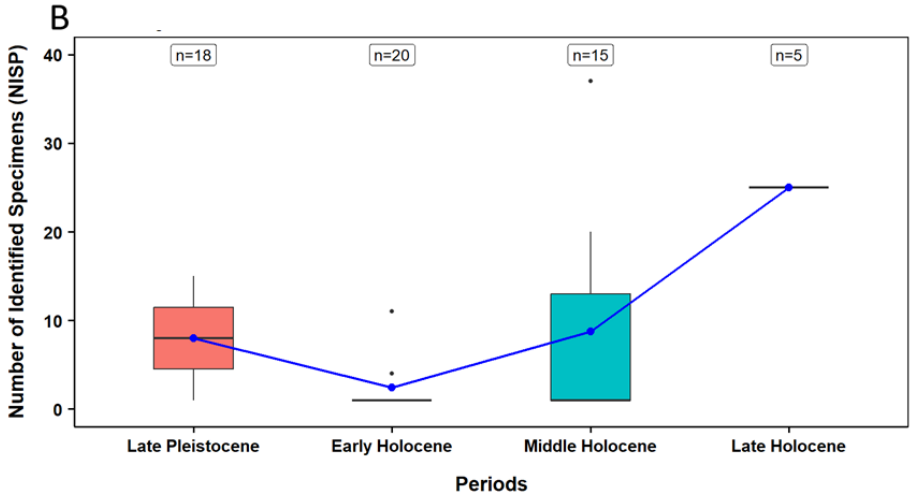
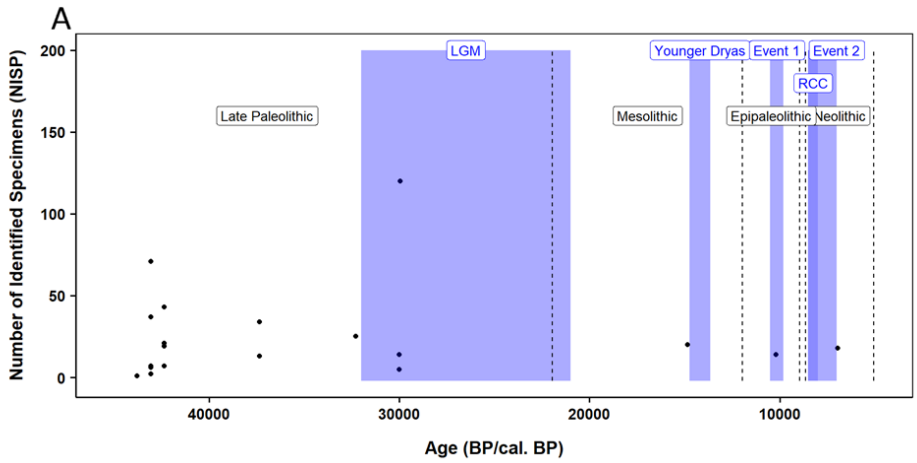


Figure S3.2.1 - Distribution of data for NISP on the turbinate monodont in the Western sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.



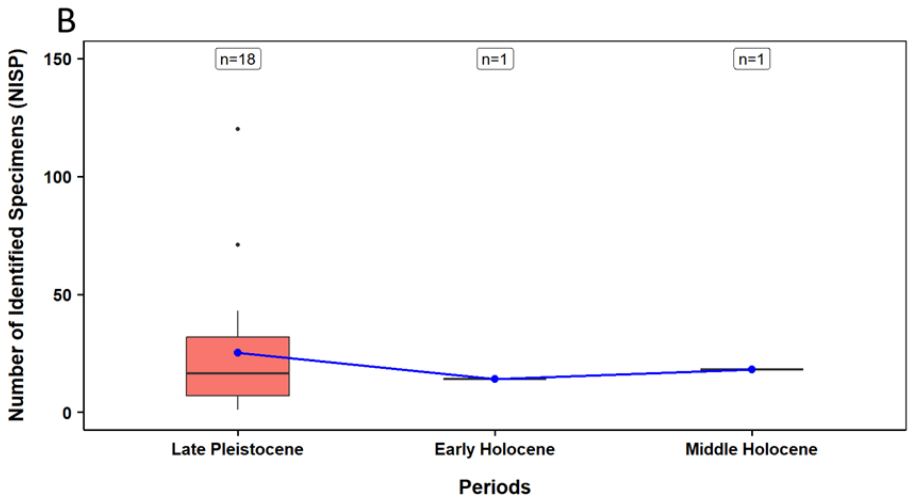


Figure S3.2.2 - Distribution of data for NISP on the turbinate monodont in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

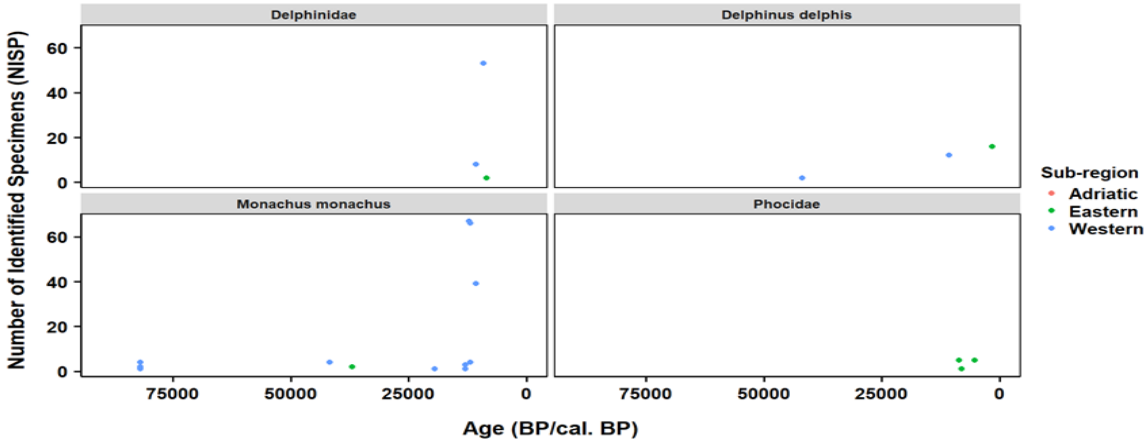


Figure S3.3 - Distribution of data for NISP for marine mammals. Colours separate the data for each sub-region of the Mediterranean Sea.

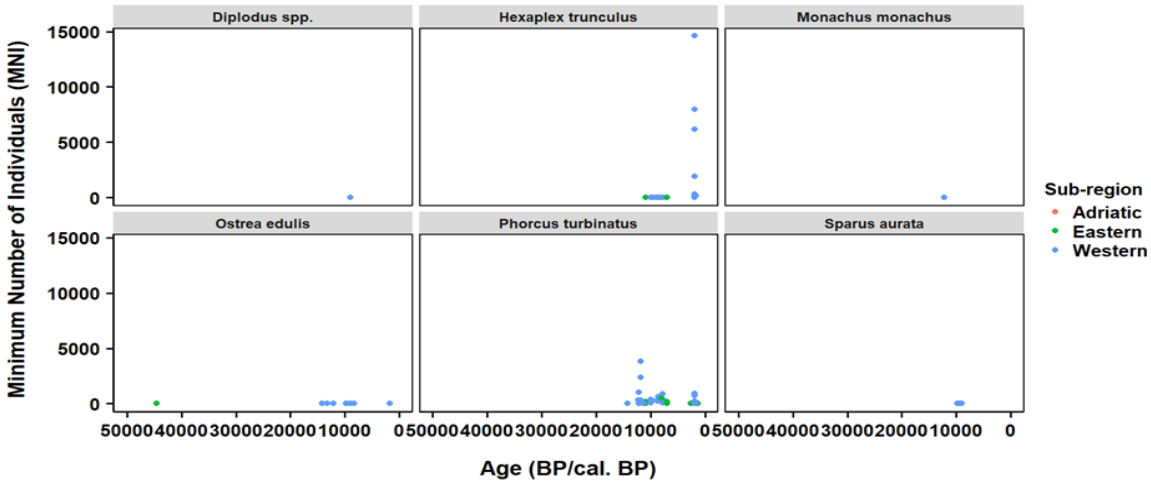


Figure S3.4 – MNI species distribution data. Colours separate the data for each sub-region of the Mediterranean Sea.

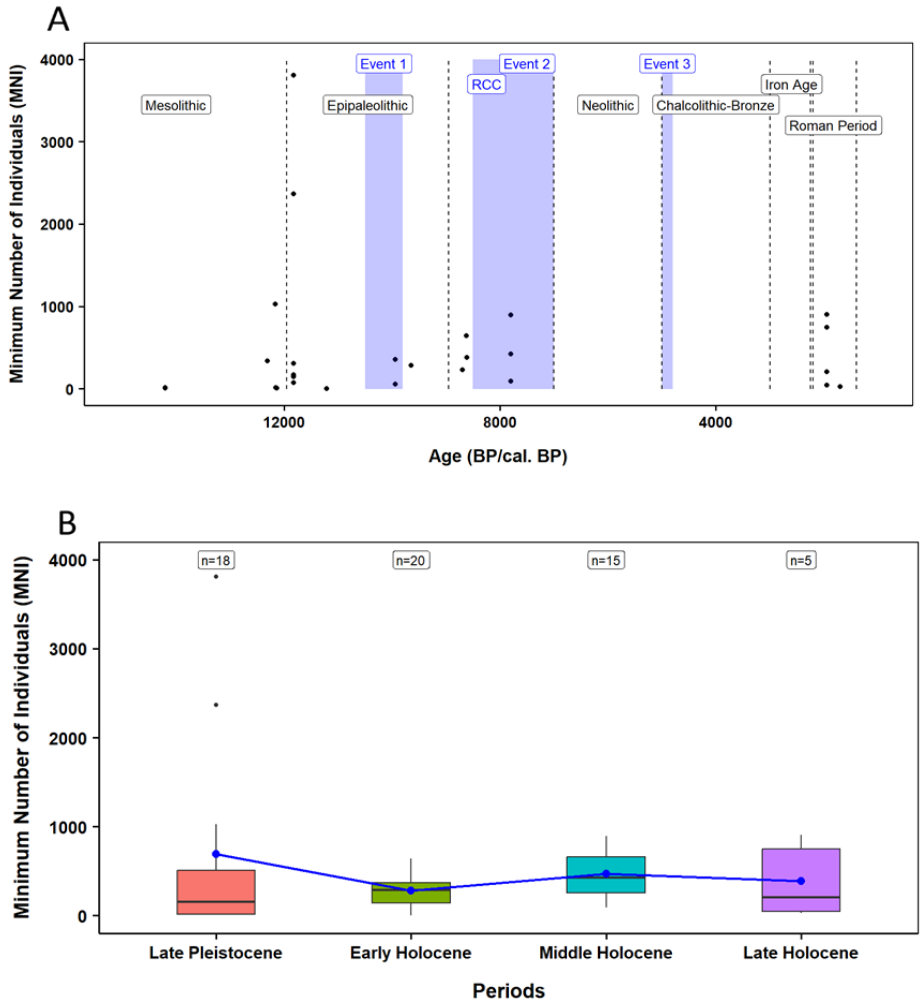
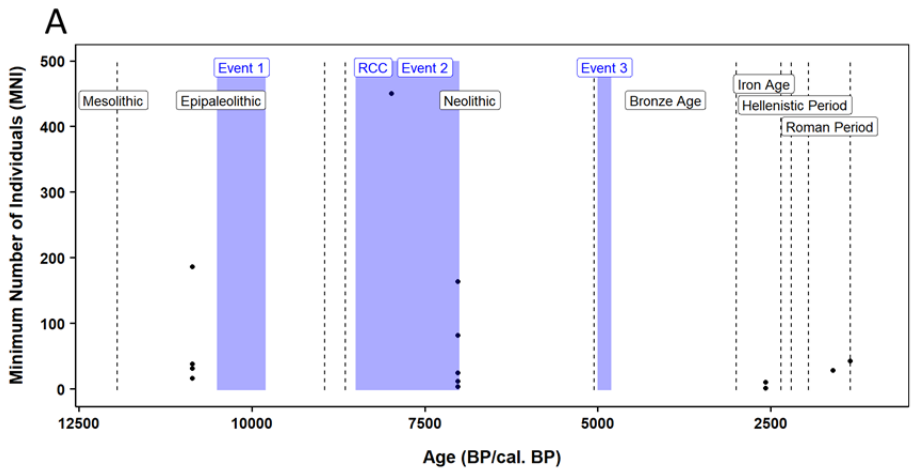


Figure S3.4.1 - Distribution of data for MNI on the turbinate monodont in the Western sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.



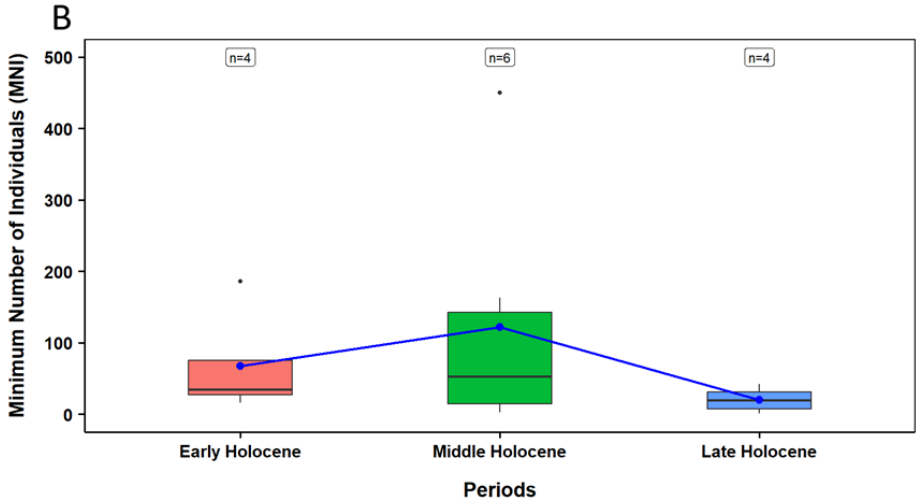


Figure S3.4.2 - Distribution of data for MNI on the turbinate monodont in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

S4. Catch records

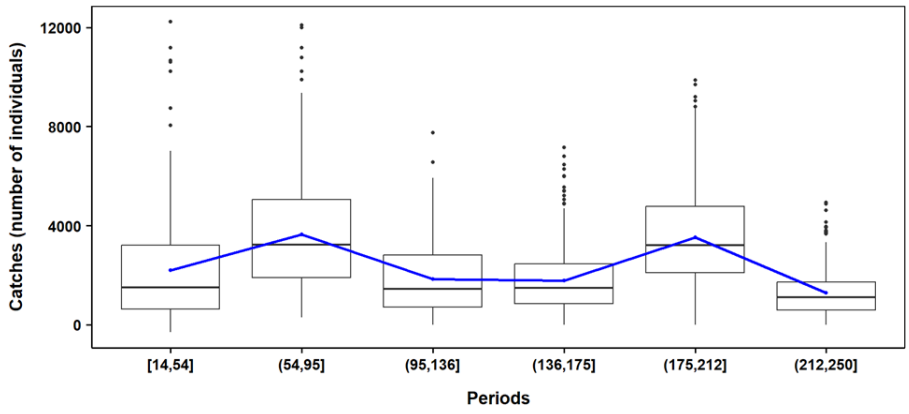


Figure S4 – Catches records of the Atlantic bluefin tuna divided into six periods, using the Jenks Natural Breaks Method, between 250–14 years BP. The blue dots, connected by the blue line, are the mean values for each period. The number of samples (n) included in each box plot is indicated above. The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

S5. Body size measures

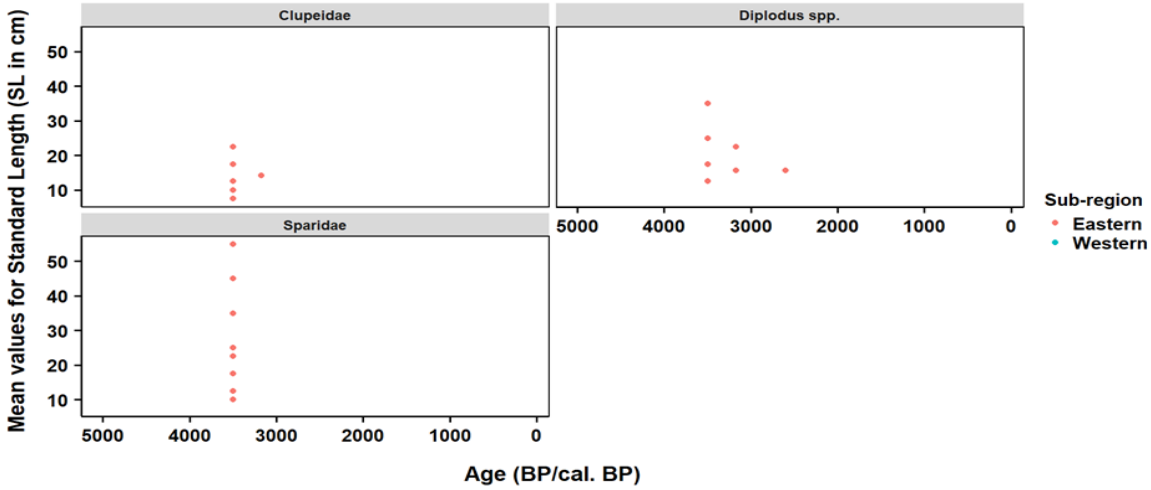


Figure S5.1 – Fishes distribution of data for Standard Length (SL). The colour indicates that the data comes from the Eastern Mediterranean Sea.

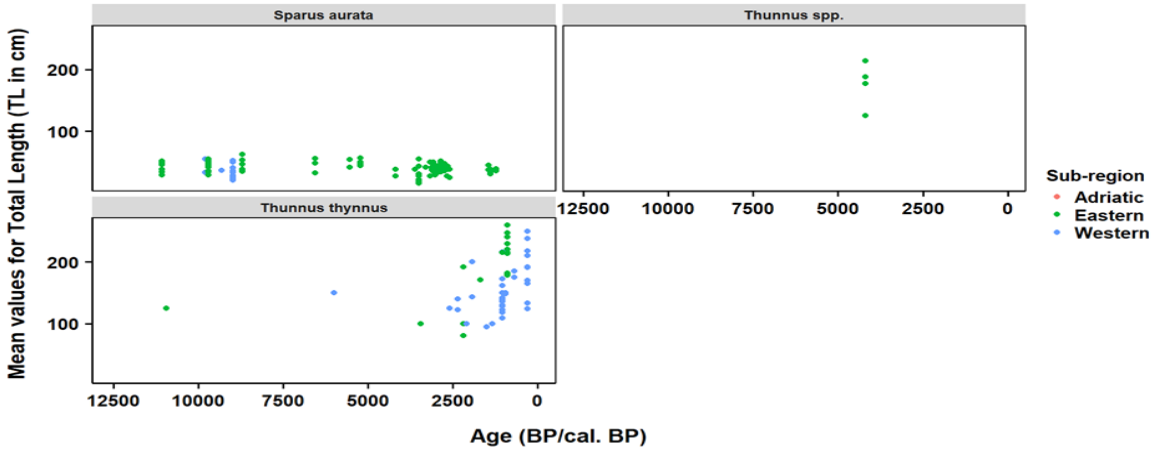
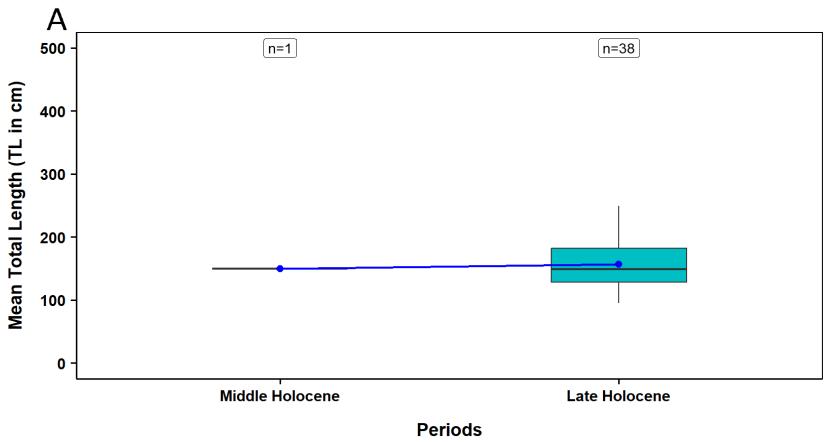


Figure S5.2 – Fishes distribution of data for Total Length (TL). The colour indicates from which sub-basin of the Mediterranean Sea the data comes.



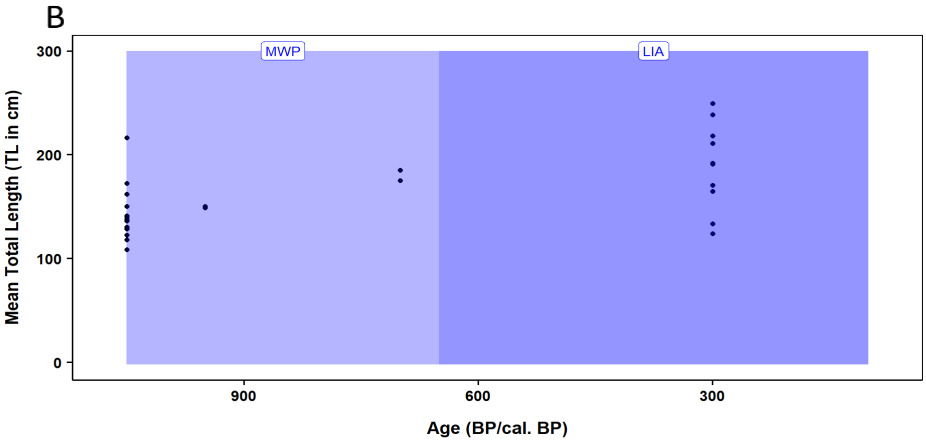


Figure S5.3 – Distribution of data for TL on the Atlantic bluefin tuna in the Western sub-region. (A) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above; (B) Total length differences between the MWP (Medieval Warm Period) and LIA (Little Ice Age).

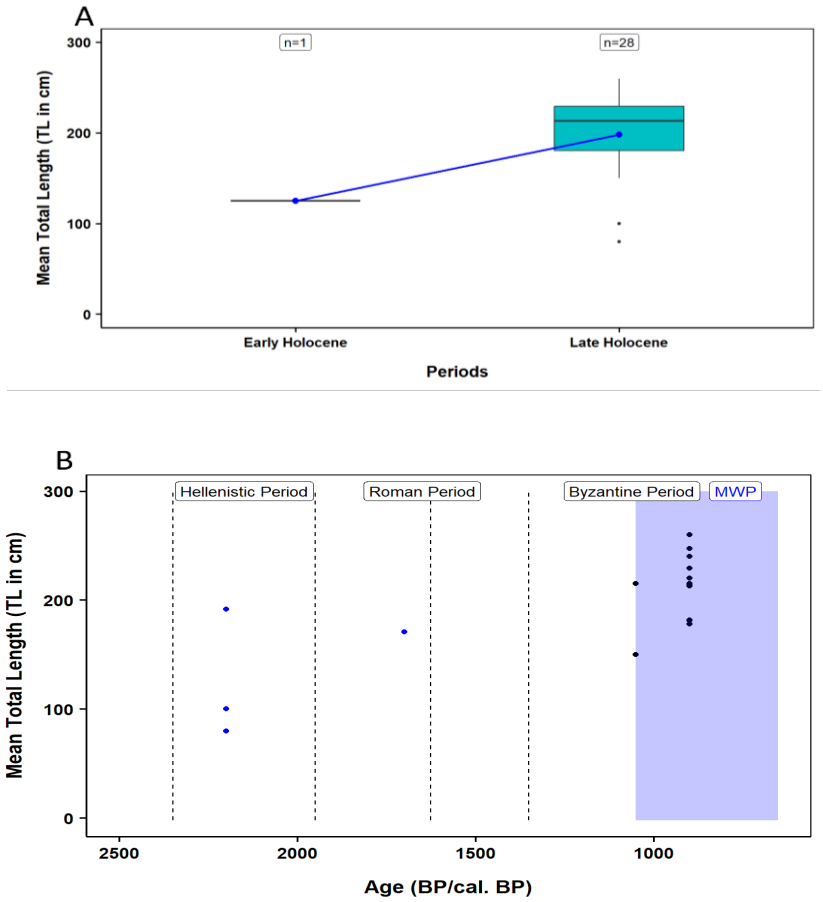


Figure S5.4 – Distribution of data for TL on the Atlantic bluefin tuna in the Eastern sub-region. (A) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n)

included in each box plot is indicated above; (B) differences between the before and during the MWP (Medieval Warm Period).

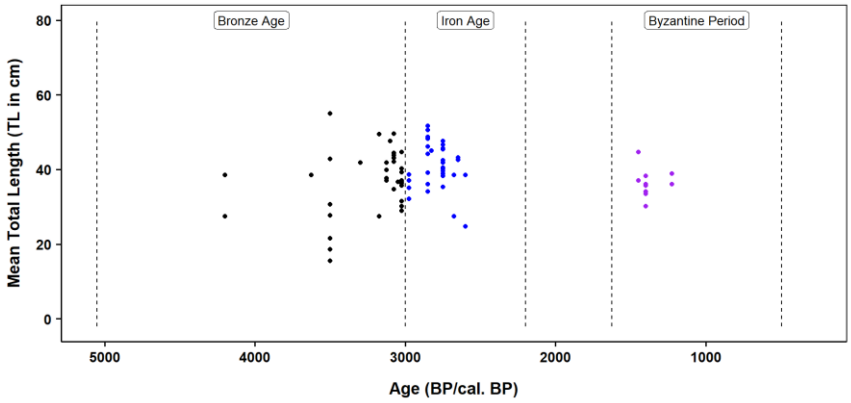


Figure S5.5 – Distribution of data for the TL on the Gilthead sea bream in the Eastern sub-region. Differences between the Bronze and Iron Ages and the Byzantine period.

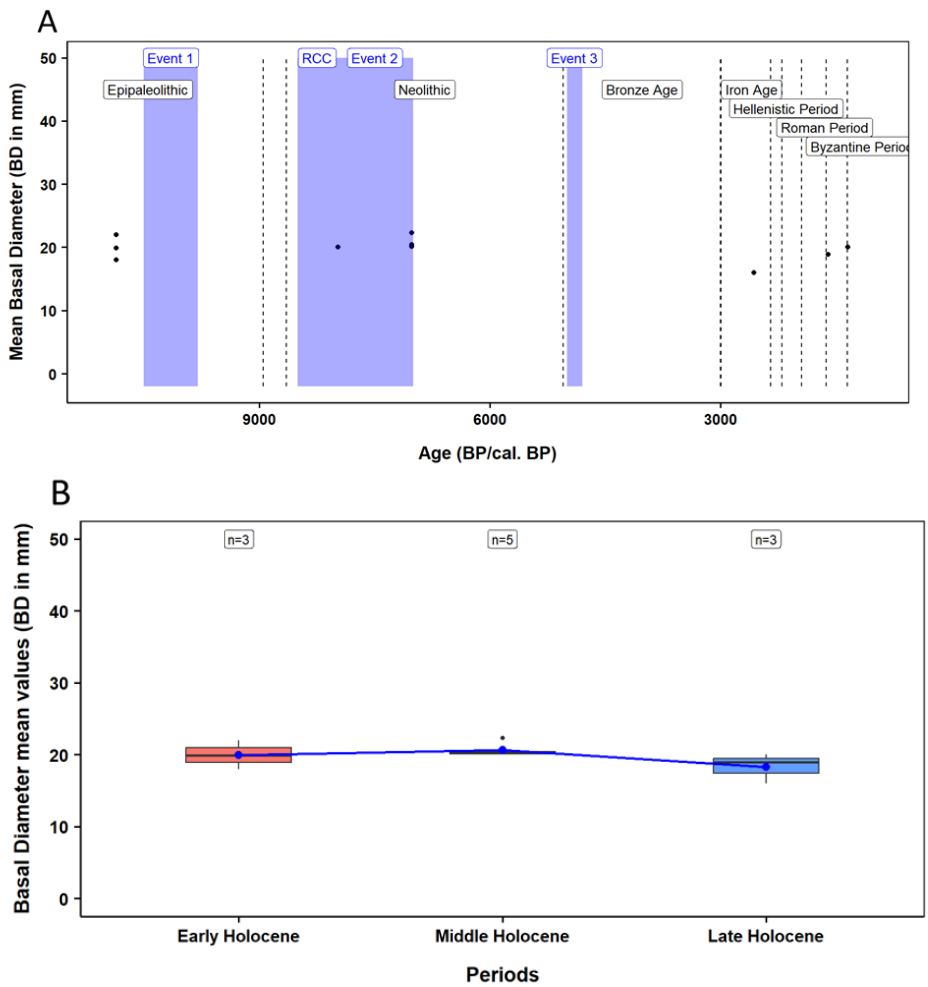


Figure S5.6 - Distribution of data for mean BD on the turbinate monodont in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

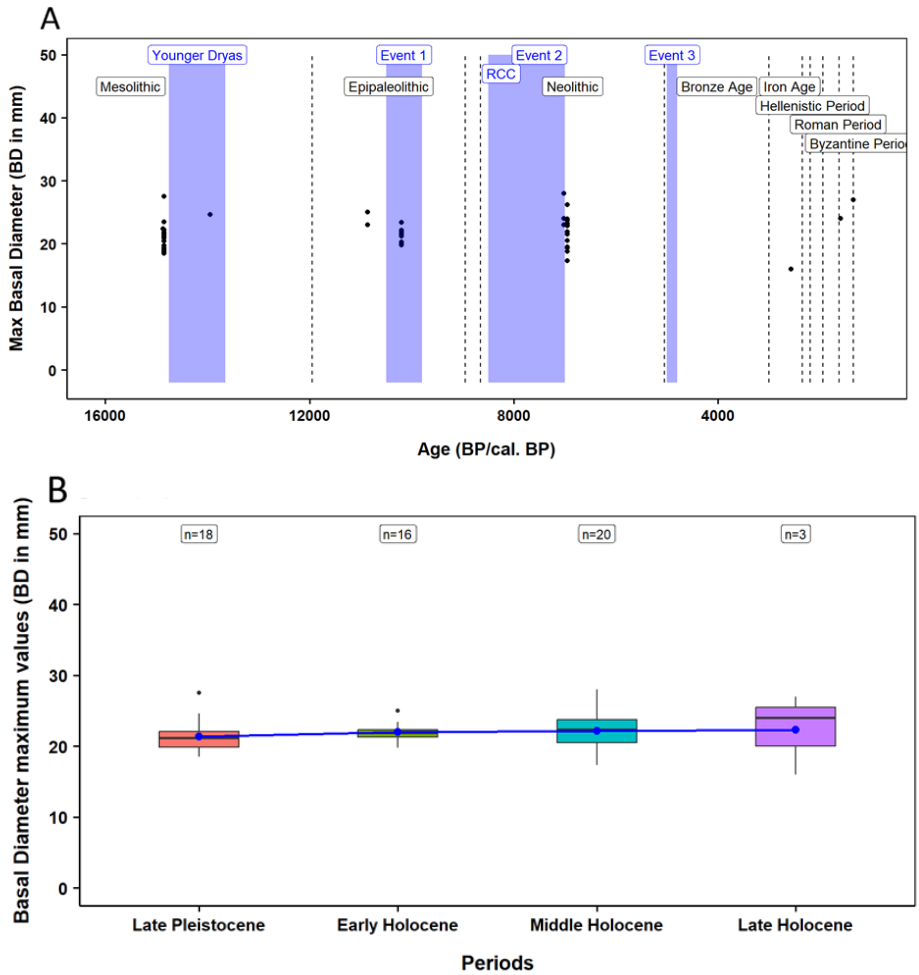


Figure S5.7 - Distribution of data for maximum values of BD on the turbinate monodont in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

S6. Stable isotopic data

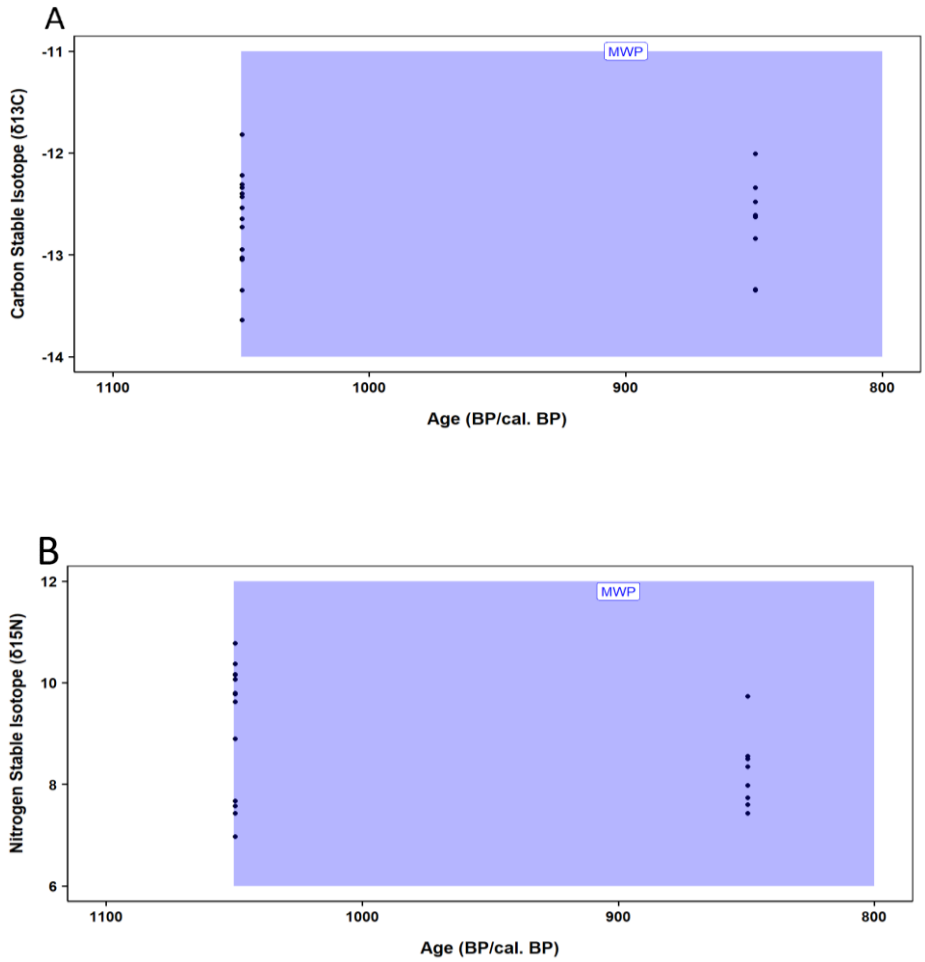
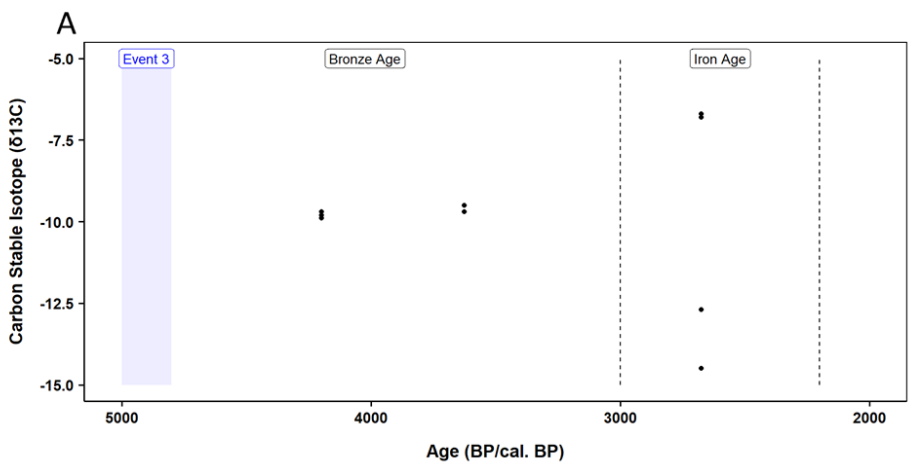


Figure S6.1 – Distribution of data for the δ^{13}C and δ^{15}N of the Atlantic bluefin tuna from the Western and Eastern sub-regions. (A) The δ^{13}C values fall within the Medieval Warm Period (MWP); (B) The δ^{15}N values fall within the Medieval Warm Period (MWP).



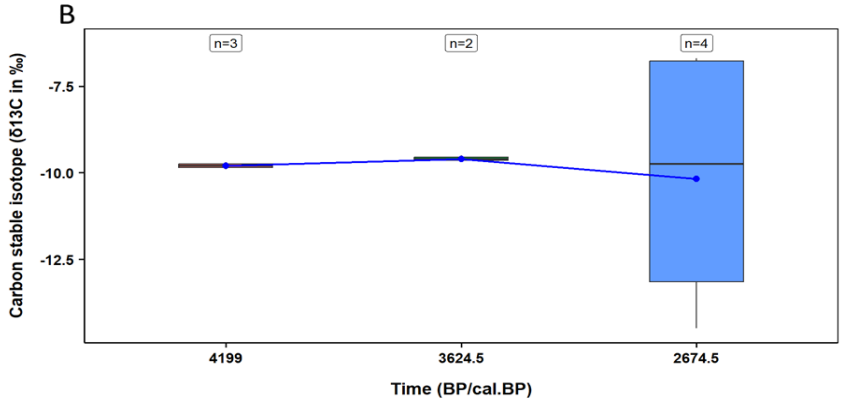


Figure S6.2 – Distribution of data for the δ^{13}C of the gilthead sea bream from the Eastern sub-region. (A) The δ^{13}C values fall between the Bronze and Iron Ages; (B) Boxplots of the differences between data with three mean ages. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

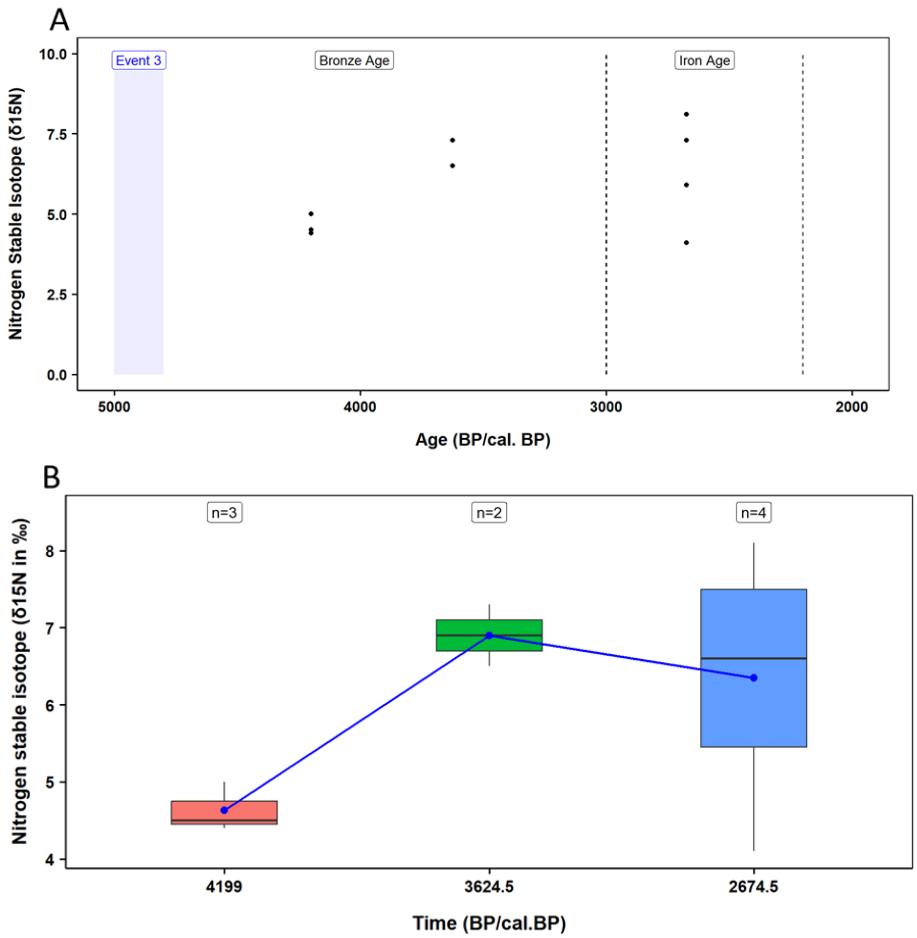


Figure S6.3 – Distribution of data for the δ^{15}N of the gilthead sea bream from the Eastern sub-region. (A) The δ^{15}N values fall between the Bronze and Iron Ages; (B) Boxplots of the

differences between data with three mean ages. The blue dots are the mean values for each period and the bars are the standard deviation. The number of samples (n) included in each box plot is indicated above.

References Supplementary Material

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