

**DANIELA DE OLIVEIRA LEAL**

**Climate versus Pre-industrial Human Impacts on Marine  
Mammals, Fishes, and Molluscs in the Mediterranean Sea  
over the last 130 ka**



**UNIVERSIDADE DO ALGARVE**

Faculdade de Ciências e Tecnologia

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Mammals, Fishes, and Molluscs in the Mediterranean Sea  
over the last 130 ka**

**Mestrado em Biologia Marinha**

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**UNIVERSIDADE DO ALGARVE**

Faculdade de Ciências e Tecnologia

**2023/2024**

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**Climate versus Pre-industrial Human Impacts on Marine Mammals, Fishes, and Molluscs in the Mediterranean Sea over the last 130 ka**

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## Resumo

Os ecossistemas marinhos estão entre os sistemas mais diversificados e de maior valor socio-económico do mundo. Estes fornecem inúmeros bens e serviços, incluindo provisão, regulação, culturais e de suporte. O Mar Mediterrâneo está localizado entre três continentes - África, Europa e Ásia - encontrando-se a uma latitude média entre 45-30°N. Esta bacia é considerada a maior do mundo, ocupando 0,7% de toda a área global da superfície oceânica. Abrigando cerca de 7,5% da diversidade marinha mundial, o Mar Mediterrâneo é considerado o segundo maior hotspot de biodiversidade a nível mundial. Contudo, os ecossistemas de todo o mundo têm sido alvo de modificações desde os tempos ancestrais, mesmo antes do início da evolução humana. O Mar Mediterrâneo testemunhou a evolução de muitas comunidades, desde os nómadas caçadores-coletores até ao sedentarismo do Neolítico e à consequente implementação de sociedades e civilizações, como o Império Romano, que em determinado momento deteve todo o poder social e económico desta região. Dada a sua longa existência, este mar foi alvo de diversos fenómenos climatológicos e ambientais que modificaram vários aspectos inerentes ao seu funcionamento, como as correntes, taxas de sedimentação, exposição solar, temperatura e salinidade, produtividade primária, entre outros. Atualmente, a investigação está amplamente focada em eventos considerados "recentes", mas que não possuem mais de 100 anos. Esta restrição temporária limita consideravelmente o nosso conhecimento sobre as alterações que os ecossistemas - como o Mar Mediterrâneo - já sofreram ao longo da sua história, bem como sobre as possíveis respostas biológicas dadas face a essas mudanças. Desta forma, é necessário estudar quais foram os impactos mais significativos e as respetivas respostas do ponto de vista de um ecossistema pristino, comparativamente ao estado atual do mesmo. Para tal, efetuamos uma revisão sistemática baseada no método PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses), que se focou em diversas espécies comercialmente importantes de mamíferos marinhos, peixes e moluscos dos últimos 130 000 (130 ka) anos até à Revolução Industrial. Para cada grupo taxonómico, os dados foram separados por sub-região do Mediterrâneo (Este, Oeste e Adriático). Posteriormente, os dados de espécies com informação suficiente foram comparados com alguns dos principais eventos climáticos e mudanças em períodos culturais por sub-região. Os resultados evidenciaram impactos significativos em três espécies: o molusco *Hexaplex trunculus* e os peixes *Thunnus thynnus* e *Sparus aurata*, em particular

durante o período do Holoceno (que começou há aproximadamente 11 000 anos). *Thunnus thynnus* sofreu alterações na sua abundância, tamanho do corpo, utilização de habitat e nível trófico, tanto de origem ambiental como humana. *Hexaplex trunculus* e *Sparus aurata* deverão ter sido intensivamente explorados durante certos períodos da história, o que resultou em alterações da abundância e do tamanho do corpo, respetivamente. Em termos ambientais, mudanças de temperatura podem ter levado a diferenças na abundância e na dimensão do corpo da espécie *T. thynnus*. O nosso trabalho evidencia alterações na abundância desta espécie, particularmente durante a Pequena Idade do Gelo na sub-região ocidental do Mediterrâneo, o que poderá estar relacionado com a descida da temperatura das águas do mar. Isto poderá ter alterado os seus padrões migratórios no Mediterrâneo, verificando-se mudanças na sua abundância. Em contrapartida, o aumento de tamanho observado tanto na região leste como oeste, poderá estar relacionado com alterações na temperatura das águas e pelo facto desta espécie ter uma dieta generalista. Isto poderá ter-lhe permitido alocar energias de modo a aumentar o seu tamanho corporal. Mudanças sub-regionais na produtividade primária deste ecossistema podem ter levado a diferentes usos do habitat e em variações no nível trófico desta espécie. Em particular, os dados de  $\delta^{13}\text{C}$  dos tecidos desta espécie apontam para uma distribuição mais costeira na parte ocidental do Mediterrâneo e uma preferência por zonas offshore na zona oriental. Essas possíveis preferências podem ser explicadas com base nas características do Mediterrâneo e na diferente utilização das áreas pela espécie. A sub-região ocidental é considerada uma importante zona de reprodução para esta espécie, enquanto a sub-região oriental, por ser mais profunda, permite-lhes procurar alimento em áreas mais profundas e afastadas da costa. Simultaneamente, o aumento dos valores de  $\delta^{15}\text{N}$  na sub-região ocidental do Mediterrâneo ocidental, em comparação com a oriental, poderá dever-se a diferenças na disponibilidade de nutrientes entre as duas regiões, uma vez que fenómenos locais podem aumentar a produtividade de certas regiões. Relativamente às atividades humanas, diferentes níveis de exploração destas três espécies podem ter levado a impactos tanto nas suas abundâncias como nas suas dimensões corporais. A sobre-exploração de *H. trunculus* durante a fase mais recente do Holoceno mas sobretudo durante o Império Romano, pode ter resultado em alterações significativas na sua abundância. As diferenças de abundância evidenciadas para *T. thynnus* poderão ser explicadas pela melhoria dos instrumentos de pesca ao longo da história, principalmente com o desenvolvimento de instrumentos mais sofisticados e frotas navais mais

poderosas. Embora o número de capturas de *T. thynnus* tenha sido mais elevado há cerca de 150 anos, tal pode ter ocorrido também como resultado de fenómenos de expansão populacional. Infelizmente, este tipo de informação não é acessível devido à escassez de dados históricos. Em contrapartida, a sobre-exploração de *S. aurata* poderá ter levado a um decréscimo no seu tamanho corporal, particularmente durante a fase mais recente do Holoceno. Entre a Idade do Bronze, Idade do Ferro e o Período Bizantino, a exploração desta espécie está particularmente evidenciada no leste do Mediterrâneo, o que poderá ter levado aos decréscimos observados. O nosso trabalho reuniu evidências significativas sobre impactos de origem climática e antropogénica experienciados no passado recente do Mar Mediterrâneo nestas três espécies marinhas. Essas alterações podem ter resultado indiretamente em modificações na estrutura e funcionamento do ecossistema marinho nos últimos 130 ka anos. Os resultados destacam a importância da integração de dados do passado (paleontológicos, arqueológicos e históricos) com dados biológicos contemporâneos para se obter um quadro temporal mais abrangente. Isso é essencial para compreender a história dos ecossistemas marinhos e as respostas específicas dadas pelas espécies a essas perturbações. Esta abordagem inclusiva e histórica garante a aplicação mais adequada de estratégias de gestão ambiental atuais e futuras, além da implementação de medidas de conservação mais direcionadas a cada espécie e às suas necessidades biológicas específicas.

Palavras-chave: Alterações ambientais, Alterações climáticas, Ecossistemas Marinhos, Holoceno, Impactos humanos, Mar Mediterrâneo

## Abstract

Climate change and anthropogenic activities have long been modifying marine ecosystems. The Mediterranean Sea has a long history of interactions between climate, humans, and its marine ecosystems. To evaluate these impacts, a systematic review of commercially important species of marine mammals, fishes, and molluscs over the last 130,000 (130 ka) years up until the Industrial Revolution (year 1850) was employed. The study area, the Mediterranean Sea, was classified into different sub-regions: Western, Eastern and Adriatic. The results showed significant impacts on the mollusc *Hexaplex trunculus* and two fish species *Thunnus thynnus* and *Sparus aurata*. Our results suggested that *T. thynnus* experienced changes in abundance, body size, habitat use and trophic level probably due to environmental (e.g., changes in temperature and primary productivity) and human (e.g., overfishing) impacts. *Hexaplex trunculus* and *S. aurata* were highly exploited by humans during certain periods, resulting in abundance and body size changes, respectively. This work compiled significant evidence of impacts on marine species from the Mediterranean Sea. These changes might have indirectly resulted in modifications to the structure and functioning of the marine ecosystems over the past 130 ka. These findings highlight the importance of integrating past data (paleontological, archaeological and historical) with contemporary biological data to gain a more comprehensive temporal framework. Understanding marine ecosystem history and species-specific responses to such disturbances is essential. This inclusive geohistorical approach guarantees the implementation of appropriate present and future environmental management strategies, in addition to the implementation of specialised conservation measures.

Keywords: Climate change, Environmental changes, Human impacts, Holocene, Marine ecosystem, Mediterranean Sea

# Table of Contents

|   |            |
|---|------------|
| <b>Acknowledgements</b> .....   | <b>i</b>   |
| <b>Resumo</b> .....   | <b>ii</b>  |
| <b>Abstract</b> .....   | <b>v</b>   |
| <b>Table of Contents</b> .....  | <b>vi</b>  |
| <b>Index of Figures</b> .....   | <b>vii</b> |
| <b>Index of Tables</b> .....  | <b>x</b>   |
| <b>List of Abbreviations</b> .....  | <b>xi</b>  |
| <b>CHAPTER 1: INTRODUCTION</b> .....  | <b>1</b>   |
| 1. THE MEDITERRANEAN SEA.....   | 1          |
| 1.1 Geographical Context .....  | 1          |
| 1.2 Biodiversity.....   | 3          |
| 1.2.1 Ecological Role of Marine Fauna in the Mediterranean Sea .....  | 5          |
| 2. IMPACTS IN THE MEDITERRANEAN SEA.....  | 8          |
| 2.1 Current Impacts .....   | 8          |
| 2.2 Past Impacts .....  | 10         |
| 2.2.1 Late Pleistocene-Holocene Climate Variability and its impact on Mediterranean marine biota.....   | 10         |
| 2.2.2 Past Human Activities and its impact on Mediterranean marine biota .....  | 12         |
| 2.3 The Importance of Studying the Past .....   | 15         |
| 3. THE AIM OF THIS WORK.....  | 16         |
| 4. OBJECTIVES AND HYPOTHESES .....  | 16         |
| 5. METHODOLOGY APPLIED: PRISMA GUIDELINES.....  | 16         |
| 6. REFERENCES .....   | 17         |
| <b>CHAPTER 2: CLIMATE VERSUS PRE-INDUSTRIAL HUMAN IMPACTS ON MARINE MAMMALS, FISHES, AND MOLLUSCS IN THE MEDITERRANEAN SEA OVER THE LAST 130 KA</b> ..... | <b>30</b>  |
| ABSTRACT .....  | 30         |
| INTRODUCTION .....  | 31         |
| MATERIALS AND METHODS.....  | 35         |
| RESULTS .....   | 42         |
| DISCUSSION .....  | 56         |
| ACKNOWLEDGEMENTS.....   | 64         |
| REFERENCES.....   | 64         |
| SUPPLEMENTARY MATERIAL.....   | 77         |

# Index of Figures

## CHAPTER 1: INTRODUCTION

**Figure 1.1** - Thermohaline circulation with the major conveyor belt systems. The yellow dashed line represents the Atlantic Water Stream (AW), which is the surface manifestation of the zonal conveyor belt of the Mediterranean. The red dashed line represents the mid-depth of the Levantine Intermediate Water formation (LIW) of the zonal thermohaline circulation. The blue dashed line represents the meridional cells induced by deep waters. LIW branching from the zonal conveyor belt connects meridional and zonal conveyor belts. Figure and caption retrieved from Pinardi and Masetti (2000).....2

## CHAPTER 2: CLIMATE VERSUS PRE-INDUSTRIAL HUMAN IMPACTS ON MARINE MAMMALS, FISHES, AND MOLLUSCS IN THE MEDITERRANEAN SEA OVER THE LAST 130 KA

**Figure 2.1** - Mediterranean Sea and the regional divisions (Western, Eastern and Adriatic) that it was adopted in this work. Black and Marmara Sea are also indicated.....35

**Figure 2.2** - PRISMA 2020 flow diagram adapted from Page et al., 2021, highlighting the methodology and selection process used, indicating the number (n) of studies included in this review. Numbers in bold are key values related to the number of studies included in the process of the evaluation.....43

**Figure 2.3** - Mediterranean Sea map with sampling units (red circles). Each number corresponds to a unique sampling location from which the data came from. See more information regarding the name of each sampling location and the corresponding publication in Table S6.....44

**Figure 2.4** – Distribution of data for the MNI of *Hexaplex trunculus* 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 letters represent statistically significant differences between periods. The number of points (n) included in each box plot is indicated above.....46

**Figure 2.5** – Atlantic Bluefin Tuna (*Thunnus thynnus*) catches records between 250-14 years BP (1700-1936), from tuna-traps in the Western Mediterranean Sea. The black points refer to the data collected between 250-100 years BP (1700-1850), and the lighter points refer to the catch records between 99-14 years BP (1851-1936). The red points are records of SST reconstructed from the Gulf of Lions (France) (data from Jalali et al., 2016). LIA: Little Ice Age lasted until 100 years BP; Industrial fisheries: minor modifications were made to tuna traps until the 1960's (Doumenge, 1998); WWI: World War I, lasted between 36-32 years BP.....48

**Figure 2.6** – Catches records of *Thunnus thynnus* 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 points (n) included in each box plot is indicated above. The black dots are outliers.....49

**Figure 2.7** – Distribution of data for TL on *Thunnus thynnus* 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 points (n) included in each box plot is indicated above; (C) Total length differences between the MWP (Medieval Warm Period) and LIA (Little Ice Age).....50

**Figure 2.8** – Distribution of data for TL on *Thunnus thynnus* 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 points (n) included in each box plot is indicated above; (C) differences between the before and during the MWP (Medieval Warm Period).....52

**Figure 2.9** – Distribution of data for the TL of *Sparus aurata* 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 letters represent statistically significant differences between periods. The number of points (n) included in each box plot is indicated above. (C) differences between the Bronze and Iron Ages and the Byzantine Period for TL data.....53

**Figure 2.10** – Distribution of data for the  $\delta^{13}\text{C}$  of *Thunnus thynnus* between the Western and Eastern sub-regions between 1,050-850 years BP. (A) The  $\delta^{13}\text{C}$  values fall within the MWP (Medieval Warm Period); (B) Boxplots of the Western and Eastern sub-regions of the Mediterranean. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.....55

**Figure 2.11** - Distribution of data for the  $\delta^{15}\text{N}$  of *Thunnus thynnus* between the Western and Eastern sub-regions between 1,050-850 years BP. (A) The  $\delta^{15}\text{N}$  values fall within the MWP (Medieval Warm Period); (B) Boxplots of the Western and Eastern sub-regions of the Mediterranean. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.....56

## Index of Tables

### CHAPTER 2: Climate versus Pre-industrial Human Impacts on Marine Mammals, Fish, and Molluscs in the Mediterranean Sea over the last 130 ka

|  |    |
|--|----|
| <b>Table 2.1</b> - Inclusion and exclusion criteria for literature in the systematic review.....   | 39 |
| <b>Table 2.2</b> – Results from the pairwise comparisons between periods for <i>Thunnus thynnus</i> , adjusted by the Bonferroni correction method. Numbers in bold represent the periods that differ significantly from each other..... | 49 |

## List of Abbreviations

BD – Basal Diameter

BP - Before Present

DAs - Death assemblages

ka - kilo annum or thousand years

LGM - Last Glacial Maximum

LIA - Little Ice Age

MNI - Minimum Number of Individuals

MWP - Medieval Warm Period

NISP - Number of Identified Specimens

RCC - Rapid Climate Change

RRA - Reported Relative Abundance

SL - Standard Length

SST – Sea Surface Temperature

TL - Total Length

$\delta^{13}\text{C}$  - Carbon Stable Isotope

$\delta^{15}\text{N}$  - Nitrogen Stable Isotope

# CHAPTER 1: INTRODUCTION

## 1. THE MEDITERRANEAN SEA

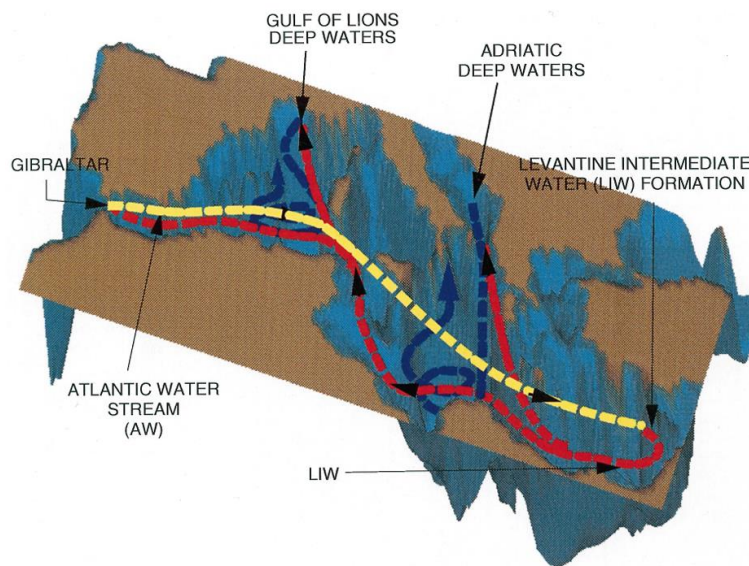
### 1.1 Geographical Context

The Mediterranean Sea, or *mare nostrum*, is a latitudinal basin within the northern hemisphere's temperate zone (Bas, 2009). It is a transcontinental semi-enclosed sea that borders Europe, Asia, and Africa (Coll et al., 2010). It is considered the largest sea in the world (approximately 3 million km<sup>2</sup>, and a maximum depth of approximately 5,300 m; Coll et al., 2010) with a surface area of around 2.5 million km<sup>2</sup> (Notarbartolo Di Sciara, 2016), corresponding to only 0.7% of the global ocean surface area (Sabelli & Taviani, 2014).

It is currently connected to the Atlantic Ocean through the Strait of Gibraltar, to the Marmara Sea through the Dardanelles Strait, and to the Black Sea through the Bosphorus Strait. It is also connected to the Red Sea and the Indian Ocean through the Suez Strait in the southeast since it was artificially opened in 1869 (Por, 1971). According to Spalding et al. (2007), the overall biogeographic complexity of the Mediterranean Sea makes this area a unique province within the Temperate Northern Atlantic realm, including seven ecoregions: (1) Adriatic Sea, (2) Aegean Sea, (3) Levantine Sea, (4) Tunisian Plateau/Gulf of Sidra, (5) Ionian Sea, (6) Western Mediterranean, and (7) Alboran Sea.

There are two straits - Sicily (between Italy and Tunisia) and Otranto (between Italy and Albania) – that act as physical barriers separating this basin into three regions: the Western and Eastern sub-basins, and the Adriatic Sea (Millot & Taupier-Letage, 2005; Rio et al., 2007; Robinson et al., 2009). The straits of the Mediterranean Sea represent a significant geomorphological feature because they connect the various sub-basins and control the flow of vast quantities of water, exerting a great influence on the oceanographic dynamics within the Mediterranean but also in the neighbouring seas (Astraldi et al., 1999). Therefore, the Mediterranean Sea presents a unique circulation and current system, globally classified as a 'concentration basin' (Bethoux, 1979; Hopkins, 1985; Pinardi et al., 2006; Bas, 2009). Since the evaporation rates in the Mediterranean are higher, a density gradient is formed across the Strait of Gibraltar, creating an inflow of cool, less saline Atlantic water at the surface, and an outflow of warmer, more saline (and therefore denser) Mediterranean water at the bottom layer. As the Atlantic inflow water reaches the Eastern Mediterranean, it warms up, becomes

saltier, and eventually sinks before circulating westward and exiting through the Strait of Gibraltar as Mediterranean outflow water (Robinson et al., 2009).



**Figure 1.1** - Thermohaline circulation with the major conveyor belt systems. The yellow dashed line represents the Atlantic Water Stream (AW), which is the surface manifestation of the zonal conveyor belt of the Mediterranean. The red dashed line represents the mid-depth of the Levantine Intermediate Water formation (LIW) of the zonal thermohaline circulation. The blue dashed line represents the meridional cells induced by deep waters. LIW branching from the zonal conveyor belt connects meridional and zonal conveyor belts. Figure and caption retrieved from Pinardi and Masetti (2000).

The mean annual sea surface temperature (SST) is highly influenced by seasonal conditions, with gradients from west to east and north to south (Hopkins, 1985) and the overall climate is characterised by hot and dry summers and cool and humid winters (Bosc et al., 2004). The basin exhibits strong environmental gradients (Danovaro et al., 1999), which are particularly evident in the contrasting nutrient regimes between the Eastern and Western pelagic regions, with the former generally characterised by oligotrophic conditions, as indicated by Notarbartolo Di Sciara (2016). Regarding the system's primary productivity, the Mediterranean has a much lower productive capacity than that estimated for most other oceanic regions (Bas, 2009). However, despite this prevailing oligotrophy of this basin (Coll et al., 2010), with a demarcated gradient from east to west, coastal areas can be enriched by sub-regional factors such as changing wind conditions, currents, and fluvial discharges (Zavatarelli et al., 1998; Bosc et al., 2004; Estrada, 2010). The Mediterranean Sea features

narrow continental shelves and a wide-open sea area. Consequently, a significant proportion of this semi-enclosed sea can be categorised as deep sea (Coll et al., 2010). In contrast to the Atlantic Ocean, the Mediterranean Sea lacks thermal boundaries in its deep sea (starting at 100-110m depth), exhibiting a lack of temperature decrease with depth (Emig & Geistdoerfer, 2005).

As defined by Lejeusne et al. (2009), the Mediterranean Sea has been described as a "miniature ocean" or a "giant mesocosm". All the features mentioned above, make this semi-enclosed basin one of the most studied in the world (El-Geziry & Bryden, 2010), with its intricate characteristics playing a crucial role in harbouring an immense amount of biodiversity (Coll et al., 2010).

## **1.2 Biodiversity**

The Mediterranean Sea is the world's second-largest biodiversity hotspot (IUCN-MED, 2009), sheltering approximately 17,000 species, excluding microbial diversity for its uncertainties (Coll et al., 2010), which accounts for 7.5% of total marine diversity in the world (Coll et al. 2010; Danovaro et al. 2010). This amount of richness is the result of a complex relationship of factors, mentioned above, such as the geological history, its mid-latitude geographic position (between 45-30°N), hydrological regimes, underwater topography, and coastal morphology (Taviani 2002; Sardà et al. 2004; Danovaro et al. 2010).

The Mediterranean Sea exhibits two key characteristics concerning its biodiversity: overall, the region is highly diverse and displays a decrease in species richness from northwest to southeast (Coll et al., 2010). The Western sub-region boasts a higher species richness, primarily due to a significant influx of species from the Atlantic Ocean and the broader range of physicochemical conditions experienced there (Coll et al., 2010). The Eastern sub-region, particularly the southeastern area, has the lowest species richness in the Mediterranean Sea, mostly due to specific oceanographic conditions, such as high salinity (Ovchinnikov, 1966; Pérès, 1967; Por & Dimentman, 2006). Additionally, the Adriatic Sea exhibits low species richness due to multiple factors, such as shallow waters towards the northern part, higher input of freshwater compared to the rest of the basin, and a broad range of temperatures

(Theocharis et al., 1993; Por & Dimentman, 2006). Given this unique isolation from the Mediterranean Sea, the Adriatic Sea also comprises many endemic species (Coll et al., 2010).

The connection between the Mediterranean Sea and the two oceans is different (Bas, 2009; Por 2009). The Suez Canal, which links the Mediterranean Sea to the Indian Ocean, has facilitated the influx of numerous non-indigenous species (Por, 1971). In contrast, the Strait of Gibraltar connects the Mediterranean to the Atlantic Ocean, resulting in a significant influence of Atlantic Ocean currents on the nearby marine environment (Bas, 2009). Due to the basin's intricate characteristics, such as its climate and hydrology, both cold and tropical/subtropical species coexist in the Mediterranean Sea (Tortonese, 1985; Boudouresque, 2004; Coll et al., 2010). In the Western basin, a higher number of cold-temperate species are found, making it more biologically similar to the Atlantic Ocean. In contrast, the Eastern basin exhibits higher biological similarity with the Indo-Pacific because it is inhabited by a higher number of subtropical species. Many species still face constraints in migrating between the Eastern and Western subregions, with the Siculo-Tunisian Strait serving as a genetic mixing point (e.g., *Octopus vulgaris*, Fadhloui-Zid et al., 2021; *Solea solea*, Bahri-Sfar et al., 2011).

The study conducted by Coll et al. (2010) aimed to estimate the diversity of species across the Mediterranean Sea. These authors (Coll et al., 2010) concluded that the Mediterranean Sea is inhabited by a substantial proportion of metazoan and macrophyte species compared to other oceans or seas around the world. In particular, it accounts for approximately 84% of metazoan species and 47% of macrophyte species. A more detailed analysis of these figures reveals that, for instance, the phylum Mollusca has 4.02% of its species in this basin (Coll et al., 2010). In contrast, subphylum Vertebrata, particularly the taxonomic group of fish, have 3.95% and other vertebrates make up 8.94% of the total. Furthermore, this basin is home to a considerable number of endemic species, representing 20.2% of the total number (Coll et al., 2010). This is the reason why the Mediterranean Sea is considered the second-largest biodiversity hotspot in the world, according to IUCN-MED (2009).

The Mediterranean Sea is also known for its emblematic endemic species, which have been receiving increasing efforts of conservation throughout the years. The Mediterranean Monk Seal, *Monachus monachus* (Hermann, 1779), is classified as Critically Endangered by the IUCN Red List of Threatened Species (Aguilar & Lowry, 2010). The Mediterranean subpopulation of

Loggerhead Sea Turtle, *Caretta caretta* (Linnaeus, 1758), which is considered of Least Concern by the IUCN Red List of Threatened Species, uses many areas within the basin as nesting sites. (Casale, 2015). A variety of marine mammals, including the common dolphin (*Delphinus delphis* Linnaeus, 1758), which is classified as endangered on the IUCN Red List of Threatened Species (Bearzi, 2012), have experienced a decline in population numbers due to environmental changes and anthropogenic pressures (Bearzi et al., 2003). The endemic species *Posidonia oceanica* (Linnaeus) Delile, 1813, is also important because it creates seagrass meadows, contributing as a forming habitat species, such as nurseries for several species, and to the overall Mediterranean's productivity. Migratory species like the Atlantic Bluefin Tuna (*Thunnus thynnus* (Linnaeus, 1758)) also used the Mediterranean Sea as their spawning grounds, travelling long distances to meet the favourable conditions for their reproduction (MacKenzie et al., 2009). Therefore, this large ecosystem supports a variety of biodiversity from the pelagic to the benthic zones, from microorganisms to large marine mammals (Coll et al., 2010). It also encompasses many habitats in its coastal zones, such as 150 globally significant wetlands for migratory and seabirds, as well as over 5,000 islands and islets, according to Gili et al. (1998) and Sardà et al. (2004, 2009).

### **1.2.1 Ecological Role of Marine Fauna in the Mediterranean Sea**

The marine fauna of the Mediterranean Sea encompasses a wide variety of organisms, including many species of marine mammals, fishes and molluscs, that play specific ecological roles in the overall marine ecosystem (Beaugrand et al., 2018). Marine mammals, fishes and molluscs perform multiple ecological functions that are vital for the proper functioning of marine ecosystems (e.g., Wallach et al., 2015; Palomera et al., 2007; Ysebaert et al., 2019).

Marine mammals occupy high trophic-level positions in the Mediterranean Sea food web (Coll et al., 2010), with certain species being top predators in this ecosystem. This position ensures their role as top-down regulators of the food web (Bowen, 1997). Most marine mammals, like cetaceans, are highly migratory species. As they move across systems, they promote the cycling of nutrients between them (Kitchell et al., 1979). An example of such horizontal transfer relies on the migration of sperm whales (*Physeter macrocephalus* Linnaeus, 1758) between regions like the Atlantic Ocean and the Southern Ocean which facilitate nutrient cycling across vast distances, impacting the productivity and nutrient dynamics of these

marine ecosystems (Lavery et al., 2010). Marine mammals also excrete nutrient-rich waste, which can enhance primary productivity in oligotrophic waters (Kanwisher and Ridgway, 1983), such as the Mediterranean waters. These animals tend to digest food during prolonged surface periods, deep diving for foraging purposes (Sparling et al., 2006). In contrast to primary consumers like zooplankton, which help distribute and sink nutrients, marine mammals can uplift nutrients towards the surface, creating an upward pump – The Whale Pump, enriching surface waters (Roman & McCarthy, 2010). This process opposes the traditional biological pump, which generally moves nutrients from pelagic waters towards the deep sea. Although the Mediterranean Sea is relatively small compared to other large ecosystems, it encompasses twelve resident marine mammal species – one seal, the Mediterranean Monk Seal, *Monachus monachus*, and eleven cetaceans, some of which are the Fin Whale (*Balaenoptera physalus* (Linnaeus, 1758)) that present throughout the entire basin to more localized species like the Rough-Toothed Dolphins (*Steno bredanensis* (Lesson, 1828)) which is found particularly in the Levantine Sea (Notarbartolo Di Sciara, 2016). It is therefore evident that marine mammals play a pivotal role in marine ecosystems, functioning as key indicators of the overall health of these systems (NOAA, 2020).

Fishes are a highly diverse taxonomic group, with ongoing debates regarding the estimates of Mediterranean fish species, due to new species coming into the basin or with reclassifications of previously known species (Coll et al., 2010). As estimated by Coll et al. (2010), there is an endemic richness gradient of fish species. This gradient becomes more prominent as latitude increases, with the north side having high richness and the Adriatic Sea acting as an endemism hotspot. There is also a spatial pattern for the invasive species, with the highest exotic species richness occurring on the Israeli coast (Coll et al., 2010). Therefore, fish is a highly diverse taxonomic group with many species occupying different trophic levels of the food web, from herbivores, like *Sarpa salpa* (Linnaeus, 1758) (Verlaque, 1990) to carnivores, such as *Diplodus annularis* (Linnaeus, 1758) (Bauchot & Hureau, 1990), to top predators like *T. thynnus* (Battaglia et al., 2012). Top predators represent a specific functional group that plays a pivotal role in regulating the food webs in which they reside (Wallach et al., 2015). Top predators regulate lower trophic levels, whereas functional groups such as small pelagics regulate this food web from a mid-position ('wasp-waist' control; Cury et al., 2000), due to their substantial biomass at intermediate levels of the food web (Palomera et al., 2007). Examples of small

pelagics of great importance in the Mediterranean Sea include *Engraulis encrasicolus* (Linnaeus, 1758), the European anchovy, and *Sardina pilchardus* (Walbaum, 1792) the European pilchard, due to their high biomass and commercial value (Palomera et al., 2007). Other species exert their influence according to their migratory nature. An emblematic case regards *T. thynnus*, which, like many other highly migratory species, contributes to the horizontal transfer of energy and matter across the system (Nathan et al., 2008). This species is known to migrate between the Atlantic Ocean and the Mediterranean Sea (Andrews et al., 2022).

According to Coll et al. (2010), molluscs represent 18% of the entire marine fauna of the Mediterranean Sea and encompass about 4% of all diversity of molluscs in the world. Molluscs are one of the most important groups in terms of species richness in the Mediterranean Sea, occurring in a wide range of habitats, ranging from brackish lagoons to bathyal depths (Sabelli & Taviani, 2014). In addition, it is notable but unsurprising that the taxonomic classification of the alien species ascribed by Coll et al. (2010) revealed that Mollusca was the phylum with the highest number of recorded alien species at approximately 33%. This fauna also encompasses an enormous diversity of species which play a variety of ecological roles in the marine ecosystems they belong to (Vinther, 2014; D'Souza & Shenoy, 2023). Filter feeders like bivalves, such as the European flat oyster (*Ostrea edulis* Linnaeus, 1758), are present throughout the Mediterranean Sea and play pivotal roles in the ecosystem they inhabit. Some of the key ecological roles include improving water quality through ecological restoration, enhancing ecosystem reliability and stability, creating diverse habitats and facilitating the movement of chemical elements, as suggested by Ostroumov (2005). Other molluscs are herbivorous and occupy higher trophic levels compared to filter feeders. For example, grazers, like the genus *Phorcus*, are ecologically highly important algae grazers (Sousa et al., 2018). Species that graze on algae can control their populations, reducing the chances of overgrowth of certain harmful species, which can, potentially, alter the ecosystem in terms of productivity, water quality and species diversity and composition (Aguilera & Navarrete, 2007). There are also highly predatory species among molluscs, like the banded dye-murex (*Hexaplex trunculus* (Linnaeus, 1758); Morton & Harper, 2007). This species is an opportunistic feeder, exhibiting both carnivory and scavenging habits. They feed on a variety of bivalves, including gastropods, barnacles, tunicates, bryozoans, carrion and its conspecifics, by drilling holes into their shells

to feed on them (Morton & Harper, 2007). Like grazers, predatory species also contribute to their ecosystem by controlling the populations of species they prey on. Therefore, this diverse fauna helps maintain the health and complexity of ecosystems' food webs and habitat structure (Coen & Bishop, 2015) in the Mediterranean Sea.

## **2. IMPACTS IN THE MEDITERRANEAN SEA**

The Mediterranean Sea, a source of ancient civilisations and a hotspot of biological diversity, is undergoing profound changes (Coll et al., 2010). This ecosystem has been shaped by a complex interplay of natural and anthropogenic factors, and this dynamic continues to influence the current Mediterranean's biodiversity (Coll et al., 2010). Understanding these impacts requires a comprehensive examination of current and historical influences, highlighting the importance of studying the impact of past climate variability and human activities. This understanding is crucial for anticipating future changes and guiding conservation and management efforts.

### **2.1 Current Impacts**

With the rapid development of technology and industrialisation, trade, energy, and other sectors, humans are constantly impacting marine ecosystems and their inherent biodiversity. The impacts caused by humans range from overfishing and aquaculture to polluting the marine ecosystems, eutrophication processes, the entrance of invasive or non-indigenous species, and habitat loss and degradation, among others (Halpern et al., 2008; Bas, 2009; Lacoue-Labarthe et al., 2016). Specifically, global change results in ocean warming, acidification and deoxygenation, which combine and strongly influence biogeochemical processes (Gruber, 2011; Doney et al., 2012; Pörtner, 2012; Baumann, 2016, 2019). The ocean absorbs heat generated on Earth and greenhouse gases (e.g., carbon dioxide, CO<sup>2</sup>) from the atmosphere, which causes continued warming and subsequent acidification of the marine environment (IPCC, 2021). This warming will ultimately cause the oceans to become more deoxygenated, due to reduced oxygen solubility, increased respiration rates and increased ocean stratification (Diaz & Rosenberg, 2008; Oschlies et al., 2017; Levin, 2018; Laffoley & Baxter, 2019). The Mediterranean Sea is no exception, as acidification is already happening

(Meier et al., 2014; Howes et al., 2015) and the combination with factors like rapid warming, growth of human population and increased frequency of extreme weather events will affect deeply the fauna and flora of the region in near the future (Lacoue-Labarthe et al., 2016).

The immense amount of biodiversity held by the Mediterranean Sea contributes to several human economic sectors, such as tourism, cultural heritage, and commerce (Lacoue-Labarthe et al., 2016). According to Lacoue-Labarthe et al. (2016), in the Mediterranean Sea, fisheries and aquaculture represent 1% of world landings and 2% of the economic value, with the fishery sector being more concentrated in the southern Mediterranean countries. With the development of fishing gears, such as trawl nets, humans have been exploiting the basin's coasts over the years (Bas, 2009), resulting in overexploitation of targeted species like small pelagics (Palomera et al., 2007) and large migrators (Lacoue-Labarthe et al., 2016). The development of bottom-trawling, which is a non-selective fishing method, caused habitat degradation (Hall-Spencer, 1999; Tudela, 2004; Pusceddu et al., 2005). *Thunnus thynnus*, a large migratory species, is one of the few well-documented species with an intense and long exploitation history, that has been supporting one of the first commercial fisheries in the Mediterranean Sea (García-Vargas & Florido del Corral, 2010; Di Natale, 2014). Due to its extensive exploitation throughout the years, the Eastern Atlantic and Mediterranean stocks are being managed by the baselines established in 1970, when the data for this species started to be more accurately collected (Andrews et al., 2022), by the ICCAT (International Commission for the Conservation of Atlantic Tunas).

The artificial opening of the Suez Canal in 1869, which connects the Mediterranean Sea to the Red Sea triggered the entrance of a multitude of non-indigenous species into the first basin (Galil, 2000). This corridor has allowed the introduction of hundreds of species, making up more than 46% of the marine species inhabiting the Eastern Mediterranean basin at present (European Environmental Agency, 2021). This linked with the progressive increase in temperatures has also allowed invasive warm-water fish species, and invertebrates like molluscs and algae to expand their distributional ranges becoming a significant part of the southern Mediterranean biota (Bianchi, 2007; Lasram and Mouillot, 2009; Lejeune et al., 2010).

Habitat loss and degradation are some of the most important threats to marine biodiversity, as well as to the structure and function of marine ecosystems (Lacoue-Labarthe et al., 2016).

With its progression, it can lead to the decrease of species richness and/abundance, as well as allow the thriving of opportunist species (Airoldi et al., 2008). On a broader scale, habitat fragmentation can also affect the connectivity, integrity and functioning of the ecosystem processes, decreasing the stability of the population and leading to isolation (Thrush et al., 2006). The Mediterranean Sea holds diversified habitats, highly productive, from seagrass meadows to mollusc reefs, and coralligenous reefs to macroalgae assemblages (Lacoue-Labarthe et al., 2016). The development of Marine Protected Areas (MPAs) is an international protective measure that strives for the preservation of habitats (Lacoue-Labarthe et al., 2016).

The aforementioned impacts represent some of the current impacts in the Mediterranean Sea. However, this marine ecosystem has long experienced a multitude of impacts throughout its history, from both climatic (Lionello et al., 2023) and anthropogenic origins (Coll et al., 2010). Consequently, it is erroneous to consider these impacts as either recent or novel to the history of the basin.

## **2.2 Past Impacts**

This section provides an overview of the Late Pleistocene and Holocene periods, with particular emphasis on climate variability. It also provides an analysis of the human presence and activities in the Mediterranean during these periods, as well as an examination of the impact of both climate and human activities on the Mediterranean marine biota.

### **2.2.1 Late Pleistocene-Holocene Climate Variability and its impact on Mediterranean marine biota**

The global climate in the last 130 ka has been characterised by large-amplitude variability at various scales, from decadal (attributed to fluctuations in solar irradiance) to multi-millennial (due to the Milankovich cycles) (Mayewski et al., 2004; Alley & Agustsdottir, 2005; Moberg et al., 2005). The multi-millennial climatic variability led to glacial-interglacial cycles both in the Late Pleistocene (129-11,7 ka BP; Head et al., 2021) and the Holocene (11,7 ka before 2000 CE; Common Era, sets the baseline of the year 0 according to the Gregorian Calendar; Stuiver & Reimer, 1986), which also had important consequences in the Mediterranean Sea (Lionello et al., 2023). In this semi-enclosed sea, the glacial-interglacial cycles have affected the

ecosystem in both direct and indirect ways. This is due to direct modifications in circulation and atmospheric conditions, as well as variations in sea level over the past million years, indirectly. These changes have ranged from a 10m increase to a 130m decrease in sea level relative to the present (Lionello et al., 2023). During this period, there were two major events, the Last Glacial Maximum (LGM, 30-19 ka, approximately, Lionello et al., 2023) and the Last Interglacial or Holocene (which started around 11 ka, Stuiver & Reimer, 1986). Throughout the LGM, the global mean sea level dropped 120-130m compared to today's sea level, while the mean global temperature was 4-7°C lower than it is today (Grant et al., 2012; Rohling et al., 2017; Tierney et al., 2020). In the Mediterranean Sea, the temperature changes were not uniform throughout the basin (Lionello et al., 2023). The Western Mediterranean suffered a stronger cooling event, with minus 4 to minus 8°C, while the Eastern was more moderated, with the Aegean Sea dropping 6°C and the open Ionian and Levantine basins dropping less than 2° up to 4°C (Hayes et al., 2005; Kuhlemann et al., 2008). The final phase of the last deglaciation was interrupted by another cooling event, the Younger Dryas, which lasted approximately between 12.8 and 11.7 ka, until the onset of the Holocene period (Benjamin et al., 2017).

During the Holocene, the basin was affected by centennial-to-millennial-scale events (Lionello et al., 2023). There were several cooling events, particularly the ones experienced between 8.6-8.0 (or 7.8) ka, between 6-5.2 ka, 3.1-2.9 ka and during the Little Ice Age which occurred between 0.6-0.15 ka ago (Rohling et al., 1997; Mercone et al., 2001; Clare et al., 2008; Rohling et al., 2019). Stable isotopic data from the Gulf of Taranto (Italy) reveal that there were periods of relatively warm conditions, such as the Roman Warm Period (RWP, 2.5-2.0 ka) (Grauel et al., 2013). This period transitioned into the Roman Classical Period (RCP, 2.0-1.8 ka), followed by the wetter Dark Ages Cold Period (DCP, 1.5-1.25 ka), and then to the Medieval Warm Period, which started warmer and more humid but gradually became drier, leading to the arid Little Ice Age (Grauel et al., 2013).

The ocean-climate cycles experienced throughout the last 130 ka had an important influence on the marine species. Temperature fluctuations and lowered sea levels facilitated the displacement of coastal populations, and the emergence of new species due to vicariant processes, extinctions, and colonization from other territories (Magoulas et al., 2006, with references therein). Both freshwater and pelagic species were affected by the glacial activity

(Bigg et al., 2007; Debes et al., 2008), with coastal species being particularly affected (Wares & Cunningham, 2001; Maggs et al., 2008). Therefore, the current distribution of the northern hemisphere species is the result of historical vicariant processes during these glaciations (Wilson & Veraguth, 2010). During the LGM, the temperatures dropped significantly across the Mediterranean (Lionello et al., 2023). Although some species can tolerate negative temperatures or near 0°C, most temperate species are unable to tolerate it (Alheit et al., 2012). Therefore, many species might have experienced dramatic distributional shifts or bottlenecks related to changes in temperature (Alheit et al., 2012). Apart from changes in distribution, environmental changes, including temperature oscillations, also impact species' abundance (McCauley et al., 2015), body size (Daufresne et al., 2009; Baudron et al., 2014), and ecosystem functioning (Pontavice et al., 2019). These environmental changes can also influence the ecosystem's food web structure by, for instance, changing the nutrient availability in the water column and by modifying the light energy reaching the shallow waters with direct impacts on producers and consumers (Richardson & Schoeman, 2004; Müren et al., 2005).

### **2.2.2 Past Human Activities and its impact on Mediterranean marine biota**

Climatic variability was not the only factor influencing the settlement of several taxonomic groups. The history of human interactions with marine fauna is extensive (Margalef, 1985; Hughes, 1994; Boudouresque, 2004; Bas, 2009). Human populations have long depended on ecosystem services, particularly in terms of food provision, cultural and recreational activities and transportation (Madariaga, 1964; Neumann et al., 2015; Mehvar et al., 2018). The progressive use of resources changed dramatically over human history, as people changed their lifestyles from hunter-gatherers to unified communities until reaching the organisation and structure of a hierarchical society (Lotze et al., 2006 with references therein).

This progression brought several developments in the way people used natural resources, such as clothing items, food provision, and the production of various tools, among others. Some of the earliest evidence of human interactions with marine resources in the Mediterranean Sea dates from the Palaeolithic period, continuing until the Mesolithic and Neolithic periods (between 20,000-4,000 Before Christ (BC); Coll et al., 2010). Although most lines of research suggested that marine resources only played a minor role in humans' diet,

the prehistoric record offers a lot of examples of marine resource exploitation (Theodoropoulou, 2023).

Zooarchaeological records are present in a multitude of locations throughout the basin, spanning from the Strait of Gibraltar (Stringer et al., 2008) in Las Cuevas de Nerja in Spain (Morales & Roselló, 2004) to a submerged Neolithic settlement site on the coast of Israel (Zohar et al., 2001). The remains found at these archaeological sites are highly diverse. In Spain, some archaeological sites displayed indications of overfishing of specific species. In the Eastern Mediterranean, in Israel, 90% of the remains belonged to a single species, the grey triggerfish (*Balistes capriscus*, Gmelin, 1789), indicating extensive exploitation impacting fish size. Therefore, humans have been exploiting marine faunal resources since the early times, although for different purposes and with different impacts.

Particularly, humans have been exploiting cetaceans for thousands of years, progressing from the opportunistic use of stranded animals or carcasses to active hunting (Clark, 1947; Kandel & Conard, 2003; Monks, 2005). They used these animals for their meat and blubber served as food. The blubber was also used as fuel in oil-burning lamps and their bones served as tools for production (Clark, 1947; Mulville, 2002; Pétilion, 2008). The joint effects of intensive human exploitation across history with other anthropogenic impacts such as habitat degradation and ship strikes, which are recent, have reduced whale populations around the world, and in some cases, populations have been extirpated (Clapham et al., 1999; Baker & Clapham, 2004). The emblematic Mediterranean monk seal is another example of a marine mammal which suffered a drastic reduction in its distribution and abundance over time, due to intensive exploitation (Karamanlidis et al., 2015, with references therein). In the past, this species was easily hunted due to its sedentary behaviour (Adamantopoulou, 2011). This species was hunted for their skin, which provided waterproof garments (González, 1999; Johnson & Lavigne, 1999; Johnson, 2004), and also their blubber for food provision (Kıraç & Savaş, 1996; Johnson & Lavigne, 1999; Johnson, 2004). This species was distributed across the Black and Mediterranean Seas and in the North Atlantic, specifically from Cabo Blanco to the northern part of Spain, including the Azores, Madeira and the Canary Islands (Johnson et al., 2006; González, 2015). However, nowadays there are only some small populations of this species scattered across the Mediterranean and Atlantic waters, with a total abundance estimated to be less than 700 individuals (Karamanlidis et al., 2015).

Human settlements often occurred along the coastlines of the Mediterranean Sea, as it was easier to access and exploit shallow marine resources (Milner et al., 2007; Schöne & Surge, 2014; Thomas, 2015) such as molluscs and fish species. An example of an important mollusc was *O. edulis*, which was highly harvested in the past for food provision during prehistoric times (Kristensen, 1997; Gercken & Schmidt, 2014). During the ancient Greek period, it was believed that the consumption of certain molluscs and other invertebrates was beneficial to treat and prevent some health problems and diseases (Voultsiadou et al., 2010). Gastropods such as *H. trunculus* were highly exploited for their purple pigments to dye clothes, during the Iron Age until the thirteenth century in the Eastern Mediterranean (Gertwagen, 2008) and during the Roman times in the Western Mediterranean (Oliver, 2015).

Fishing activities were always present in the Mediterranean Sea. During the Pontic economy (approximately between the end of the 4<sup>th</sup> and the 1<sup>st</sup> centuries Before Christ (BC) in the ancient region of Pontus in northeastern Anatolia; Britannica, 2018), the exportation of fish to the Aegean Sea was highly important, with fish products such as salt fish (*tarichos*) and fish sauce (*garum*) mainly made from *E. encrasicolus* (Bekker-Nielsen & Enghoff, 2006). The exploitation of fish was extensive in some parts of the Mediterranean: there are historical records dating from the Imperial Period (or Imperial Rome, 20-360 Anno Domini (AD), Milwaukee Public Museum, 2022) that present evidence of overfishing in the Western Mediterranean Sea (Trakadas, 2006). An intensively and highly exploited resource over Mediterranean history was the *T. thynnus* (Longo & Clark, 2012; Andrews et al., 2023). Its exploitation was conducted in a sustainable way in the Eastern Atlantic and Mediterranean Sea, due to the type of fishing gear used, the tuna traps (De la Serna et al., 2012), such as *la tonnara* in Italy (Longo & Clark, 2012) and *almadrabas* in Spain (De la Serna et al., 2012). These traps caught the fish near the shoreline based on their spawning behaviours (Longo & Clark, 2012). However, with the development of new industrial fishing gears and systems, these tuna traps have been replaced by more sophisticated technology and the population of *T. thynnus* started to decline (Longo & Clark, 2012).

To sum up, the history of human interactions with marine fauna is extensive and multifaceted. As a result, some species experienced some degree of constraint, and this probably affected the species' biology, ecology, or functionality. Consequently, it is essential to ascertain the extent of the impact that these interactions have had on the marine fauna.

### **2.3 The Importance of Studying the Past**

Most studies conducted nowadays prioritise looking at what is happening to habitats, ecosystems and oceanic processes based on short-term data (last 100 years). However, these short-term data are already biased, because they have already been modified by previous human activities and climate change, and therefore they are not representative of pristine marine ecosystems (Agiadi & Albano, 2020). The historical, archaeological and paleontological record, on the other hand, incorporates data covering hundreds to thousands, and millions of years. Leveraging the geohistorical record allows us to obtain both the long-term and pristine baseline data on marine ecosystems that are otherwise unavailable from modern monitoring records (Dietl & Flessa, 2011). Archaeological remains are also good past indicators of commercial trading, exploitation and human consumption (Van Neer et al., 2005). At the same time, historical records such as catch records are good indicators of species presence in certain areas or the environmental conditions experienced through certain periods (Lotze et al., 2006). Both paleontological and archaeological records are fundamental to understanding the degree of exploitation towards certain species. However, because of the human selection bias, they are not reliable enough to evaluate entire ecosystems (Agiadi & Albano, 2020). Quantitative measures that enable the definition of reliable baselines and the differentiation between human and non-human sources of disturbance are the fossil record, such as surface death assemblages (DAs, Dietl et al., 2015). In optimal conditions, DAs demonstrate a high degree of fidelity to their corresponding living assemblages, when appropriately sampled (e.g., Agiadi & Albano, 2020, with references therein), which makes them reliable records for past environmental conditions (Kidwell, 2015; Kowalewski, 2017).

For this reason, archaeological, palaeontological and historical records are suitable for studying changes in environmental conditions in the past, to establish baselines with credible confidence and avoid the potential for bias in the face of the already considerable pressures exerted on ecosystems by human activities.

### **3. THE AIM OF THIS WORK**

This study aims to unravel the climatic and anthropogenic impacts on three taxonomic groups – marine mammals, fishes and molluscs – distributed in the Mediterranean Sea, over the last 130 ka.

### **4. OBJECTIVES AND HYPOTHESES**

To answer the main purpose of this work, several key objectives are addressed, with subsequent hypotheses formulation.

Firstly, it is necessary to understand if climatic changes and human activities have impacted the targeted species in the Mediterranean Sea over the last 130 ka. Therefore, we propose that both factors likely affected the species living in this marine ecosystem, due to environmental fluctuations and anthropogenic activities that might have occurred in this period.

Next, we strive to understand how climatic changes over the last 130 ka in the Mediterranean Sea have impacted species in different ways. We hypothesize that temperature and other environmental oscillations have affected the targeted species, as climate change might have influenced marine ecosystems.

Simultaneously, it is crucial to assess how past human activities over the last 130 ka in the Mediterranean Sea have influenced species. We hypothesize that human activities, such as resource exploitation, might have significantly impacted the targeted species, due to interactions between humans and marine fauna.

### **5. METHODOLOGY APPLIED: PRISMA GUIDELINES**

The three taxonomic groups selected for this study have inhabited the Mediterranean Sea for a longer period than the study timeframe. Consequently, to gain a more comprehensive understanding of the various impacts that have shaped their evolution, we have conducted a systematic review following the PRISMA guidelines, as outlined by Page et al. (2021). PRISMA stands for “Preferred Reporting Items for Systematic Reviews and Meta-Analyses”. The methodology is widely used for conducting systematic reviews due to its structural approach,

which ensures transparency and completeness throughout the entire process (Page et al., 2021). It was decided that this method should be employed to obtain a comprehensive overview of the records from the targeted species across the Mediterranean Sea over the time interval used in this study.

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## **CHAPTER 2: CLIMATE VERSUS PRE-INDUSTRIAL HUMAN IMPACTS ON MARINE MAMMALS, FISHES, AND MOLLUSCS IN THE MEDITERRANEAN SEA OVER THE LAST 130 KA**

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### **ABSTRACT**

Climate change and anthropogenic activities have long been modifying marine ecosystems. The Mediterranean Sea has a long history of interactions between climate, humans, and its marine ecosystems. To evaluate these impacts, a systematic review of commercially important species of marine mammals, fishes, and molluscs over the last 130,000 (130 ka) years up until the Industrial Revolution (year 1850) was employed. The study area, the Mediterranean Sea, was classified into different sub-regions: Western, Eastern and Adriatic.

The results showed significant impacts on the mollusc *Hexaplex trunculus* and two fish species *Thunnus thynnus* and *Sparus aurata*. Our results suggested that *T. thynnus* experienced changes in abundance, body size, habitat use and trophic level probably due to environmental (e.g., changes in temperature and primary productivity) and human (e.g., overfishing) impacts. *Hexaplex trunculus* and *S. aurata* were highly exploited by humans during certain periods, resulting in abundance and body size changes, respectively. This work compiled significant evidence of impacts on marine species from the Mediterranean Sea. These changes might have indirectly resulted in modifications to the structure and functioning of the marine ecosystems over the past 130 ka. These findings highlight the importance of integrating past data (paleontological, archaeological and historical) with contemporary biological data to gain a more comprehensive temporal framework. Understanding marine ecosystem history and species-specific responses to such disturbances is essential. This inclusive geohistorical approach guarantees the implementation of appropriate present and future environmental management strategies, in addition to the implementation of specialised conservation measures.

## **INTRODUCTION**

Marine ecosystems are among the world's most diverse and socio-economically valuable systems (Millennium Ecosystem Assessment, 2005; Halpern et al., 2008). Marine ecosystems provide several ecosystem services, from which human populations benefit (Liquete et al., 2013). These services include provision (fisheries and aquaculture), regulation, support (shoreline protection) and cultural services (Doney et al., 2012; Bernhardt & Leslie, 2013; Liquete et al., 2013). The Mediterranean Sea is one of the numerous marine ecosystems worldwide that have long provided resources to human populations (Gibbs, 2004; Madariaga, 1964; Neumann et al., 2015; Mehvar et al., 2018) and sheltered a significant amount of biodiversity (Coll et al., 2010). This basin constitutes a transcontinental semi-enclosed sea bordering Europe, Asia, and Africa (Coll et al., 2010). Sheltering 7.5% of the world's marine diversity (Coll et al. 2010; Danovaro et al. 2010), it is the second-largest biodiversity hotspot globally (IUCN-MED, 2009).

Like many marine ecosystems worldwide, climate warming and human activities are currently impacting the Mediterranean Sea, causing significant effects on biodiversity (Lotze et al., 2006; Coll et al., 2010; Moullec et al., 2019). The most significant hazards in this region are habitat loss and degradation, overexploitation of marine resources, pollution, invasions of non-indigenous species, and climate change (Halpern et al., 2008; Coll et al., 2010; Côté et al., 2016). These factors are increasingly affecting habitat quality, prey availability, and species phenological patterns with subsequent effects on the productivity, fitness, and distribution of marine species (Pauly et al., 1998; Planque et al., 2010; Howarth et al., 2014). During the last few decades, the Mediterranean Sea has experienced a temperature increase higher than the global average (Lionello et al., 2014), with an increase of around 0.4°C in the most recent decades (Macias et al., 2013). This change exerts a strong influence on the Mediterranean biodiversity (Bianchi, 1997; CIESM, 2008; Lejeusne et al., 2010) by changing species distribution and abundance (Heller, 1863; Lejeusne & Chevaldonné, 2005; Garrabou et al., 2009). This semi-enclosed basin has been a hub of ancient civilizations that have influenced its shorelines (Anthony et al., 2014) and utilized its resources since ancient times (Coll et al., 2010). One notable impact of human activity was the industrialisation of fishing gear, which brought consequences for various species, habitats, and ecosystems (Tudela, 2004). Overall, this large marine ecosystem is experiencing heterogeneous impacts from both natural and human origin, which raises an overload of uncertainties regarding its future prosperity and its inherent biodiversity.

However, in resemblance to many other marine ecosystems, the Mediterranean Sea has long experienced several environmental changes and human impacts throughout its history, either due to natural climatic variations (e.g., glacial and interglacial cycles, Lionello et al., 2023; e.g., rapid climate changes events, Berger et al., 2016) or due to the evolution of societies and consequent exploitation of its resources (Lotze et al., 2006; Coll et al. 2010; Colonese et al., 2011; Marzano, 2013). The glacial and interglacial cycles have directly caused modifications in circulation and atmospheric conditions and caused variations in sea levels over the last million years, indirectly (Lionello et al., 2023). During the Holocene (11,7 ka before 2000 CE; Common Era, sets the baseline of the year 0 according to the Gregorian Calendar; Stuiver & Reimer, 1986) the basin was affected by centennial-to-millennial-scale events (Lionello et al., 2023), changing between warming and cooling events, such as the Medieval Warm Period (MWP,

1,250 - 600 years ago) and the Little Ice Age (LIA, 600-150 years ago, Grauel et al., 2013; Lionello et al., 2023 with references therein), respectively. In the past, humans also impacted marine ecosystems (Lotze et al., 2006 with references therein). Some authors, (Jackson et al., 2001) investigated the impact of human activity on a range of coastal ecosystems. Their findings revealed that the overfishing of shellfish and large vertebrates was the primary human-induced impact observed in all the studied ecosystems. Even ancient civilisations which exploited on a small scale brought severe local impacts. Some of them were related to strong resource depletion (Rick & Erlandson, 2008; Lotze & Worm, 2009), such as the decrease in the distribution range of the sea cows (sirenians) due to aboriginal hunting in the Pacific Rim during the Late Pleistocene (129-11,7 ka BP; Head et al., 2021; Estes et al., 1989). Hence, the Mediterranean Sea's biodiversity has been impacted by a combination of environmental changes and the growth of human populations, which have had continued development of sophisticated technology (Tudela, 2004), transport networks and a vast array of trade activities (Lotze et al., 2006; Gertwagen et al., 2008).

Most ecological research prioritises understanding what is happening to ecosystems based on local surveys lasting a few years or based on short-term data from the last 100 years, not considering the ecosystems' long-term changes (Jackson, 1997; Dayton et al., 1998). These short-term data analyses did not address the ecosystem dynamics, which occur in multi-temporal scales and the life span of multiple ecologically important species (Jackson, 2001 with references therein). Paleoecological, archaeological, and historical data provide the solution for this as they constitute long-term records essential to fully understanding the marine ecosystem history (Jackson, 2001). These data help to differentiate between human-induced and natural perturbations to the marine ecosystems and were focused on reconstructing past environmental conditions (Leiva-Dueñas et al., 2018, with references therein). Therefore, it is necessary to have a well-dated time series that offers a foundation for proper current management and conservation efforts (Jackson, 2001).

There are two main types of objectives regarding past studies and analyses of the use of marine resources. While paleoecological studies use marine organisms as proxies for paleoclimatic and paleoenvironmental reconstructions (e.g., Richardson, 2001; Dettman et al., 2004; Wanamaker et al., 2008), archaeological studies use marine remains as proxies to understand human subsistence strategies (e.g., Bosch et al., 2018; Branscombe et al., 2020).

Paleoecological studies can use a variety of resources, such as the stable oxygen isotope ( $\delta^{18}\text{O}_{\text{shell}}$ ) values derived from bivalves' shells to reconstruct paleoclimate archives on ocean temperature (Butler et al., 2013; Reynolds et al., 2013; Doré et al., 2020). Additionally, some authors used the differences in oxygen and carbon stable isotopes ( $\delta^{18}\text{O}$  and  $^{13}\text{C}$ ) to infer differences in salinity and proportion of carbon and its dietary sources, respectively (Sisma-Ventura et al., 2019, with references therein). Archaeological studies use  $\delta^{18}\text{O}$  to understand the seasonality of shellfish exploitation in the Adriatic and Eastern Mediterranean Sea (Bosch et al., 2018; Branscombe et al., 2020). However, these types of studies did not focus on what happened in the marine ecosystem itself. Thus, the lack of knowledge regarding the changes brought upon the marine ecosystems reveals a gap in this type of research.

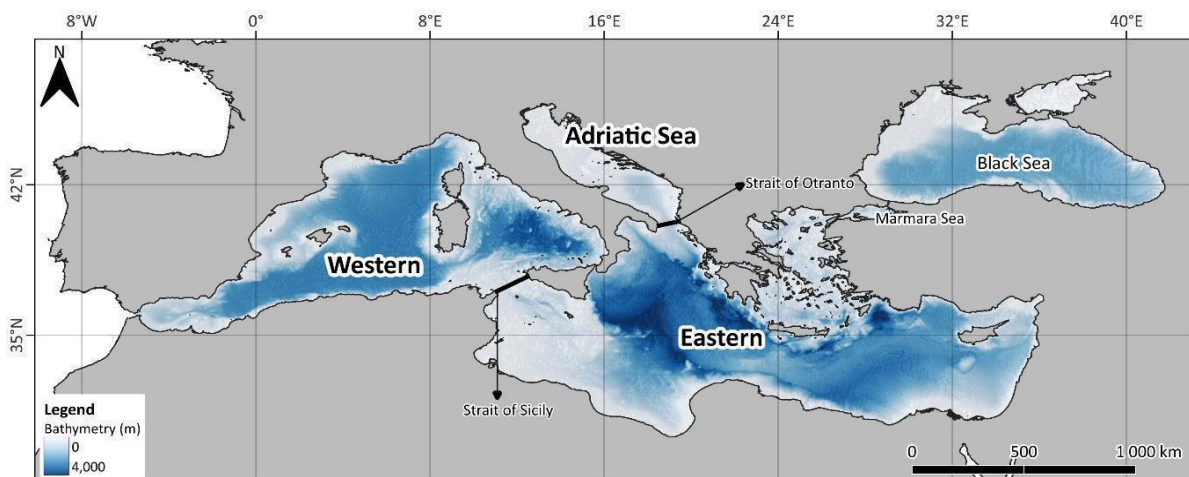
To address this gap, we conducted a systematic review of three taxonomic groups - marine mammals, fishes and molluscs - on the Mediterranean Sea over the last 130 ka to fully understand what were the implications of both climate and human impacts on marine ecosystems. The systematic review was done following the PRISMA guidelines, as outlined by Page et al. (2021). The PRISMA method (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) ensures transparency and completeness throughout the entire process (Page et al., 2021). We have selected these three taxonomic groups based on their long historical presence in the Mediterranean Sea, along with their ecological importance (Coll et al., 2010).

This work aims to understand how climatic changes over the last 130 ka in the Mediterranean Sea have impacted species in different ways and their specific responses to these impacts. To achieve this, we hypothesise that: (a) past climatic changes and human activities experienced over the last 130 ka in the Mediterranean Sea likely affected species living in this marine ecosystem, (b) the climatic changes might have impacted targeted species from different taxonomic groups, through temperature or other environmental oscillations, and (c) human activities, such as resource exploitation, might have also impacted the targeted species. This is an important key step for improving the overall management and conservation efforts of marine ecosystems in the Mediterranean Sea, as understanding the past responses of marine taxonomic groups allows for a better identification of both current and future climate and human impacts facilitating more effective conservation and management strategies.

## MATERIALS AND METHODS

### Study Area

The study was carried out in the Mediterranean Sea (Figure 2.1), which is the largest and deepest semi-enclosed sea in the world (extending approximately 3 million km<sup>2</sup> and reaching a maximum depth of around 5,300 m) (Coll et al., 2010). It is nowadays connected to the Atlantic Ocean on the west side through the Strait of Gibraltar. To the northeast, it is connected to the Marmara Sea through the Dardanelles Strait, and further to the Black Sea through the Bosphorus Strait. In the southeast part, it is connected with the Indian Sea and the Red Sea through the Suez Strait. Physical boundaries established by the straits of Sicily (between Italy and Tunisia) and Otranto (Italy and Albania) separate the Mediterranean into three regions: the Western and Eastern sub-basins, and the Adriatic Sea (Millot & Taupier-Letage, 2005; Rio et al., 2007; Robinson et al., 2009), which we have adopted for this work.



**Figure 2.1** - Mediterranean Sea and the regional divisions (Western, Eastern and Adriatic) that were adopted in this work. Black and Marmara Sea are also indicated.

### Periods timetable

Several time classification schemes apply to the different parts of the Mediterranean region for the studied time interval. To be able to correlate events between the regions and to employ a unified scheme in this study, we have created a table with all the available schemes, including geologic and cultural (see Table S1). This decision was made because archaeologists and palaeontologists commonly utilize distinct terminologies or words to describe similar

periods across both human and geologic histories. Consequently, the table incorporates both the geological terms settled by the Global Boundary Stratotype Section and Points from the International Commission on Stratigraphy (ICS, <https://stratigraphy.org/gssps/>), as well as the cultural terms and some terms related to environmental events that we have identified in the literature. Given the three distinct regions within this basin, we have selected the names separately to capture a wider range of terms. The periods comprised in this table are dated based on the years Before Present system. This system assigns the year 0 to 1950, a consequence of the nuclear testing initiated in the mid-20<sup>th</sup> century, which altered the carbon isotope ratio in the atmosphere and, consequently, affected radiocarbon dating (Taylor & Bar-Yosef, 2014). All conversions to this system were made using the package “rcarbon” (Crema & Bevan, 2020) in Rstudio (version 4.3.2).

### **Systematic Literature Review**

In the present study, a bibliographic search was conducted of peer-reviewed scientific articles, reviews, data articles and book chapters on the climatic and anthropogenic impacts on commercially important species of marine mammals, fish and molluscs in the Mediterranean Sea over the last 130 ka, up to the Industrial Revolution (year 1850). This global phenomenon varies in its onset around the world. Therefore, for this work, we considered the Industrial Revolution to have started in 1850 around the Mediterranean Sea (Abram et al., 2016). We decided to focus on commercially relevant species most commonly found in records referring to the use, consumption and/or exploitation during the past. This work was conducted using the PRISMA 2020 methodology (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Page et al., 2021). PRISMA is a complete, transparent tool that helps synthesize existing knowledge on a particular topic in a comprehensive and structured way. This methodology is comprised of several steps: (1) a systematic selection of peer-reviewed articles using search engines; (2) removal of duplicate entries from search engines and two screening processes based on predetermined inclusion/exclusion standards (one on titles and abstracts, the other to the full article), (3) identification of other potential studies with relevant data via secondary literature, and (4) the extraction of information from both sources (search engines and secondary literature) into a database based on targeted parameters.

## Choice of Species

Given the amount of diversity the Mediterranean Sea holds and its long history of interaction between marine resources and humans (Coll et al., 2010 with references therein), we have decided to focus our study on commercially important species of marine mammals, fishes, and molluscs that are historically well-documented within the basin. Thus, a primary search was conducted on Google Scholar with the combination of several keywords such as: “fish exploitation”, “marine mammal hunting”, “mollusc harvesting”, “archaeology”, “historical remains”, “Mediterranean”, “Late Pleistocene” and “Holocene”. This resulted in a total of seven species and one well-represented family. We chose two marine mammal species, *Delphinus delphis* Linnaeus, 1758 and *Monachus monachus* (Hermann, 1779); two fish species, *Engraulis encrasicolus* (Linnaeus, 1758) and *Thunnus thynnus* (Linnaeus, 1758); and three mollusc species, *Ostrea edulis* Linnaeus, 1758, *Hexaplex trunculus* (Linnaeus, 1758), and *Phorcus turbinatus* (Born, 1778). The Sparidae family was highly mentioned throughout the search, with *Sparus aurata* Linnaeus, 1758 being the only species particularly mentioned, but given the current commercial importance of *Diplodus* species, the following species were also included, as they inhabit the Mediterranean waters: *Diplodus annularis* (Linnaeus, 1758); *Diplodus bellottii* (Steindachner, 1882); *Diplodus cervinus* (Lowe, 1838); *Diplodus levantinus* Fricke, Golani & Appelbaum-Golani, 2016; *Diplodus puntazzo* (Walbaum, 1792); *Diplodus sargus* (Linnaeus, 1758); and *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817). On the other hand, small pelagics are globally important fish that highly contribute to the fisheries economies nowadays, therefore three species that inhabit these waters were also included: *Sardina pilchardus* (Walbaum, 1792); *Sardinella aurita* Valenciennes, 1847; and *Sardinella maderensis* (Lowe, 1838). The final search included a total of seventeen species, two marine mammals, twelve fishes, and three molluscs.

## Search Process

The searches were conducted in English. The databases used to retrieve the information were Elsevier’s Scopus (<https://www.scopus.com/>) and the Web of Science Core Collection (<https://webofknowledge.com/>). The search covered the interval from 1911 until the cut-off date, February 12, 2024. We searched using the “All fields” mode, which explores all the searchable fields using one query, including “title”, “abstract”, and “keywords”. The strings

used in the search were grouped into six main categories with a specific set of keywords within – taxa, with currently scientifically accepted names for each species, reported by WoRMS Editorial Board (<https://www.marinespecies.org>), the most commonly used unaccepted names found in literature and their respective common names; area/region of interest with its subdivisions, timeframe, anthropogenic and climatic impacts, and theme. The keywords from each topic were interspersed with the Boolean operator “OR”, while when a new topic changed, the operator was “AND”. The impact topic terms were used together in the same query to avoid restrictive results (see Table S2 to check all strings used within each category).

### **Screening Process and Data Gathering**

Once the searches were done in both search engines, the datasets were merged, the duplicates were removed, and the remaining articles were screened. The screening was divided into two steps. In the first step, the titles and abstracts were screened regarding the targeted species, study area and timeframe. Only the articles meeting the first inclusion criteria in Table 2.1 were downloaded and fully read. In the second screening, only the papers with quantitative data, which also met the inclusion criteria of Table 2.1 based on the full-text screening, were included in the database. See Table S3 for the compilations of scientific articles used to build the database.

With this information, a database was built with a set of parameters that referred to the information of the included articles, the general information regarding the article, the location of the data (coordinates), the type of assemblage from where the data comes from (natural or archaeological as base categories), and the respective age (absolute and relative age). In some cases, when the coordinates were not provided by the authors, but the area where the site is located was indicated, we placed the coordinates as a medium point of the region. We also gathered information on some Effect Measures, such as the datation method used, the time interval covered by the study or the sampling effort.

Regarding the specific parameters meant to be used in subsequent analyses, we collected data on the Number of Identified Specimens – NISP (Grayson, 1984), the Minimum Number of Individuals – MNI (Lyman, 1994; 2003; 2008), catches, Reported Relative Abundance (RRA), body size (fishes body length and molluscs basal diameter) and stable isotope data ( $\delta^{13}\text{C}$  and

$\delta^{15}\text{N}$ ). As different authors expressed the same type of information in different units, the respective metrics were standardised on the database. In light of the various dating techniques employed in the articles under consideration, we have utilized the traditional years "Before Present" (BP) system in this study. However, certain articles in our analysis presented their dates in calibrated Before Present (cal. BP), a separate system that accounts for fluctuations in atmospheric carbon. When we encountered an age expressed in cal. BP, we assumed that value. Thus, any age described in this study is presented as "BP/cal. BP". See S4 for the explanation of the modifications made to the database.

**Table 2.1** - Inclusion and exclusion criteria for literature in the systematic review.

|                         | Inclusion criteria  | Exclusion criteria  |
|-------------------------|---|---|
| <b>First screening</b>  |   |   |
| 1                       | The study focuses on the selected species of marine mammals, fishes and molluscs          | The study was conducted on non-targeted taxa or non-targeted species      |
| 2                       | The study was conducted in the Mediterranean Sea or in a specific region within the basin | The study was conducted outside the study area                            |
| 3                       | The study focuses on the Late Pleistocene and Holocene, until the Industrial Revolution   | The study focuses on other time periods, not covered in the present study |
| <b>Second screening</b> |   |   |
| 1                       | The study focuses on the selected species of marine mammals, fishes and molluscs          | The study was conducted on non-targeted taxa or non-targeted species      |
| 2                       | The study was conducted in the Mediterranean Sea or in a specific region within the basin | The study was conducted outside the study area                            |
| 3                       | The study focuses on the Late Pleistocene and Holocene, until the Industrial Revolution   | The study focuses on other time periods, not covered in the present study |
| 4                       | Open access document  | No access to the document   |
| 5                       | Reviews included quantitative data  | Reviews including qualitative and/or descriptive data                     |
| 6                       | The literature used is in English   | The literature is in any other language.                                  |
| 7                       | Climate or human impacts on the targeted species  | Out of topic  |

## Analyses

Given the method used to gather the data used in this study, we have decided to generally approach the outcome of the systematic review, and a full analysis regarding the database. All the maps presented in this work were created using Free and Open Source QGIS version 3.34.3 (QGIS.org). The bathymetry data was obtained from GEBCO (General Bathymetric Chart of the Oceans) (GEBCO Compilation Group, 2022). All original graphical representations were made with the "ggplot2" package (Wickham, 2016) and statistical analyses were conducted in R version 4.3.2 (R Core Team, 2023).

## **Systematic Review Analyses**

In this work, we focused on the distribution of the selected species across the Mediterranean Sea within the timeframe. We grouped the sites where the data came from into sampling units since different articles presented the same sampling locations. Therefore, we decided to map these sampling units across the study area. The sampling sites located in both the Black and Marmara Seas were included in the Eastern Mediterranean sampling units, given the reduced number within these seas and to standardize the number of regions inside the basin. The data regarding the Effort Measures were meant to be used as a way to understand the effort put by the authors in research of this particular species across the Mediterranean. However, this information was not further explored, due to the primary focus of this work being the analyses of impacts of climate and/or humans on these species throughout time.

## **Data Analyses**

We first visualized the dispersion of the data through time, subsetting the data inside each parameter by each sub-region of the Mediterranean Sea. Data from both Marmara and the Black Sea were incorporated into the Eastern sub-basin when assessments regarding different regions were done.

The variables NISP, MNI and Reported Relative Abundance had data on most of the searched species, so we plotted the records separately by taxonomic group. Looking at the overall data, we first excluded the outliers. Then if some data was clustered around a time interval, we would only focus on that period.

For the species with the most data, further analyses were done to evaluate particular changes throughout time for each sub-region. This methodology was applied for variables such as NISP, MNI, body size and stable isotope data. This data dispersion was plotted with some of the major climatic events experienced in the Mediterranean Sea over the last 130 ka, such as the Last Glacial Maximum (LGM, Lionello et al., 2023). We decided to address specifically the climatic events in which temperature changes were the main environmental factor influencing the marine ecosystem. This data dispersion was also plotted against the changes in cultural periods across the basin, such as the transition between the Epipaleolithic/Mesolithic and Neolithic periods (Stiner & Kuhn, 2006). As the names used and the durations of the cultural

periods differed across the basin, this information was considered for each region. All the information regarding the climatic and cultural events is displayed in Table S5. Then we divided the data based on the four geologic periods (Late Pleistocene, Early, Middle and Late Holocene), and proceeded with statistical analyses. If in each plot there were clusters of data that seemed to visually follow a trend (either decreasing or increasing), this was further assessed by subdividing the data according to the climatic and/or anthropogenic events.

Only *T. thynnus* presented data related to catches, but this data was limited to a period of centuries rather than thousands of years. Given the fact that long-term fluctuations in catches can be considered as a proxy of abundance according to Ravier and Fromentin (2001), we decided to assess them for differences in time and to evaluate trends. We also incorporated data from after the year 1850 (between 1700 and 1936) from Polanco-Martínez et al. (2018), as the fisheries of *T. thynnus* are historically important. To see if some fluctuations are correlated to climatic or human events, we incorporated data on the Sea Surface Temperature (SST) and major environmental events, such as the Little Ice Age (Briffa, 2000), and major historical human events, such as World War I and the beginning of industrialized fishing in the 19<sup>th</sup> century (Longo & Clark, 2012). The data on SST was recovered from the Paleo Data Search of the National Oceanic and Atmospheric Administration (Jalali et al., 2021; NCEI-NOAA).

The body size parameters gathered were Total and Standard Lengths (TL and SL, respectively) for fish and Basal Diameter (BD) for molluscs. Each set of data was plotted by species across time. Given the lack of data regarding SL, no further statistical analyses were done. Further analyses on TL and BD were conducted for the geologic periods and respective subdivisions of data.

Information on stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) was available for several species but given the lack of data and uncertainty when the specific species was not given, we decided to focus only on *T. thynnus* and *S. aurata* which had the most data across the timeframe. For *T. thynnus* the data covered the same interval, therefore a comparison between sub-regions was performed. For *S. aurata* the analyses focused on differences between intervals, within the same sub-region. These intervals are not considered periods, as a set of only three ages was presented. Further analyses were conducted for the geologic periods and respective subdivisions of data.

## Statistical Analyses

First, we assessed the normality (Shapiro-Wilk test) and corresponding homoscedasticity/equal variances for all parameters gathered (Levene's test from the "car" package, Fox & Weisberg, 2019). If the comparison was between two groups, a two-sample Student *t*-test or a Mann-Whitney *U* test was done. If we assessed multiple groups, we used an ANOVA, Welch ANOVA or Kruskal-Wallis depending on whether the assumptions of normality and homoscedasticity were respectively met. In case there were significant differences between multiple groups, an *ad hoc* approach would be the next step. In case an ANOVA was performed, the corresponding *post-hoc* test would be a Tukey's HSD (Honestly Significant Difference) test. If a Kruskal-Wallis was performed, then a pairwise Wilcoxon test was applied to determine which levels of the independent variable differ from each other. We selected a statistical significance threshold of  $p\text{-value} < 0.05$ . When analyses involved more than two pairwise comparisons, the Bonferroni method was applied to adjust the *p-values* for multiple comparisons, reducing the probability of making a Type I error (false-positive, Sedgwick, 2012). We used the Mann-Kendall test (Hipel & McLeod, 1994; Libiseller & Grimvall, 2002) from the R package "trend" (Pohlert, 2023), to determine whether the catches data for *T. thynnus* contained statistically significant trends (monotonic trend). The rationale for selecting this test was its non-parametric nature, which obviates the need for the time series to be normally distributed. To assess for significant changes, we decided to divide the data based on the Jenks Natural Breaks Classification (Jenks, 1977), from the "classInt" package (Bivand, 2023). This clustering approach optimizes the grouping of data points into classes by minimizing the variance within groups and maximizing the variance between groups.

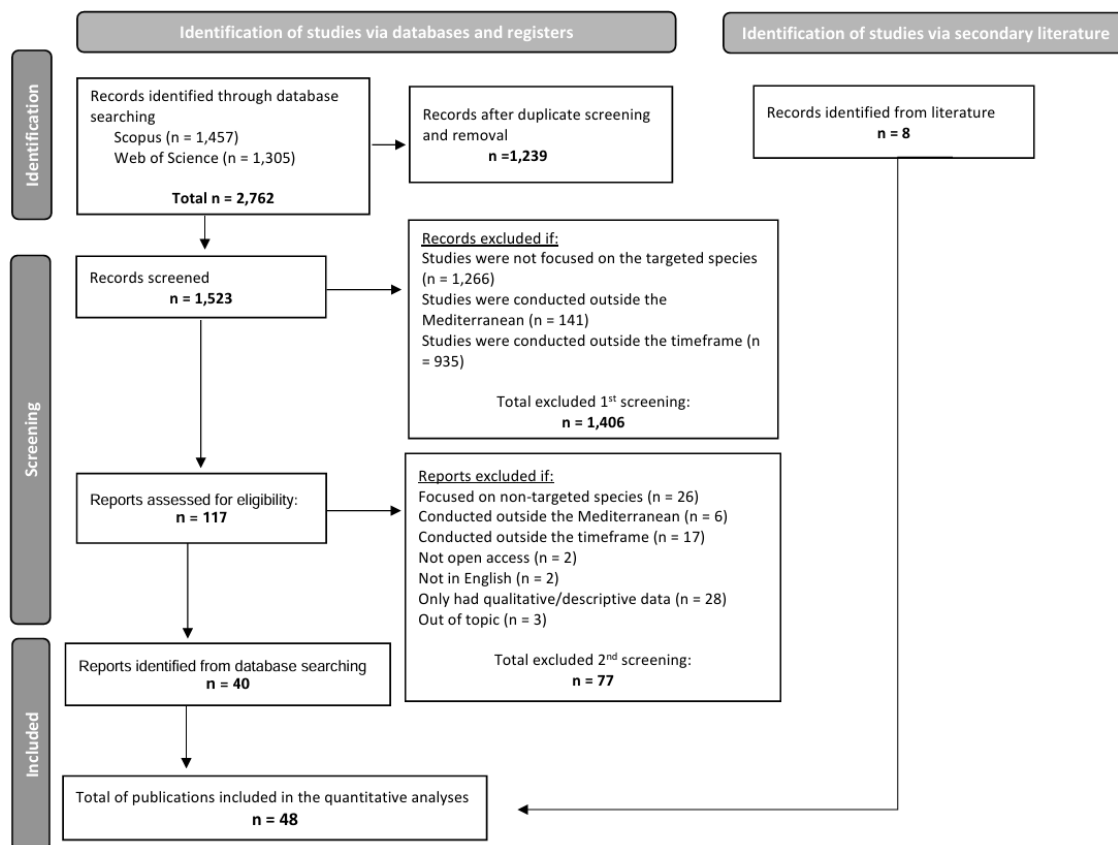
## RESULTS

### Systematic Literature Review

A total of 2,762 publications were retrieved from both Web of Science and Scopus. After removing duplicates, 1,523 publications were screened. From the first screening, 117 publications were considered eligible for full-text screening. From the second screening, 40 publications were included for gathering information and subsequent analyses. Secondary literature was selected by reviewing the full text of the publications. Based on this review, we included 8 additional publications in the analyses (Figure 2.2). In total, 48 publications were

used to build the database. The publications were also categorised based on their primary focus, which was either related to the species as indicators of past environmental conditions or changes or related to previously identified impacts upon them. With this classification, 42 of the total number of publications analysed targeted species as indicators and 15 assessed specific impacts.

The search covered seventeen species, but the results did not represent them all equally. For instance, no results were found for *Diplodus bellottii*, *D. cervinus*, *D. levantinus*, and *D. puntazzo*. Instead, the search yielded data on twenty-three taxa: Clupeidae, Delphinidae, Phocidae, Sparidae, and Scombridae families. *Diplodus* spp., *Thunnus* spp., *Phorcus* spp., and *Monodonta* sp. genus. *Delphinus delphis*, *D. annularis*, *D. sargus*, *D. vulgaris*, *E. encrasicolus*, *H. trunculus*, *M. monachus*, *O. edulis*, *P. turbinatus*, *S. pilchardus*, *S. aurita*, *S. maderensis*, *S. aurata* and *T. thynnus* species.

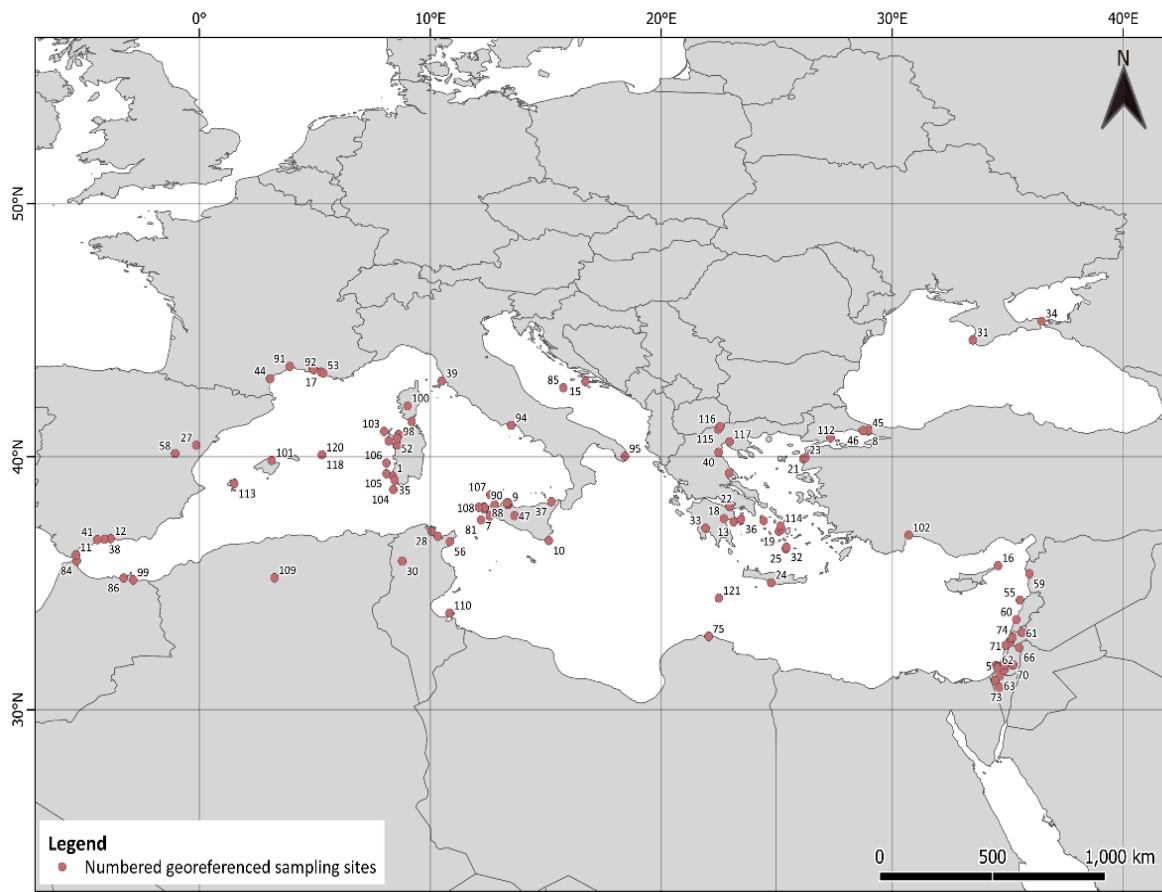


**Figure 2.2** - PRISMA 2020 flow diagram adapted from Page et al., 2021, highlighting the methodology and selection process used, indicating the number (n) of studies included in this

review. Numbers in bold are key values related to the number of studies included in the process of the evaluation.

### Systematic Review Analyses

The sampling units are dispersed throughout the Mediterranean area, with higher concentrations in some countries than others (Figure 2.3). The Western and Eastern sub-regions have more sampling units containing targeted species remains than the Adriatic Sea. Additionally, isolated sample units are in the Black and Marmara Seas, most likely because these location names were not included in the search strings. The countries presenting a high concentration of sampling units are Spain, Italy, Greece, and Israel (Figure 2.3, see also Table S6 for detailed information on each sampling unit). Additionally, most of the sampling units are in the coastal areas, while some are situated inland.



**Figure 2.3** - Mediterranean Sea map with sampling units (red circles). Each number corresponds to a unique sampling location from which the data came from. See more information regarding the name of each sampling location and the corresponding publication in Table S6.

### **NISP distribution**

The results obtained for NISP differ greatly between species. The dataset includes information on most species, except for *D. annularis*, *S. pilchardus*, *S. aurita*, and *S. maderensis*. The taxonomic group with the highest quantity of data belong to fish, followed by molluscs, and then by marine mammals. Following the exclusion of outliers, the data is mainly distributed between 12,500–100,000 years BP for fish, 50,000–100,000 years BP for molluscs, and 9,000–500 years BP for marine mammals (see supplementary material S7.1, S7.2 and S7.3). Most of the data is distributed between the Western and Eastern sub-regions, with only a few data from the Adriatic Sea. Within these sub-regions, *S. aurata*, *T. thynnus*, and *P. turbinatus* have the highest amount of data.

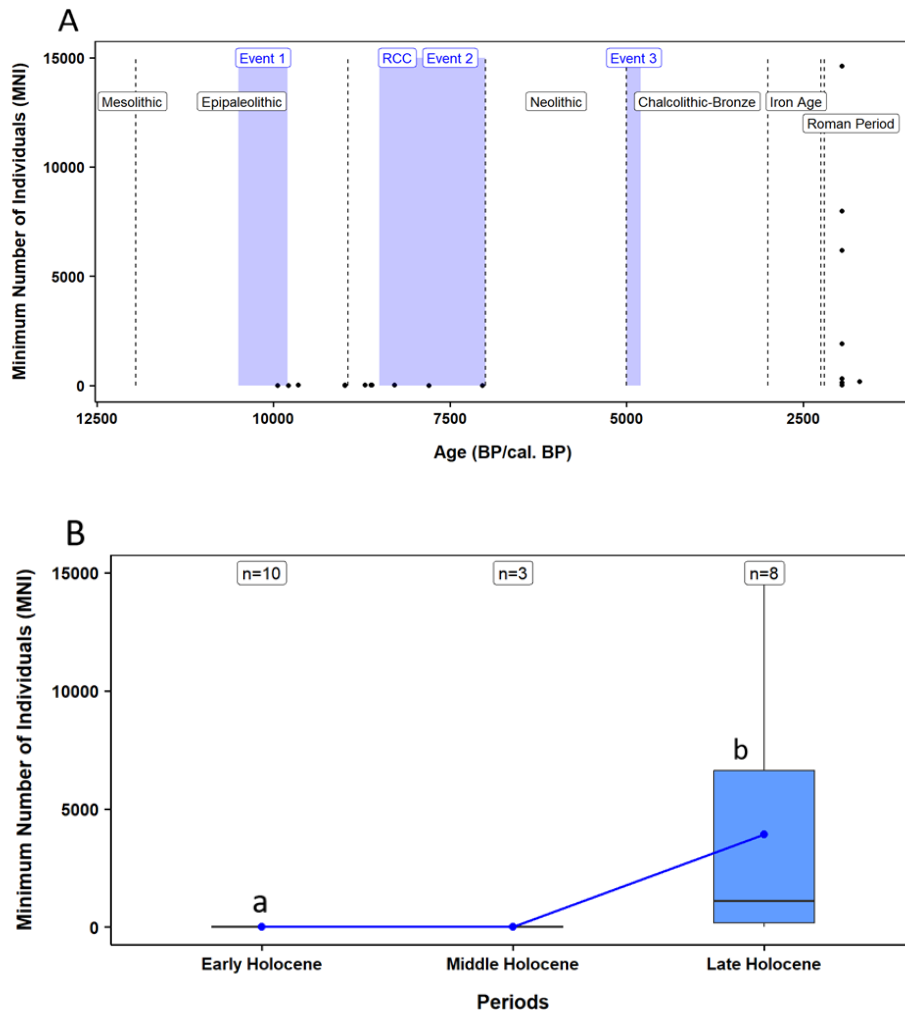
Concerning fish, the data for the two fish species covers the entire time interval. The remaining fish species exhibit fewer data and a more segregated distribution across sub-regions. The data from *P. turbinatus* is distributed across all the sub-regions. Two peaks are observed, the first around 30,000–45,000 years BP in the Eastern sub-region and the second between 50,000–15,000 years BP, with most of the records in the Western sub-region. In terms of marine mammals, *M. monachus* presents a peak in data availability around 12,500 years BP, with the most pronounced increase.

The only species with enough data to use for further analyses were *S. aurata* and *T. thynnus* for fish species, and *P. turbinatus* for molluscs. For the subsequent analyses, we separate the data between sub-regions and evaluate them separately. For these three species, sufficient information is available to evaluate the differences between the Western and Eastern sub-regions. Despite the comparisons made between periods for each region, no significant outcomes are found (see supplementary material S7.1.1B-S7.1.4B and S7.2.1B-S7.2.2B).

### **MNI distribution**

Five species and one genus presented data for MNI (see supplementary material S8.1). The data is predominantly distributed between 100,000-17,000 years BP. Both *P. turbinatus* and *H. trunculus* show data for most of the periods. The first species exhibits data from the Western and Eastern sub-regions. The statistical tests do not reveal any significant differences between the periods for both regions (see supplementary material S8.1.1B and S8.1.2B). For

*H. trunculus*, the results from the Kruskal-Wallis test indicate significant differences between periods in the Western sub-region ( $H_2 = 15.792$ ;  $p\text{-value} = 0.0004$ ). Furthermore, the pairwise comparisons reveal that the data from the Early and Late Holocene are statistically different from each other ( $p\text{-value} = 0.0013$ ; Figure 2.4B).



**Figure 2.4** – Distribution of data for the MNI of *Hexaplex trunculus* 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 letters represent statistically significant differences between periods. The number of points (n) included in each box plot is indicated above.

### Reported Relative Abundance (RRA)

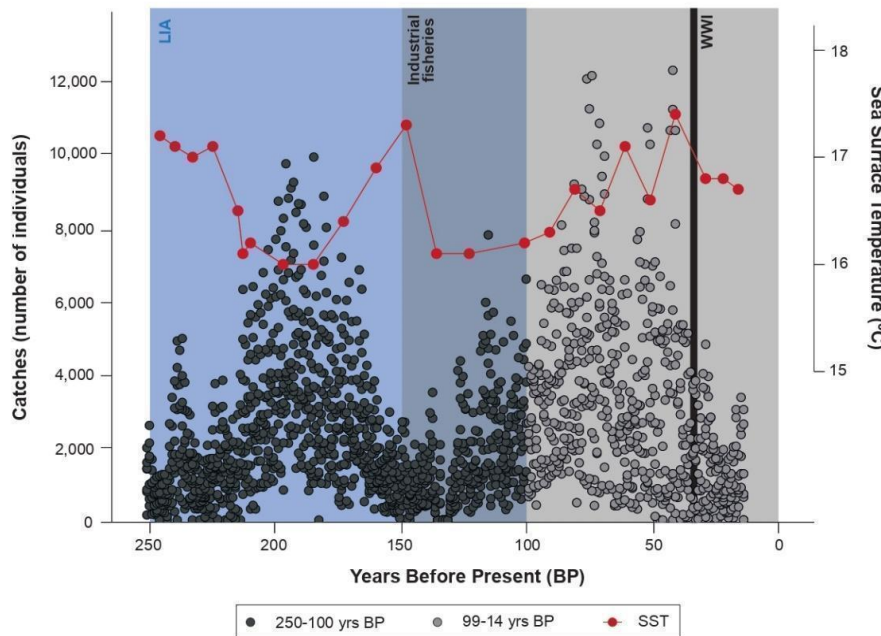
The RRA data were firstly separated based on the taxonomic group and subsequently by sub-region and assemblage type. Data for this parameter are available for all taxonomic groups,

except for Phocidae and Delphinidae families. Most of the data from all species are from archaeological sites. Consequently, we decided not to analyse this variable, as any conclusions made would incorporate important human bias: RRA from archaeological sites largely reflect human preferences for the exploitation of these species, rather than the relative abundance of the species in the natural population at that time. Nevertheless, it is possible to identify specific clusters and gaps in the information available for each taxon. About fish species, the data is predominantly derived from the Western and Eastern sub-regions, in contrast to the Adriatic Sea, which extends from 15,000-100,000 years BP. The species with the most data is *E. encrasicolus*, from the Eastern and Adriatic basins. *Sparus aurata* also presents a lot of data, with information available for each sub-region. Concerning the latter, the data is scattered across the time interval and the sub-regions. The Sparidae family presents a cluster of data from the Western Mediterranean, with the majority of the points falling within the range of 7,500-12,500 years BP. This suggests a decreasing trend towards the present (supplementary material S9.1). In terms of molluscs, the majority of the data originates from the Western and Eastern sub-regions, with a temporal range spanning between 50,000-100,000 years BP. The mollusc species presenting the most data are *H. trunculus* and *P. turbinatus*. *Hexaplex trunculus* has data predominantly from the Western sub-region, with a peak of RRA occurring around 1,950 years BP. In contrast, *P. turbinatus* has data from both the Western and Eastern basins, with a temporal separation between the two, ranging from approximately 30,000 to 15,000 years BP (supplementary material S9.2). Regarding marine mammal species, both species present scattered data through time, with high values for RRA coming from archaeological/natural assemblages in the Adriatic Sea and low values from archaeological settings in the Western Mediterranean Sea (supplementary material S9.3).

### ***Thunnus thynnus* catches records**

The data regarding the number of catches of *T. thynnus* ranged from zero catches to approximately 12,500 (number of individuals) through the time interval (250–14 years BP) (Figure 2.5). It is possible to identify two peaks in the number of catches for this species. The first peak occurs around 200 years BP, with about 10,000 individuals caught during the LIA event. The second peak occurred between 75-45 years BP, with approximately 12,000 tunas caught after the industrialisation of fisheries gears. Additionally, there were three moments

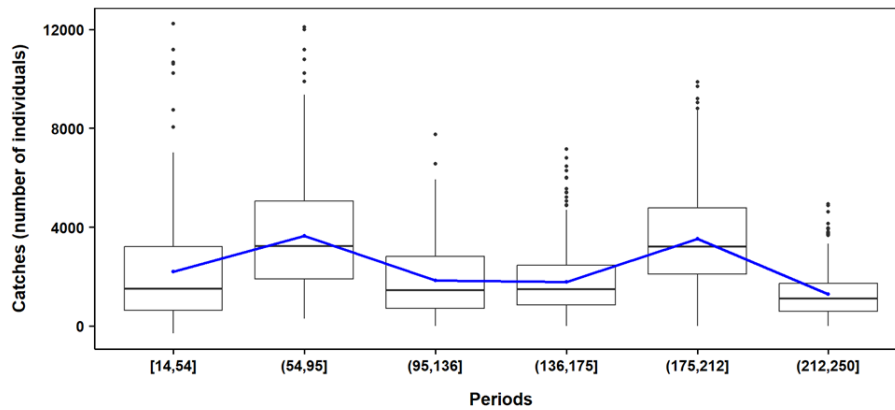
of a decline in the catch record. On the other hand, the SST exhibited a range of 16 to 17.4°C throughout the entire interval. However, the SST trend revealed that the peaks are synchronised with a decrease in temperature, while an increase is observed during the drops.



**Figure 2.5** – Atlantic Bluefin Tuna (*Thunnus thynnus*) catches records between 250-14 years BP (1700-1936), from tuna-traps in the Western Mediterranean Sea. The black points refer to the data collected between 250-100 years BP (1700-1850), and the lighter points refer to the catch records between 99-14 years BP (1851-1936). The red points are records of SST reconstructed from the Gulf of Lions (France) (data from Jalali et al., 2016). LIA: Little Ice Age lasted until 100 years BP; Industrial fisheries: minor modifications were made to tuna traps until the 1960's (Doumenge, 1998); WWI: World War I, lasted between 36-32 years BP.

The Mann-Kendall test ( $S$ ) result suggests a significant decreasing trend ( $S = -3.98e^5$ ; Kendall's tau coefficient =  $-2.39e^{-1}$ ;  $p$ -value  $< 2.2e^{-16}$ ;) in the catches variable.

Based on the Jenks Natural Breaks Method we divided the data into six periods (Figure 2.6). We find statistically significant differences between some periods according to the Kruskal-Wallis test ( $H_5 = 407.55$ ;  $p$ -value  $< 2.2e^{-16}$ ; Table 2.2).



**Figure 2.6** – Catches records of *Thunnus thynnus* 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 points (n) included in each box plot is indicated above. The black dots are outliers.

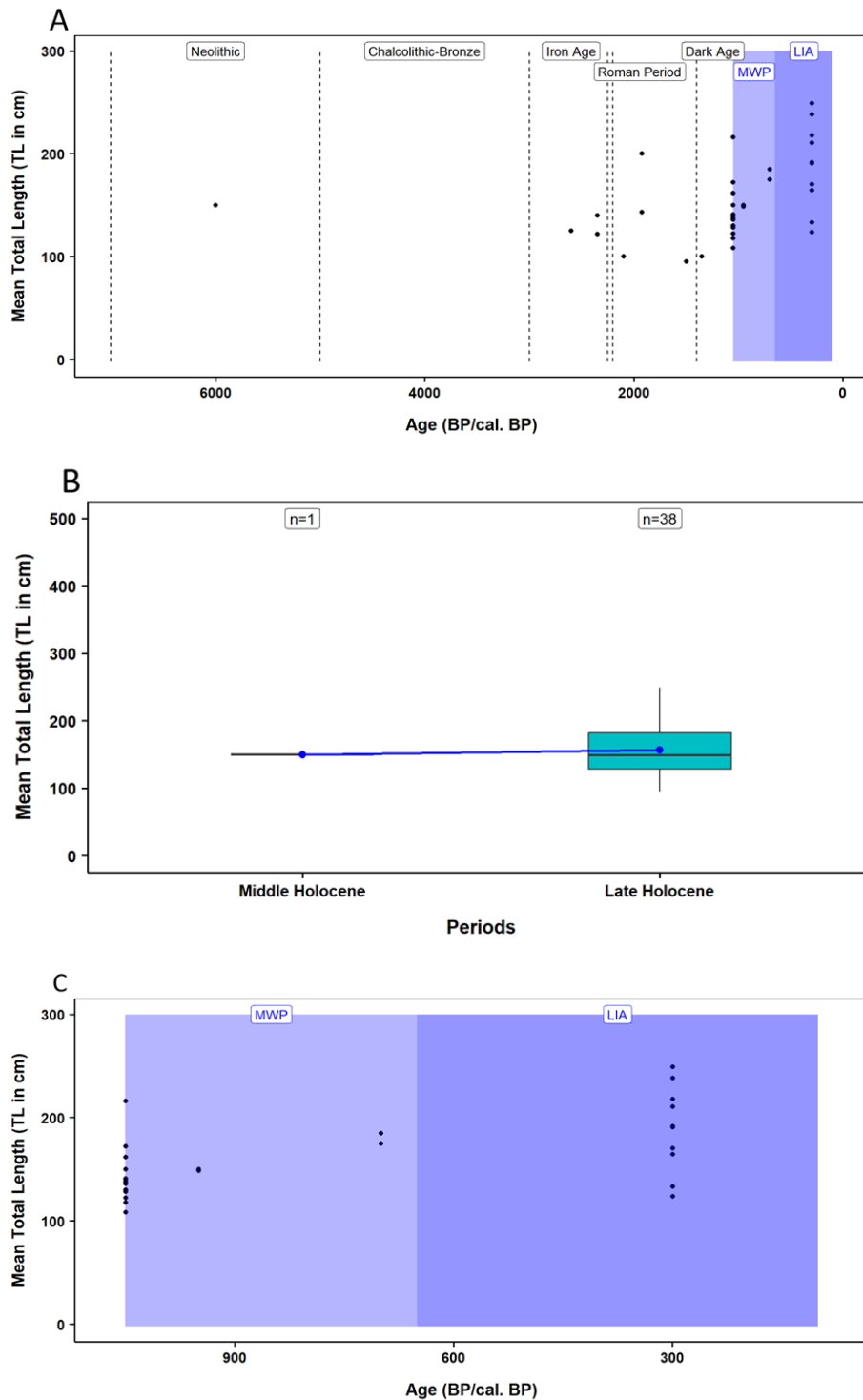
**Table 2.2** – Results from the pairwise comparisons between periods for *Thunnus thynnus*, adjusted by the Bonferroni correction method. Numbers in bold represent the periods that differ significantly from each other.

|           | [14,54]  | (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] | 6.00E-04 | < 2E-16 | 3.00E-04 | 1.10E-05  | < 2E-16   |

### Fishes' standard and total length

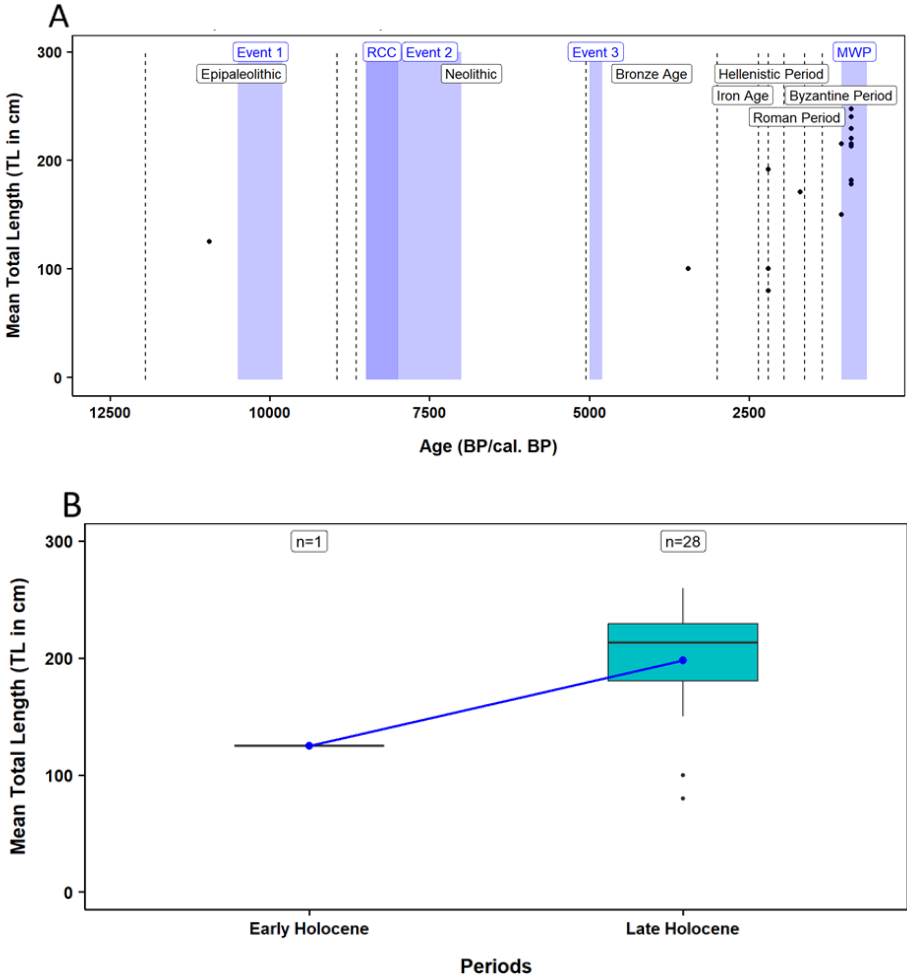
The results gathered regarding the SL and TL are displayed in supplementary material S10.1 and S10.2, respectively. Given the limited number of data and restricted distribution in time and by sub-region, no further analyses were performed on data for SL. For TL, analyses were performed on *S. aurata* and *T. thynnus*, excluding *Thunnus* spp.

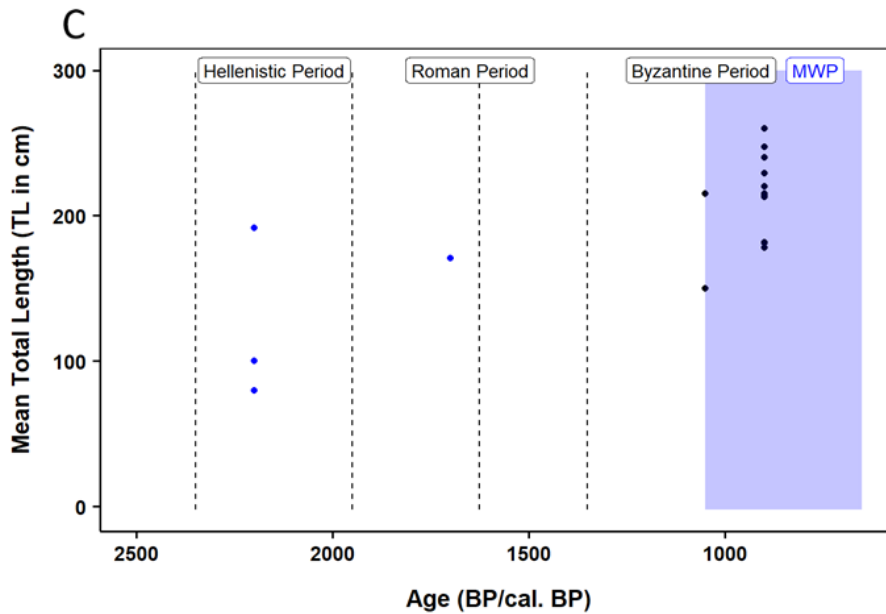
The data from *T. thynnus* exhibits a normal distribution ( $W = 0.9593$ ;  $p\text{-value} = 0.1686$ ) with non-significantly different variances between geologic periods ( $F = 2.103$ ;  $p\text{-value} = 0.1554$ ) for the Western sub-region. Our analysis reveals that there are no statistically significant differences between the geologic periods (Figure 2.7B;  $t_{37} = 0.16577$ ;  $p\text{-value} = 0.8696$ ). However, there are statistically significant differences in TL between the Medieval Warm Period and the Little Ice Age climatic periods (Figure 2.7C;  $t_{15.141} = 2.967$ ;  $p\text{-value} = 0.01$ ).



**Figure 2.7** – Distribution of data for TL on *Thunnus thynnus* 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 points (n) included in each box plot is indicated above; (C) Total length differences between the MWP (Medieval Warm Period) and LIA (Little Ice Age).

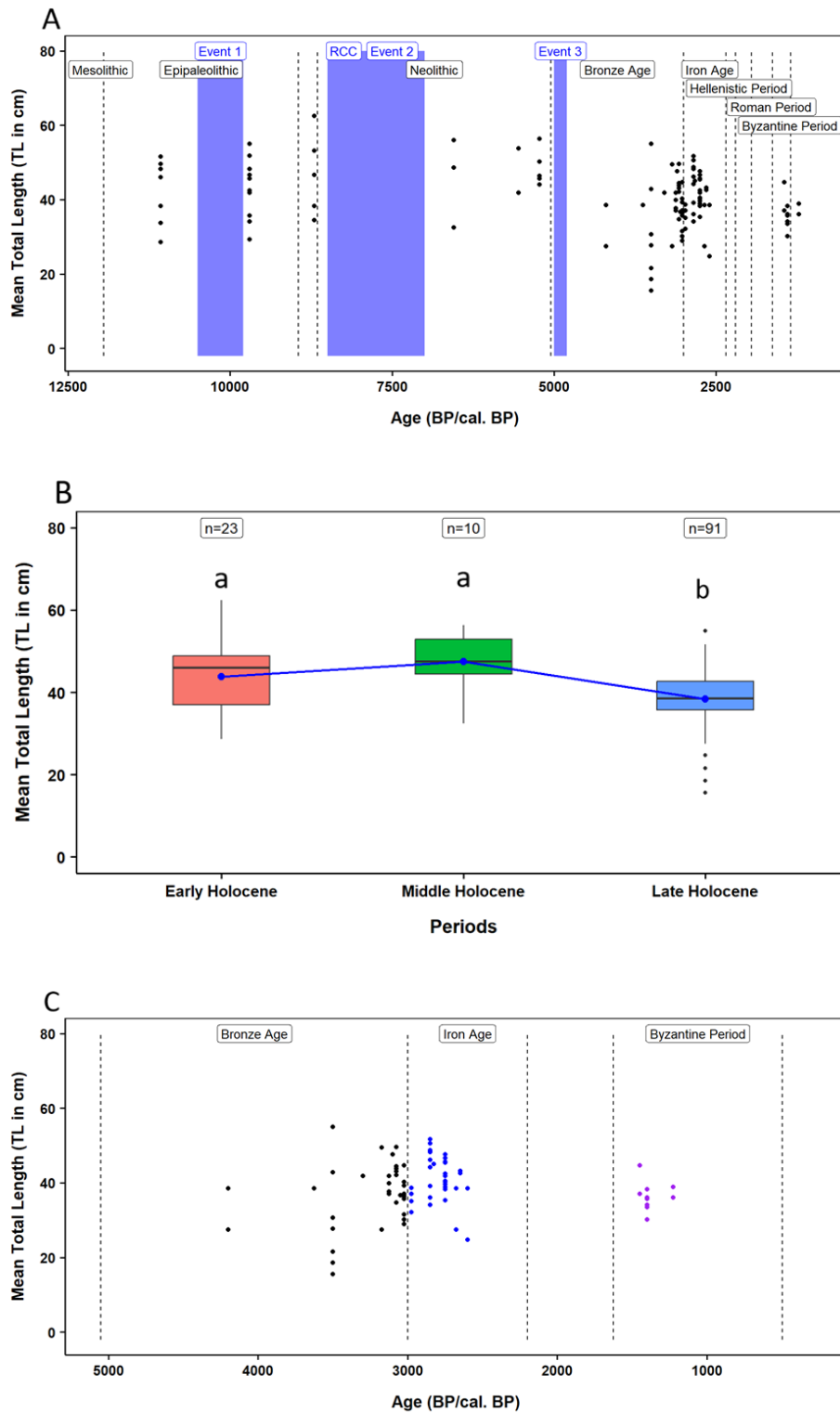
Regarding the data from the Eastern sub-region, the distribution is non-normally distributed ( $W = 0.9091$ ;  $p\text{-value} = 0.0163$ ) with non-significantly different variances ( $F = 0.9167$ ;  $p\text{-value} = 0.3468$ ). The statistical analysis between geologic periods does not yield significant differences ( $W = 3$ ;  $p\text{-value} = 0.2088$ ). However, analysis regarding the “before” and “during” of the beginning of the Medieval Warm Period reveal significant differences (Figure 2.8C;  $W = 8$ ;  $p\text{-value} = 0.01035$ ), although the amount of data differs from “before” and “during”.





**Figure 2.8** – Distribution of data for TL on *Thunnus thynnus* 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 points (n) included in each box plot is indicated above; (C) differences between the before and during the MWP (Medieval Warm Period).

The information regarding *S. aurata* is limited to the Eastern sub-region. This data exhibits a normal distribution ( $W = 0.9898$ ;  $p\text{-value} = 0.4921$ ), and non-significantly different variances between geologic periods ( $F_2 = 1.5013$ ;  $p\text{-value} = 0.227$ ). We find statistically significant differences between the Early and the Late Holocene ( $p\text{-value} = 0.0061$ ) and between the Middle and Late Holocene ( $p\text{-value} = 0.001$ ). This is illustrated in Figure 2.9B. Further investigation into potential differences between the Bronze and Iron Ages and the Byzantine Period yields statistical differences between the three periods ( $H_2 = 8.501$ ;  $p\text{-value} = 0.014$ , Figure 2.9C). Nevertheless, the comparisons between periods reveal no significant differences.



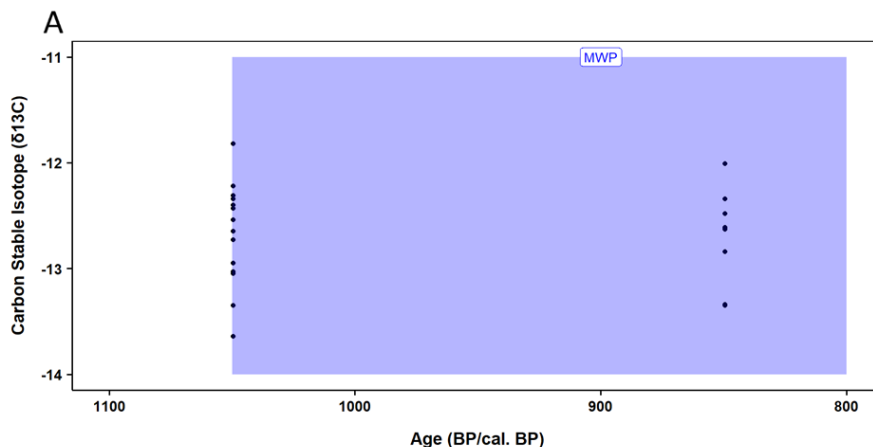
**Figure 2.9** – Distribution of data for the TL of *Sparus aurata* in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The letters represent statistically significant differences between periods. The number of points (n) included in each box plot is indicated above. (C) differences between the Bronze and Iron Ages and the Byzantine Period for TL data.

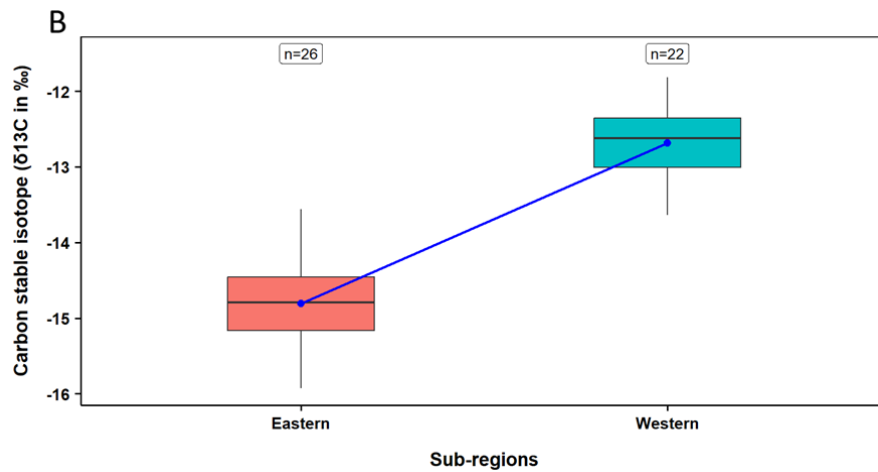
### Molluscs basal diameter (BD)

The results obtained regarding BD metrics are presented in the supplementary material, S11.1 and S11.2. The only species for which information is available regarding body size was *P. turbinatus* but restricted to the Eastern sub-region for both mean and maximum values of basal diameter. Upon assessment of both sets of data for normality and homoscedasticity, both are found to exhibit a non-normal distribution ( $W_{mean} = 0.9102$ ;  $p\text{-value}_{mean} = 0.245$ ;  $W_{maximum} = 0.9794$ ;  $p\text{-value}_{maximum} = 0.4367$ ). However, the same is not presented for the homoscedasticity between values. For mean values, the periods do not differ from each other in terms of variance ( $F_{mean} = 1.2519$ ;  $p\text{-value}_{mean} = 0.3365$ ), while for maximum values, the variance differs significantly ( $F_{maximum} = 4.4836$ ;  $p\text{-value}_{maximum} = 0.0071$ ). The results performed for the mean values indicate no significant differences between the periods ( $F = 2.021$ ;  $p\text{-value} = 0.195$ , S11.1B). The same result is found when assessing the maximum values ( $F = 0.3701$ ;  $p\text{-value} = 0.7767$ , S11.2B).

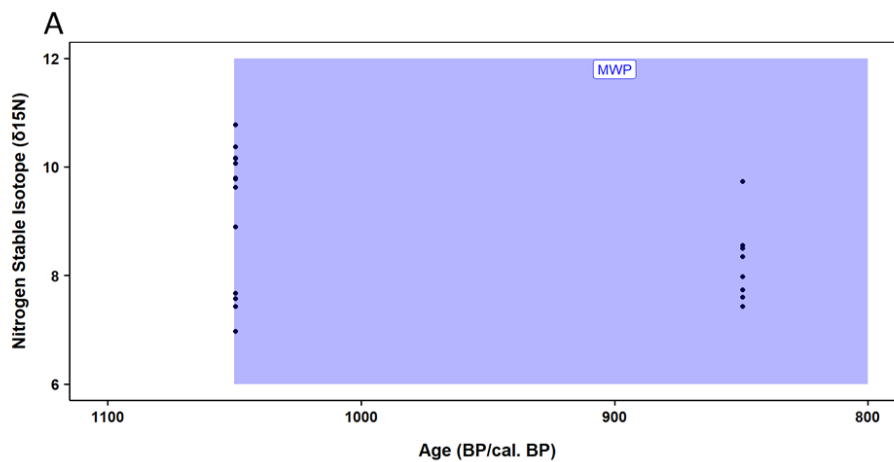
### *Thunnus thynnus* stable isotopic data

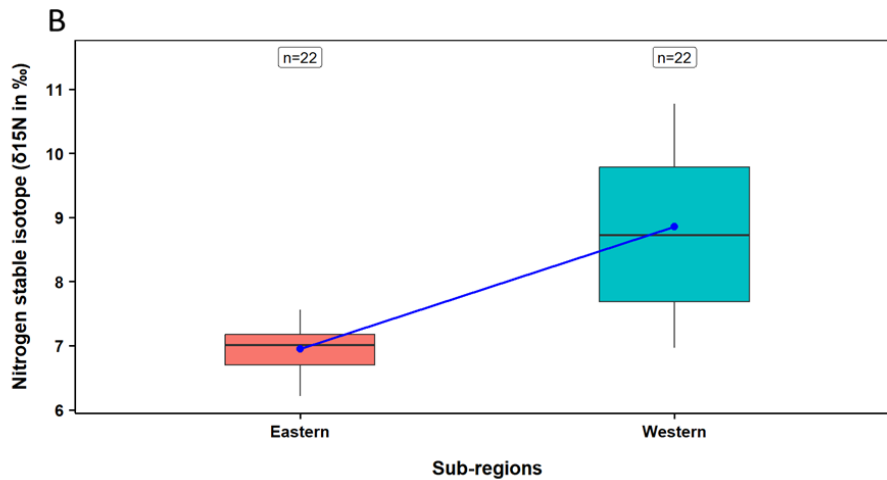
All data of stable isotopes of *T. thynnus* fall within a single major climatic event, the Medieval Warm Period (MWP, see Figures 2.10A and 2.11A). After assessing for normality ( $W_{\delta^{13}C} = 0.9335$ ;  $p\text{-value}_{\delta^{13}C} = 0.0091$ ;  $W_{\delta^{15}N} = 0.8727$ ;  $p\text{-value}_{\delta^{15}N} = 0.0002$ ) and homoscedasticity ( $F_{\delta^{13}C} = 1.141$ ;  $p\text{-value}_{\delta^{13}C} = 0.291$ ;  $F_{\delta^{15}N} = 41.743$ ;  $p\text{-value}_{\delta^{15}N} = 0.8.626e^{-8}$ ) for both stable isotopes. Statistical analyses reveal significant differences between the Western and Eastern sub-regions for the same period (850–1,050 years BP) for both  $\delta^{13}C$  ( $W = 1$ ;  $p\text{-value} = 3.927e^{-9}$ ) and  $\delta^{15}N$  ( $W = 16$ ;  $p\text{-value} = 1.2e^{-7}$ , Figures 2.10B and 2.11B).





**Figure 2.10** – Distribution of data for the  $\delta^{13}\text{C}$  of *Thunnus thynnus* between the Western and Eastern sub-regions between 1,050-850 years BP. (A) The  $\delta^{13}\text{C}$  values fall within the MWP (Medieval Warm Period); (B) Boxplots of the Western and Eastern sub-regions of the Mediterranean. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.





**Figure 2.11** - Distribution of data for the  $\delta^{15}\text{N}$  of *Thunnus thynnus* between the Western and Eastern sub-regions between 1,050-850 years BP. (A) The  $\delta^{15}\text{N}$  values fall within the MWP (Medieval Warm Period); (B) Boxplots of the Western and Eastern sub-regions of the Mediterranean. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

### ***Sparus aurata* stable isotopic data**

The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for *S. aurata* belong to the Bronze and Iron Ages. For both stable isotopes, there are a few data points from each major geologic period (see Figures S12.1A and S12.2A). After assessing for the normality ( $W_{\delta^{13}\text{C}} = 0.8855$ ;  $p\text{-value}_{\delta^{13}\text{C}} = 0.1794$ ;  $W_{\delta^{15}\text{N}} = 0.9172$ ;  $p\text{-value}_{\delta^{15}\text{N}} = 0.3695$ ) and homoscedasticity ( $F_{\delta^{13}\text{C}, d.f.=2} = 45.719$ ;  $p\text{-value}_{\delta^{13}\text{C}} = 0.0002$ ;  $F_{\delta^{15}\text{N}, d.f.=2} = 3.7329$ ;  $p\text{-value}_{\delta^{15}\text{N}} = 0.0885$ ) of the data for the geologic periods, the statistical analysis reveals no significant differences between periods ( $H_{\delta^{13}\text{C}, d.f.=2} = 0.70028$ ;  $p\text{-value}_{\delta^{13}\text{C}} = 0.705$ ;  $F_{\delta^{15}\text{N}, d.f.=2} = 2.344$ ;  $p\text{-value}_{\delta^{15}\text{N}} = 0.177$ ). However, the  $\delta^{15}\text{N}$  values increase abruptly from 4,199 years BP to 3,625 years BP and then decrease towards 2,675 years BP (Figure S12.2B).

## **DISCUSSION**

The Mediterranean Sea today is heavily impacted by environmental changes and human activities (Lotze et al., 2006; Coll et al., 2010; Moullec et al., 2019) including the warming of waters (Lionello et al., 2014; Cramer et al., 2018), the alteration and/or degradation of natural habitats (Halpern et al., 2008; Coll et al., 2010), and the overexploitation of marine resources (Tudela, 2004; Moullec et al., 2019), among others. These impacts raise several questions

regarding the Mediterranean's ecosystem processes and overall functioning in the present days, bringing even more uncertainties about its sustainability in the future (Cramer et al., 2018). However, impacts such as these have long been experienced in the Mediterranean Sea, with the interchange between warm and cold periods such as the MWP (1,050-650 years BP; Briffa, 2000) and the LIA (650-100 years BP; Briffa, 2000), and successive cultural changes such as the Late Paleolithic (51,949 - 21,949 years BP; Stiner and Kuhn, 2006) and the Mesolithic (21,949 - 11,949 years BP; Stiner and Kuhn, 2006). A comprehensive understanding of the historical impacts on the Mediterranean Sea is essential for accurately assessing the marine ecosystem's past responses (Jackson, 2001). The study of the past marine ecosystems of the Mediterranean Sea can inform about its future state (Jackson, 2001). Although the method employed was a systematic review, we focused specifically on the parameters extracted from the database to better understand the climatic and anthropogenic impacts on several species across the Mediterranean Sea, particularly during the Holocene.

Even though there are limitations associated with our work, there are also relevant results that can be discussed concerning past impacts on marine ecosystems. The results reported here present the impacts of pre-industrial climate change and human activities on one mollusc (*H. trunculus*) and two fish species (*T. thynnus* and *S. aurata*), particularly during the Holocene period.

### **Caveats and mitigation measures**

The scope of this study encompasses some caveats related to the experimental design, the type and availability of data gathered, and the general context of the environmental and cultural changes that have occurred in the past.

Firstly, the experimental design of this study is biased towards economically important species. Although it is almost certain that other species were also impacted, it was not possible to include them all. Secondly, the lack of available data on the pre-set parameters for the Adriatic Sea suggests that these parameters were not the primary focus of previous studies, although data may have been collected but not yet published. The amount of available data also varies significantly between studies, lacking unified guidelines (e.g., dating systems and body size measurements) which made the gathering of information and subsequent analyses

challenging. It is not uncommon for scientific articles to present data in a format that is not readily usable. Another restriction was the resolution required to reconstruct past population sizes, thereby limiting the potential for evaluating the magnitude of past impacts. Lastly, another constraint is the duality of dating geohistorical records, in either absolute or relative time.

However, to mitigate some of these issues, we constructed a timetable with the various classification schemes available for the entire Mediterranean and its three sub-regions. This allowed for the interpretation of the records by adopting a unified absolute timescale, in years Before Present (BP).

### **Climatic Impacts**

Climatic changes directly affect species' biological rates/processes (Viitasalo et al., 2015), along with their distribution (Pinsky et al., 2013), abundance (McCauley et al., 2015), and body size (Daufresne et al., 2009; Baudron et al., 2014). Indirectly, it also affects the ecosystem functioning (Pontavice et al., 2019), by altering species interactions and populations' synchrony (match/mismatch of populations, Viitasalo et al., 2015).

Some of the impacts identified in our results might be attributed to changes in temperature and sub-regional differences in productivity across the Mediterranean Sea. Firstly, we have identified changes in the abundance and body size of *T. thynnus*, most likely linked to changes in temperature. Temperature plays a significant role in various aspects of *T. thynnus* biology, including metabolism, growth, reproduction, survival of larvae, food availability and migration patterns (Pepin, 1991; Korsmeyer & Dewar, 2001; Schaefer, 2001; Graham & Dickson, 2004).

Our study suggests a significant impact on the abundance of *T. thynnus* due to a noticeable increase in the number of catches observed in the Western sub-basin during the latter stages of the LIA (250-100 years BP). There appears to be a correlation between the decline in SST and the increase in catches from tuna traps in this region. The LIA is characterised by a decrease in temperature, which had notable climatic effects in Europe (Mann, 2002; Guiot et al., 2005). Some authors (Ravier and Fromentin, 2004) found something similar and concluded that the migration of *T. thynnus* towards the Mediterranean Sea between the 17<sup>th</sup>-20<sup>th</sup> centuries may have been caused by the cooling temperatures of the LIA event. *Thunnus*

*thynnus* travels great distances from cold feeding areas to warm, oligotrophic spawning grounds (Block et al., 2005; Rooker et al., 2007; Galuardi et al., 2010). Temperature influences the production and distribution of plankton (e.g., McGowan et al., 1998; Beaugrand et al., 2002), influencing the food availability for both juveniles and adults (Mather et al., 1995). This drives the spatial and temporal dynamics of this migratory fish (Ravier & Fromentin, 2004) between the spawning and feeding grounds. *Thunnus thynnus* was not the only species whose abundance seemingly increased during the LIA, as Calkin et al. (2001) confirmed that during this event in Alaska (1250-1890 Anno Domini (AD)) there were higher Pacific sockeye salmon abundances.

It can be hypothesised that climate change, through fluctuations in the temperature, may have also impacted the growth and subsequent body size (TL) variations of this fish during past climatic events. In changing environmental conditions, the opportunistic diet of *T. thynnus* (MacArthur, 1972; Janzen, 1973; Olesen & Jordano, 2002) may have enabled this species to increase its TL. Recent studies suggested a stronger consumer-driven control of food webs with warming (Allen et al., 2005; López-Urrutia et al., 2006). Warming boosts heterotroph abundance, strengthening consumer-resource interactions (O'Connor, 2009; Gilbert et al., 2014), and benefiting organisms of top trophic levels (Archibald et al., 2022) as *T. thynnus*. Temperate consumers have wider niche breadths, making them generalists (MacArthur, 1972; Janzen, 1973; Olesen & Jordano, 2002). This dietary flexibility together with stronger consumer-resource interactions might have granted *T. thynnus* the chance to thrive during past climatic fluctuations, allowing for the increase in TL across the entire Mediterranean basin.

Secondly, we have identified observed differences in the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios of *T. thynnus* tissues in the Mediterranean Sea between 1,050-850 years BP, which may be explained by sub-regional differences in ecosystem primary productivity. The Mediterranean Sea is an oligotrophic basin with a distinct gradient from east to west (Coll et al., 2010). This feature was also present in the past, with pronounced events of declines in primary productivity in the Eastern (e.g., Kuhnt et al., 2008) and enhanced productivity in the Western sub-region (e.g., Incarbona et al., 2010; Nieto-Moreno et al., 2011).

The  $\delta^{13}\text{C}$  values are good indicators of sources of primary production in marine systems (Hobson et al., 1994; France, 1995), as their signatures change between primary producers

(DeNiro & Epstein, 1981; Inger & Bearhop, 2008), but are generally maintained across trophic levels (DeNiro & Epstein, 1978; Guiry, 2019). Several factors can alter the carbon values, including terrestrially derived carbon inputs, different quantities of resuspended carbon from the sediment or the deep sea (Barnes et al., 2009; Magozzi et al., 2017), raining patterns and temperature variability (Rao et al., 2017) and the predominant primary producer sources (McCormack et al., 2019). The higher values of the  $\delta^{13}\text{C}$  observed in the Western sub-region suggest that *T. thynnus* may have demonstrated a preference for coastal waters in these areas, whereas, in the Eastern sub-region, they appear to have preferred offshore areas. This proves to be consistent with its use of the Western part for spawning (Oray & Karakulak, 2005; Rooker et al., 2008; Alemany et al., 2010). Studies suggest that fish from the Central-Eastern Mediterranean tend to forage in more offshore waters, due to the opportunity for deep-diving (Wilson & Block, 2009; Battaglia et al., 2013; Olafsdottir et al., 2016) and/or due to less benthic-pelagic coupling (Magozzi et al., 2017; Pinzone et al., 2019).

The  $\delta^{15}\text{N}$  values increase with the trophic level and are used to estimate the trophic position of an organism in the food web (Sigman et al., 2009). The increased values of the  $\delta^{15}\text{N}$  values of *T. thynnus* in the Western compared to the Eastern Mediterranean are most likely due to differences in nutrient availability between the two regions. The Mediterranean Sea is regulated by bottom-up processes, where nutrient availability drives the structure and functioning of the entire food web (Coll et al., 2009; Macias et al., 2014; Piroddi et al., 2017). Despite the prevailing oligotrophy of this basin (Coll et al., 2010) with a demarcated gradient from east to west, coastal areas can be enriched by local factors such as fluctuating wind conditions, currents, and fluvial discharges (Bosc et al., 2004; Estrada, 2010; Zavatarelli et al., 1998). Changes in primary producers, and thus, in bottom-up control might cause temporal and/or spatial changes in the trophic level of the above species in the food web. In the past, local changes in nutrient input, combined with the fact that *T. thynnus* has a generalist diet (MacArthur, 1972; Janzen, 1973; Olesen & Jordano, 2002), allowed the organisms to thrive in the Western Mediterranean. On the other hand, the greater oligotrophy of the Eastern Mediterranean results in a more specialised prey selection. Nevertheless, for the Mediterranean Sea as a whole, a study conducted by Andrews et al. (2023) on long-time series isotopic data from eastern Atlantic, Mediterranean and Black Sea locations between the 1<sup>st</sup>

century to 1941 Common Era found no significant change in *T. thynnus* trophic position across millennia, despite the large modifications of the marine ecosystems that have taken place.

### **Anthropogenic Impacts**

Humans have shaped marine ecosystems since discovering their potential to provide food resources (Jackson, 2001). Since prehistorical times, humans have exerted a significant impact on various marine ecosystems, particularly through the overexploitation of particular groups of species (e.g., Estes et al., 1989). Some of the changes identified in our results might be attributed to exploitation by humans, such as changes in the abundance of *H. trunculus* and *T. thynnus*.

Our study highlights the extensive exploitation of *H. trunculus* in the Late Holocene (4,200 years BP to present days; Stuiver & Reimer, 1986), but particularly during the Roman Period (2,249-1,400 years BP; Roberts et al., 2011). This gastropod inhabits the intertidal region of the coastline (Bonanno et al., 2016), being easily accessible by either hunter-gatherers who consume on a small scale or by civilisations who exploit them at industrial levels. During the Roman Period, *H. trunculus* along with two other 'murex' molluscs - *Bolinus brandaris* and *Stramonita haemastoma* - were intensely harvested to be used in the Mediterranean to produce Purple dye (Oliver, 2015), also known as Royal purple, Tyrian purple or even Imperial purple (Reese, 1980).

*Thunnus thynnus*' abundance seems to have been more influenced by human activity after the introduction of industrial advancements to fishing equipment (this study). The exploitation of this large predator is well-documented across the Mediterranean Sea, from the beginning of the 7<sup>th</sup> millennium BC (Before Christ; Desse & Desse-Berset, 1994) until nowadays. The intensive exploitation of this species in the Mediterranean Sea has led to a drastic decline in recent years (Fromentin and Powers, 2005), with the population facing a potential collapse (MacKenzie et al., 2009), as seen with the decreasing monotonic trend (this study). The continued fishing activity went through several modifications but had as a baseline the natural migrating routes of the animals towards the enclosed sea (e.g., Berthelot, 1869; Farrugio, 1981; Mather et al., 1995). Although the number of catches was higher after 150 years BP, this may have been the result of slight modifications to the tuna traps or the result

of phenomena of population expansion, which translates to a higher number of catches. Nevertheless, to provide a more detailed explanation for this increase after 150 years BP, a longer time series is required.

The anthropogenic removal of species like the ones mentioned above might have caused changes in their past abundances. The reduction of consumer populations causes major changes in ecosystem structure and function, triggering cascade effects throughout the pelagic food web (Pauly et al., 1998; Essington et al., 2002; Scheffer et al., 2005). A similar impact was observed in sea cows (manatees), whose uncontrolled exploitation that began 4,000 years ago by aboriginal hunters, inevitably led to their extinction in 1768 due to the actions of European fur traders (Estes et al., 1989). The exploitation of sea otters by Aboriginal Aleuts began 2,500 years ago, leading to a significant decrease in their population and an increase in the size of sea urchins, their natural prey (Simenstad et al., 1978). The overfishing of sea otters and competitive predators of sea urchins has led to profound changes in the kelp forests, due to the lack of top-down control over sea urchins that graze on kelp (Jackson et al., 2001).

Secondly, our results indicated that intensive exploitation can lead to changes in body size, as demonstrated by the case of both *T. thynnus* and *S. aurata*. In addition to the impact of climate change on organism growth, another potential explanation for the observed increase in TL for *T. thynnus* across time intervals is that human activities did not significantly affect the species. This is based on the hypothesis that a reduction in exploitation may have allowed this species to grow. According to Sarmiento (1757), there was a significant decrease in tuna catches in Spain between the mid-16<sup>th</sup> and 18<sup>th</sup> centuries, likely linked to the previous overexploitation of this predator. In prior centuries, prey and juvenile stages of *T. thynnus* were overexploited, and disturbance of the seabed near tuna traps in Andalusia (Spain's Atlantic coast) might have altered their migration routes further from shore (García, 2016).

The intensive exploitation of *S. aurata* during the Late Holocene in the Eastern sub-region led to a decrease in its TL (this study). This species was subjected to significant exploitation from multiple Mediterranean locations during the Holocene period, including the hypersaline Bardawil Lagoon in Egypt (Guy et al., 2018). Analyses of oxygen isotopes in teeth revealed changes in size patterns, suggesting shifts in the exploitation of this species. The reduction in body size is evident in the archaeological remains from the Late Bronze Age (3,550–3,200

years BP) until the Byzantine Period (1,680–1,360 years BP). This reduction is likely due to an intensive harvest of younger individuals (Guy et al., 2018). *Sparus aurata* is not the only species with a long history of exploitation, as evidenced by numerous examples from around the world (e.g., Jackson, 2001). Guiry et al. (2021) conducted an analysis of numerous archaeological sheepshead bones (*Archosargus probatocephalus*) from New Orleans, USA. Their findings indicated a steady decrease in the average estimated fish's SL between 1720 and the 1840's. This decline probably results from long-term fishing activities in the area. A reduction in the average fish catch size is indicative of a clear response to overfishing, which may be attributed to the utilisation of size-selective fishing gear (such as gill netting, a common practice at the time; Goode, 1887). The intense harvesting of species with consequences of size reductions dramatically changes the nature of trophic interactions in marine ecosystems (Shackell et al., 2009; Cheung et al., 2012; Garcia et al., 2012).

## Conclusions

This work shows the significance of past climatic and anthropogenic impacts on the species, and therefore, on this large marine ecosystem. These impacts affected the abundance, body size and trophic ecology of these species. In particular, *T. thynnus* was likely impacted by both climatic changes, especially due to temperature fluctuations and sub-regional differences in the primary productivity of the ecosystem, while *H. trunculus* and *S. aurata* were probably impacted by human activities, through extensive gathering or fishing. The removal of certain links in food webs brings several changes to the well-functioning of the ecosystem. For instance, the decline of top predators, such as *T. thynnus*, may deeply impact the marine ecosystem with consequences in the food web of each region, through trophic cascades and modifications of certain predator-prey interactions.

The integration of paleoecological, archaeological and historical data with contemporary biological information provides a more comprehensive temporal framework, which is essential for comprehending marine ecosystem history and species-specific responses to such disturbances. This allows for a better understanding of how short-term trends investigated nowadays, might fit within multi-temporal scale cycles. Despite this, the lack of such integration hinders progress in effectively addressing environmental challenges and limits the potential for present and future holistic solutions. Consequently, we need to collaborate in a

multidisciplinary way in developing more extensive and inclusive approaches to marine ecosystem conservation and current environmental management.

Moreover, we propose additional efforts to address the limitations associated with the integration of information from past studies. Further research and management strategies should be directed towards species that are particularly vulnerable and at an elevated risk of collapse (e.g., *M. monachus*), to implement species-specific conservation measures. Thus, a comprehensive understanding of how marine ecosystems have responded in the past to certain impacts represents a valuable asset for present and future studies and policy-making endeavours aimed at preserving the marine biodiversity of the Mediterranean Sea.

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## SUPPLEMENTARY MATERIAL

### S1. Geological, cultural and climatic periods timetable

**Table S1** – List of designations regarding different geologic, climatic and cultural periods, divided by each sub-region of the Mediterranean, placed in time using the system years BP (Before Present). ICS stands for International Commission on Stratigraphy.

#### Quaternary System

| Years BP | Series   | Stage [ICS]                                  | Ref. Stage ICS            | Periods Western Med.                                 | Ref. W   | Periods Eastern Med.    | Ref. E  | Periods Adriatic   | Ref. A  |
|----------|----------|--|---------------------------|--|--|-------------------------|---|--|---|
| 0        | Holocene | Meghalayan (Late Holocene)<br>START 4,200 BP | Stuiver and Reimer (1986) | Industrial Period 100-0 BP / Modern Warming 100-0 BP | Briffa, 2000; Verschuren et al., 2000; Briffa & Osborn, 2002; Bradley et al., 2003; Keller, 2004; Hambrey, | Modern Warming 100-0 BP | Briffa, 2000; Verschuren et al., 2000; Briffa & Osborn, 2002; Bradley et al., 2003; Keller, |  |   |
| 50       |          |  |                           |  |  |                         |   | Late Modern 150-50 BP / Little Ice Age 650-100 BP / Little Ice Age 400-100BP | Haywood, 1997; Blondel & Aronson, 1999; Briffa, 2000; Reale, 2000; Verschuren et al., 2000; |

|     |  |  |  |   |  |   |  |  |  |
|-----|--|--|--|---|--|---|--|--|--|
|     |  |  |  |   | 2005;<br>Martín-<br>Puertas et<br>al., 2008;<br>Helama et<br>al., 2009;<br>Büntgen<br>et al.,<br>2011;<br>Roberts et<br>al., 2011  |   | 2004;<br>Hambre<br>y, 2005;<br>Martín-<br>Puertas<br>et al.,<br>2008;<br>Helama<br>et al.,<br>2009;<br>Büntgen<br>et al.,<br>2011; |  | ren et<br>al.,<br>2000;<br>Briffa &<br>Osborn,<br>2002;<br>Bradley<br>et al.,<br>2003;<br>Keller,<br>2004;<br>Hambre<br>y, 2005;<br>Lotze et<br>al.,<br>2006;<br>Martín-<br>Puertas<br>et al.,<br>2008;<br>Helama<br>et al.,<br>2009;<br>Büntgen<br>et al.,<br>2011; |
| 100 |  |  |  | Little Ice Age 650-100<br>BP / Little Ice Age 700-<br>100 BP / Little Ice Age<br>400-100 BP | Briffa,<br>2000;<br>Reale,<br>2000;<br>Verschure<br>n et al.,<br>2000;<br>Briffa &<br>Osborn,<br>2002;<br>Bradley et<br>al., 2003; | Little Ice Age 650-100<br>BP / Little Ice Age 400-<br>100BP | Briffa,<br>2000;<br>Reale,<br>2000;<br>Verschu<br>ren et<br>al.,<br>2000;<br>Briffa &<br>Osborn,<br>2002;<br>Bradley               |  |  |

|     |  |  |  |  |                              |  |                              |   |                           |
|-----|--|--|--|--|------------------------------|--|------------------------------|---|---------------------------|
| 150 |  |  |  |  | Keller, 2004;                |  | et al., 2003;                |   | Haywood, 1997;            |
| 200 |  |  |  |  | Hambrey, 2005;               |  | Keller, 2004;                |   | Blondel &                 |
| 250 |  |  |  |  | Martín-Puertas et al., 2008; |  | Hambrey, 2005;               |   | Aronson, 1999;            |
| 300 |  |  |  |  | Helama et al., 2009;         |  | Martín-Puertas et al., 2008; |   | Briffa, 2000;             |
| 350 |  |  |  |  | Büntgen et al., 2011;        |  | Helama et al., 2009;         |   | Reale, 2000;              |
| 400 |  |  |  |  | Roberts et al., 2011         |  | Büntgen et al., 2011;        | Early Modern 450-150 BP / Little Ice Age 650-100 BP / Little Ice Age 400-100 BP | Verschuuren et al., 2000; |
|     |  |  |  |  |                              |  | et al., 2011;                |   | Briffa & Osborn, 2002;    |
|     |  |  |  |  |                              |  |                              |   | Bradley et al., 2003;     |
|     |  |  |  |  |                              |  |                              |   | Keller, 2004;             |
|     |  |  |  |  |                              |  |                              |   | Hambrey, 2005;            |
|     |  |  |  |  |                              |  |                              |   | Lotze et al., 2006;       |



|       |  |  |  |  |   |  |  |  |  |
|-------|--|--|--|--|---|--|--|--|--|
| 900   |  |  |  | / High Medieval Period<br>1,049-750 BP                               | Bradley et al., 2003;<br>Keller, 2004;<br>Hambrey, 2005;<br>Ruas, 2005;<br>Martín-Puertas et al., 2008;<br>Helama et al., 2009;<br>Büntgen et al., 2011<br>Roberts et al., 2011 |  | Keller, 2004;<br>Hambrey, 2005;<br>Martín-Puertas et al., 2008;<br>Helama et al., 2009;<br>Büntgen et al., 2011; |  | Bradley et al., 2003;<br>Keller, 2004;<br>Hambrey, 2005;<br>Lotze et al., 2006;<br>Martín-Puertas et al., 2008;<br>Helama et al., 2009;<br>Büntgen et al., 2011; |
| 950   |  |  |  |  |   |  |  |  |  |
| 1,000 |  |  |  |  |   |  |  |  |  |
| 1,050 |  |  |  |  |   |  |  |  |  |
| 1,100 |  |  |  | Dark Age 1,400-1,090<br>BP / Early Medieval<br>Period 1,449-1,049 BP | Ruas, 2005;<br>Roberts et al., 2011   |  |  |  |  |
| 1,150 |  |  |  |  |   |  |  |  |  |
| 1,200 |  |  |  |  |   |  |  |  |  |
| 1,250 |  |  |  |  |   |  |  |  |  |



|       |  |  |  |  |  |   |   |                             |  |
|-------|--|--|--|--|--|---|---|-----------------------------|--|
| 2,100 |  |  |  |  |  | (Black Sea) 2,429-2,273 BP / Hellenistic  | 2020; Aiken et al., 2023                                    |                             |  |
| 2,200 |  |  |  |  |  | (Black Sea) 2,272-1,980 BP / Greek  |   |                             |  |
| 2,300 |  |  |  |  |  | Classical Period 2,449-2,350 BP / Roman   |   |                             |  |
| 2,400 |  |  |  |  |  | Classical Period 2,049-1,950 BP / Roman   |   |                             |  |
| 2,500 |  |  |  |  |  | Period 2,049-1,449 BP   |   |                             |  |
| 2,600 |  |  |  |  |  | Iron Age 3,000-2,200 BP / Middle Bronze Age to Iron Age 3,849-2,449 BP / Roman                        | Stuiver & Reime, 1986; Reale, 2000; Roberts et al., 2011    |                             |  |
| 2,700 |  |  |  |  |  | Period 2449-1400 BP / Greek Classical Period 2,449-2,350 BP   |   |                             |  |
| 2,800 |  |  |  |  |  | Archaic (Black Sea) 2,649-2,429 BP / Greek Classical Period 2,449-2,350 BP                            | Reale, 2000; Aiken et al., 2023                             | Local Market 2,849-2,449 BP | Haywood, 1997; Blondel & Aronson, 1999; Lotze et al., 2006 |
| 2,900 |  |  |  |  |  | Bronze Age (Black Sea) 4,449-2,649 BP / Early Iron Age 2,999-2,649 BP / Early Iron Age 3,149-2,749 BP | Andreu et al., 1996; Eshel et al., 2019; Aiken et al., 2023 | Agricultural 7,949-2,849 BP | Haywood, 1997; Blondel & Aronson, 1999;                    |



|       |                             |  |  |  |   |   |  |  |
|-------|-----------------------------|--|--|--|---|---|--|--|
| 4,500 | Holocene)<br>START 8,186 BP |  |  |  |   |   |  |  |
| 4,600 |                             |  |  |  |   |   |  |  |
| 4,700 |                             |  |  |  |   |   |  |  |
| 4,800 |                             |  |  |  |   |   |  |  |
| 4,900 |                             |  |  |  |   |   |  |  |
| 5,000 |                             |  |  |  |   |   |  |  |
| 5,100 |                             |  |  |  |   |   |  |  |
| 5,200 |                             |  |  |  |   |   |  |  |
| 5,300 |                             |  |  |  |   |   |  |  |
| 5,400 |                             |  |  |  |   |   |  |  |
| 5,500 |                             |  |  |  |   |   |  |  |
| 6,000 |                             |  |  |  |   |   |  |  |
| 6,500 |                             |  |  |  |   |   |  |  |
| 7,000 |                             |  |  |  |   |   |  |  |
| 7,500 |                             |  |  | Rapid Climate Change (RCC) 8,499-7,999 BP  | Krauβ et al., 2018  |   |  |  |
|       |                             |  | Neolithic 7,000-5,000 BP / Neolithic 7,449 – 5,449 BP / End of Neolithic or Neolithic-Chalcolithic transition at ~5,449 BP | Stuiver & Reime, 1986; Vacchi et al., 2017 | Neolithic 8,649-5,049 BP / Rapid Climate Change (RCC) 8,499-7999 BP / Mesolithic (Black Sea) UNTIL 7,849 BP / Neolithic (Black Sea) 7,849-6,849 BP / Chalcolithic (Black Sea) 6,849-4,449 BP / Chalcolithic Period (southern Levant) 5,999-4,999 BP | Andreu et al., 1996; Rowan & Golden, 2009; Krauβ et al., 2018; Aiken et al., 2019 |  |  |

|        |             |  |                          |  |   |  |  |   |   |
|--------|-------------|--|--------------------------|--|---|--|--|---|---|
| 8,000  |             | Greenlandian<br>(Early Holocene)<br>START 11,650<br>BP |                          | Epipaleolithic 11,949-<br>8,949 BP / Rapid<br>Climate Change (RCC)<br>8,499-7,999 BP   | Tortosa,<br>2005;<br>Sánchez,<br>2007;<br>Krauß et<br>al., 2018   | Mesolithic Age START<br>10,000 BP  | Bar-<br>Yosef,<br>1998   | Rapid Climate<br>Change (RCC) 8,499-<br>7,999 BP  | Blondel<br>&<br>Aronson<br>, 1999;<br>Lotze et<br>al.,<br>2006;<br>Krauß et<br>al., 2018  |
| 8,500  |             |  |                          |  |   |  |  |   |   |
| 9,000  |             |  |                          |  |   |  |  |   |   |
| 9,500  |             |  |                          |  |   |  |  |   |   |
| 10,000 |             |  |                          |  |   |  |  |   |   |
| 11,000 | Pleistocene | Late Pleistocene<br>131,949 -<br>11,650 BP             | Head et<br>al.<br>(2021) | Epipaleolithic or<br>Mesolithic 21,949-<br>11,949 BP / Late<br>Paleolithic Hunter-<br>gatherers at 13,500 BP<br>/ Mesolithic 14,949-<br>10,949 BP / Neolithic<br>START 11,949 BP /<br>Developed Solutrean<br>(Iberia) 20,949-17,949<br>BP / Solutrean (Iberia)<br>20,300-18,700 BP /<br>Magdalenian (Iberia)<br>17,949-11,949 BP / | Tortosa,<br>2005;<br>Stiner &<br>Kuhn,<br>2006;<br>Sánchez,<br>2007;<br>Lowe,<br>2008;<br>Pluciennik<br>, 2008;<br>D'Amore<br>et al.,<br>2009;<br>Villaverde<br>et al.,<br>2019 | Epipaleolithic or<br>Mesolithic 21,949-<br>11,949 BP / Neolithic<br>START 11,949 BP /<br>Mesolithic 14,949-<br>10,949 BP / Mesolithic<br>Age START 10,000 BP | Reale,<br>2000;<br>Stiner &<br>Kuhn,<br>2006;<br>Pluciennik,<br>2008 | Epipaleolithic or<br>Mesolithic 21,949-<br>11,949 BP / Neolithic<br>START 11,949 BP /<br>Hunter-Gatherer<br>101,949-7,949 BP /<br>Mesolithic 14,949-<br>10,949 BP | Haywood,<br>1997;<br>Blondel<br>&<br>Aronson<br>, 1999;<br>Lotze et<br>al.,<br>2006;<br>Stiner &<br>Kuhn,<br>2006;<br>Pluciennik,<br>2008 |
| 12,000 |             |  |                          |  |   |  |  |   |   |
| 13,000 |             |  |                          |  |   |  |  |   |   |
| 14,000 |             |  |                          |  |   |  |  |   |   |
| 15,000 |             |  |                          |  |   |  |  |   |   |
| 16,000 |             |  |                          |  |   |  |  |   |   |
| 17,000 |             |  |                          |  |   |  |  |   |   |
| 18,000 |             |  |                          |  |   |  |  |   |   |
| 19,000 |             |  |                          |  |   |  |  |   |   |
| 20,000 |             |  |                          |  |   |  |  |   |   |

|        |  |  |  |   |  |  |                                |   |  |
|--------|--|--|--|---|--|--|--------------------------------|---|--|
|        |  |  |  | Magdalenian or Late Paleolithic 16,500 - 10,000 BP  |  |  |                                |   |  |
| 21,000 |  |  |  | <p>Late Paleolithic 51,949-36,949 to 21,949 BP / Middle Paleolithic UNTIL 31,949 OR 28,949 BP / Late or Evolved Aurignacian (Iberia) 31,100-26,900 BP / Aurignacian (Iberia) 35,949-28,949 BP / Gravettian (Iberia) 28,949-22,949 BP / Gravetian (Iberia) 26,000-20,800 BP / Middle Solutrean (Iberia) 22,949-20,949 BP</p> | <p>Tortosa, 2005; Stiner &amp; Kuhn, 2006; Sánchez, 2007; Miller &amp; Barton, 2008; Villaverde et al., 2019</p> | <p>Late Paleolithic 51,949-36,949 to 21,949 BP</p> | <p>Stiner &amp; Kuhn, 2006</p> | <p>Late Paleolithic 51,949-36,949 to 21,949 BP / Hunter-Gatherer 101,949-7,949 BP</p> | <p>Haywood, 1997; Blondel &amp; Aronson, 1999; Lotze et al., 2006; Stiner &amp; Kuhn, 2006</p> |
| 22,000 |  |  |  |   |  |  |                                |   |  |
| 23,000 |  |  |  |   |  |  |                                |   |  |
| 24,000 |  |  |  |   |  |  |                                |   |  |
| 25,000 |  |  |  |   |  |  |                                |   |  |
| 26,000 |  |  |  |   |  |  |                                |   |  |
| 27,000 |  |  |  |   |  |  |                                |   |  |
| 28,000 |  |  |  |   |  |  |                                |   |  |
| 29,000 |  |  |  |   |  |  |                                |   |  |
| 30,000 |  |  |  |   |  |  |                                |   |  |
| 31,000 |  |  |  |   |  |  |                                |   |  |

|         |  |  |  |  |                         |  |   |   |                          |
|---------|--|--|--|--|-------------------------|--|---|---|--------------------------|
| 32,000  |  |  |  |  |                         |  |   |   | Haywood, 1997;           |
| 33,000  |  |  |  | Middle Paleolithic                                   | Djindjian et al., 2003; | Middle Paleolithic                                   | Djindjian et al., 2003;                 | Middle Paleolithic                            | Blondel & Aronson, 1999; |
| 34,000  |  |  |  | 251,949-31,949 BP / Late Paleolithic                 | Tortosa, 2005;          | 251,949-31,949 BP / Late Paleolithic                 | Stiner & Kuhn, 2006;                    | 251,949-31,949 BP / Late Paleolithic          | Djindjian et al., 2003;  |
| 35,000  |  |  |  | 51,949-36,949 to 21,949 BP / Early Upper Paleolithic | Sánchez, 2007;          | 51,949-36,949 to 21,949 BP / Early Upper Paleolithic | 40,000-30,000 BP / Aurignacian (Iberia) | 51,949-36,949 to 21,949 BP / Hunter-Gatherer  | Lotze et al., 2006;      |
| 35,000  |  |  |  | 40,000-30,000 BP / Aurignacian (Iberia)              |                         | 40,000-30,000 BP                                     |   | 7,949 BP / Early Upper Paleolithic            | Stiner & Kuhn, 2006      |
| 35,000  |  |  |  | 35,949-28,949 BP                                     |                         |  |   | 40,000-30,000 BP                              |                          |
| 36,000  |  |  |  | Middle Paleolithic                                   | Djindjian et al., 2003; | Middle Paleolithic                                   | Bar-Yosef, 1998;                        | Middle Paleolithic                            | Haywood, 1997;           |
| 40,000  |  |  |  | 251,949-31,949 BP / Middle Paleolithic               | Tortosa, 2005;          | 251,949-31,949 BP / Late Paleolithic                 | Djindjian et al., 2003;                 | 251,949-31,949 BP / Late Paleolithic          | Blondel & Aronson, 1999; |
| ...     |  |  |  | 115,949-35,949 BP / Late Paleolithic                 | Stiner & Kuhn, 2006;    | 51,949-36,949 to 21,949 BP / Early Late Paleolithic  | Stiner & Kuhn, 2006;                    | 51,949-36,949 to 21,949 BP / Pre-human BEFORE | Djindjian et al., 2003;  |
| 130,000 |  |  |  | 51,949-36,949 to 21,949 BP / Early Late Paleolithic  | Sánchez, 2007;          | 40,000-30,000 BP / Middle Paleolithic                |   | 101,949 BP / Hunter-Gatherer                  | Lotze et al.,            |
| ...     |  |  |  | 40,000-30,000 BP                                     |                         | 251,949-46,949 BP                                    |   | 101,949-7,949 BP / Early Late                 |                          |

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|--|--|--|--|--|--|--|--|----------------------------------|------------------------------------|
|  |  |  |  |  |  |  |  | Paleolithic 40,000-<br>30,000 BP | 2006;<br>Stiner &<br>Kuhn,<br>2006 |
|--|--|--|--|--|--|--|--|----------------------------------|------------------------------------|

## S2. List of Search Strings used in the search engines

**Table S2** – List of Search Strings used in the search engines, organised by theme. Each set of terms divided by theme was combined using the Boolean operator “AND”.

| Topic     | Strings  |
|-----------|--|
| Taxa      | <p>“Delphinus” OR “Monachus” OR “Dolphin*” OR “Porpoise*” OR “Monk seal*” OR “Engraulis” OR “Sardin*” OR “Sparus aurata” OR “Diplodus” OR “Clupea” OR “Alosa” OR “Thynnus” OR “Anchov*” OR “Pilchard*” OR “Bang*” OR “Black sprat*” OR “Frydr*” OR “Herring*” OR “*Bream*” OR “Gilt*” OR “Snapper*” OR “Breca*” OR “Puntazzo*” OR “Blacktail*” OR “Tun*” OR “Horse mackerel*” OR “Squid hound*” OR “Ostrea” OR “Hexaplex trunculus” OR “Phorcus turbinatus” OR “Trunculariopsis trunculus” OR “Murex trunculus” OR “Monodonta turbinata” OR “Osilinus turbinatus” OR “Oyster*” OR “Murex*” OR “Turbinate monodont”</p> |
| Area      | <p>“Mediterranean” OR “Adriatic” OR “Aegean” OR “Levant*” OR “Tunisia*” OR “Sidra” OR “Ionian” OR “Alboran” OR “Balearic” OR “Tyrrhenian” OR “Ligurian” OR “Sicil*” OR “Libyan” OR “Sardinia” OR “Marmara” OR “Cicilian” OR “Gibraltar”</p>  |
| Timeframe | <p>“Holocene” OR “Greenlandian” OR “Northgrippian” OR “Meghalayan” OR “Pleistocene” OR “Preindustrial” OR “Pre-industrial” OR “Pre industrial” OR “Historical” OR “Archaeological” OR “*Lithic” OR “Aurignacian” OR “Gravettian” OR “Solutrean” OR “Magdalenian” OR “Bronze Age” OR “Iron Age” OR “Copper Age” OR “Roman*” OR “Greek*” OR “Medieval” OR “Dark Age*” OR “Little Ice Age” OR “Byzantine” OR “Hellen*” OR “Archaic*” OR “Hunter-Gather*” OR “Hunter* Gather*” OR “Classic*” OR “Antiquity” OR “Christian*” OR “Prehuman” OR “Pre human” OR “Pre-human” OR “Modern”</p>                                    |
| Impacts   | <p>“Climat*” OR “Environment*” OR “Salin*” OR “Dissolved oxygen” OR “Productivity” OR “Invasion*” OR “Temperature*” OR “Anthropogenic*” OR “Human*” OR “Whaling” OR “Hunt*” OR “Fish*” OR “Farming” OR “Aquaculture” OR “Harvest*”</p>   |
| Theme     | <p>“Marine” OR “Maritime” OR “Sea*” OR “Ocean*” OR “Lagoon*” OR “Delta*” OR “Basin*” OR “Estuar*” OR “Shel*” OR “Coast*” OR “Margin*” OR “*Littoral” OR “Gulf*” OR “Strait*” OR “Channel*” OR “Water*” OR “Slope*” OR “Deep” OR “*Tidal”</p>   |

### S3. Articles included in the database

**Table S3** – Compilation of the scientific articles used to build the database.

| Authors  | Title  | Year | DOI                                   |
|--|--|------|---------------------------------------|
| Addis P.; Dean J.M.; Pesci P.;<br>Locci I.; Cannas R.; Corrias S.;<br>Cau A.   | Effects of local scale perturbations in the<br>Atlantic bluefin tuna ( <i>Thunnus thynnus</i> L.)<br>trap fishery of Sardinia (W. Mediterranean) | 2008 | 10.1016/j.fis<br>hres.2008.01<br>.021 |
| Agiadi K.; Albano P.G.   | Holocene fish assemblages provide<br>baseline data for the rapidly changing<br>eastern Mediterranean   | 2020 | 10.1177/095<br>9683620932<br>969      |
| Andrews A.J.; Di Natale A.;<br>Addis P.; Piattoni F.; Onar V.;<br>Bernal-Casasola D.; Aniceti V.;<br>Carenti G.; Gómez-Fernández<br>V.; Garibaldi F.; Morales-<br>Muñiz A.; Tinti F.   | Vertebrae reveal industrial-era increases in<br>Atlantic bluefin tuna catch-at-size and<br>juvenile growth                                       | 2023 | 10.1093/icesj<br>ms/fsad013           |
| Andrews A.J.; Di Natale A.;<br>Bernal-Casasola D.; Aniceti V.;<br>Onar V.; Oueslati T.;<br>Theodropoulou T.; Morales-<br>Muñiz A.; Cilli E.; Tinti F.  | Exploitation history of Atlantic bluefin tuna<br>in the eastern Atlantic and Mediterranean-<br>insights from ancient bones                       | 2022 | 10.1093/icesj<br>ms/fsab261           |
| Andrews A.J.; Pampoulie C.;<br>Di Natale A.; Addis P.; Bernal-<br>Casasola D.; Aniceti V.; Carenti<br>G.; Gómez-Fernández V.;<br>Chosson V.; Ughi A.;<br>Von Tersch M.; Fontanals-Coll<br>M.; Cilli E.; Onar V.; Tinti F.;<br>Alexander M. | Exploitation shifted trophic ecology and<br>habitat preferences of Mediterranean and<br>Black Sea bluefin tuna over centuries                    | 2023 | 10.1111/faf.<br>12785                 |

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|--|--|------|-------------------------------|
| Andrews A.J.; Puncher G.N.; Bernal-Casasola D.; Di Natale A.; Massari F.; Onar V.; Toker N.Y.; Hanke A.; Pavey S.A.; Savojardo C.; Martelli P.L.; Casadio R.; Cilli E.; Morales-Muñiz A.; Mantovani B.; Tinti F.; Cariani A. | Ancient DNA SNP-panel data suggests stability in bluefin tuna genetic diversity despite centuries of fluctuating catches in the eastern Atlantic and Mediterranean | 2021 | 10.1038/s41598-021-99708-9    |
| Andrews, AJ; Orton, D; Onar, V; Addis, P; Tinti, F; Alexander, M   | Isotopic life-history signatures are retained in modern and ancient Atlantic bluefin tuna vertebrae  | 2023 | 10.1111/jfb.15417             |
| Biard, V; Gol'din, P; Gladilina, E; Vishnyakova, K; McGrath, K; Vieira, FG; Wales, N; Fontaine, MC; Speller, C; Olsen, MT  | Genomic and proteomic identification of Late Holocene remains: Setting baselines for Black Sea odontocetes   | 2017 | 10.1016/j.jasrep.2017.07.008  |
| Bosch M.D.; Mannino M.A.; Prendergast A.L.; Wesselingh F.P.; O'Connell T.C.; Hublin J.-J.  | Year-round shellfish exploitation in the Levant and implications for Upper Palaeolithic hunter-gatherer subsistence  | 2018 | 10.1016/j.jasrep.2017.08.014  |
| Bosch M.D.; Wesselingh F.P.; Mannino M.A.  | The Ksâr 'Akil (Lebanon) mollusc assemblage: Zooarchaeological and taphonomic investigations   | 2015 | 10.1016/j.quaint.2015.07.004  |
| Branscombe T.L.; Bosch M.D.; Miracle P.T.  | Seasonal Shellfishing across the East Adriatic Mesolithic-Neolithic Transition: Oxygen Isotope Analysis of <i>Phorcus turbinatus</i> from Vela Spila (Croatia)     | 2021 | 10.1080/14614103.2020.1721695 |
| Chakroun, A; Zaghib-Turki, D   | Facies and fauna proxies used to reconstruct the MIS 5 and MIS 7 coastal environments in eastern Tunisia   | 2017 | 10.7306/gq.1312               |
| Colonese, AC; Lo Vetro, D; Landini, W; Di Giuseppe, Z; Hausmann, N; Demarchi, B;   | Late Pleistocene-Holocene coastal adaptation in central Mediterranean:   | 2018 | 10.1016/j.quaint.2018.06.018  |

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|--|--|------|----------------------------------|
| d'Angelo, C; Leng, MJ;<br>Incarbona, A; Whitwood, AC;<br>Martini, F  | Snapshots from Grotta d'Oriente (NW Sicily)  |      |                                  |
| de Pablo, JFL; Gabriel, S  | El Collado shell midden and the exploitation patterns of littoral resources during the Mesolithic in the Eastern Iberian Peninsula   | 2016 | 10.1016/j.quaint.2015.11.100     |
| Fuller B.T.; Van Neer W.;<br>Linseele V.; De Cupere B.;<br>Chahoud J.; Richards M.P.   | Fish $\delta^{13}C$ and $\delta^{15}N$ results from two Bronze/Iron Age sites (Tell Tweini & Sidon) along the Levantine coast  | 2020 | 10.1016/j.jasrep.2019.102066     |
| Ganzedo U.; Polanco-Martínez J.M.; Caballero-Alfonso Á.M.;<br>Faria S.H.; Li J.; Castro-Hernández J.J.   | Climate effects on historic bluefin tuna captures in the Gibraltar Strait and Western Mediterranean  | 2016 | 10.1016/j.jmarsys.2016.02.002    |
| Guy S.-V.; Thomas T.; Irit Z.;<br>Andreas P.; Dorit S.; Omri L.;<br>Ayelet G.; Guy B.-O.   | Tooth oxygen isotopes reveal Late Bronze Age origin of Mediterranean fish aquaculture and trade  | 2018 | 10.1038/s41598-018-32468-1       |
| Hunt C.O.; Reynolds T.G.; El-Rishi H.A.; Buzaian A.; Hill E.;<br>Barker G.W.   | Resource pressure and environmental change on the North African littoral: Epipalaeolithic to Roman gastropods from Cyrenaica, Libya  | 2011 | 10.1016/j.quaint.2011.04.045     |
| Lo Presti, V; Antonioli, F;<br>Palombo, MR; Agnesi, V;<br>Biolchi, S; Calcagnile, L; Di Patti, C; Donati, S; Furlani, S;<br>Merizzi, J; Pepe, F; Quarta, G;<br>Renda, P; Sulli, A; Tusa, S | Palaeogeographical evolution of the Egadi Islands (western Sicily, Italy). Implications for late Pleistocene and early Holocene sea crossings by humans and other mammals in the western Mediterranean | 2019 | 10.1016/j.jearthsci.2019.04.027  |
| Longo S.B.; Clark B.   | The Commodification of Bluefin Tuna: The Historical Transformation of the Mediterranean Fishery  | 2012 | 10.1111/j.1471-0366.2011.00348.x |

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New challenges in archaeopalynology: Pollen analysis on Roman bivalve shells from south-western Europe and North Africa

2023 10.1016/j.rev  
palbo.2023.1  
04876

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|---|---|------|--|
| Lotze, HK; Coll, M; Dunne, JA   | Historical Changes in Marine Resources, Food-web Structure and Ecosystem Functioning in the Adriatic Sea, Mediterranean   | 2011 | 10.1007/s10<br>021-010-<br>9404-8            |
| Lucarini G.; Wilkinson T.; Crema E.R.; Palombini A.; Bevan A.; Broodbank C. | The MedAfriCarbon Radiocarbon Database and Web Application. Archaeological Dynamics in Mediterranean Africa, ca. 9600–700 BC  | 2020 | 10.5334/joad<br>.60                          |
| Mannino M.A.; Thomas K.D.; Leng M.J.; Di Salvo R.; Richards M.P.            | Stuck to the shore? Investigating prehistoric hunter-gatherer subsistence, mobility and territoriality in a Mediterranean coastal landscape through isotope analyses on marine mollusc shell carbonates and human bone collagen | 2011 | 10.1016/j.qu<br>aint.2011.05.<br>044         |
| Mannino M.A.; Thomas K.D.; Leng M.J.; Piperno M.; Tusa S.; Tagliacozzo A.   | Marine resources in the mesolithic and neolithic at the Grotta dell'Uzzo (Sicily): Evidence from isotope analyses of marine shells  | 2007 | 10.1111/j.14<br>75-<br>4754.2007.0<br>0291.x |
| Mercier L.; Mouillot D.; Bruguier O.; Vigliola L.; Darnaude A.M.            | Multi-element otolith fingerprints unravel sea-lagoon lifetime migrations of gilthead sea bream <i>Sparus aurata</i>  | 2012 | 10.3354/me<br>ps09444                        |

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|---|---|------|-----------------------------------|
| Mion L.; André T.; Mailloux A.; Sternberg M.; Morales Muniz A.; Rosello-Izquierdo E.; Llorente Rodríguez L.; Herrscher E.       | Contribution to Mediterranean medieval dietary studies: Stable carbon and nitrogen isotope data of marine and catadromous fish from Provence (9th–14th CE)                            | 2022 | 10.1016/j.dib<br>.2022.10801<br>6 |
| Morales-Pérez J.V.; Pérez Ripoll M.; Jordá Pardo J.F.; Álvarez-Fernández E.; Maestro González A.; Aura Tortosa J.E.             | Mediterranean monk seal hunting in the regional Epipalaeolithic of Southern Iberia. A study of the Nerja Cave site (Málaga, Spain)  | 2019 | 10.1016/j.quaint.2017.11.050      |
| Mouchi V.; Godbillot C.; Dupont C.; Vella M.-A.; Forest V.; Ulianov A.; Lartaud F.; de Rafélis M.; Emmanuel L.; Verrecchia E.P. | Provenance study of oyster shells by LA-ICP-MS  | 2021 | 10.1016/j.jas.2021.10541<br>8     |
| Oliver A.V.   | An ancient fishery of Banded dye-murex ( <i>Hexaplex trunculus</i> ): Zooarchaeological evidence from the Roman city of Pollentia (Mallorca, Western Mediterranean)                   | 2015 | 10.1016/j.jas.2014.11.026         |
| Onar V.; Yelda Olcay-Uçkan B.; Öztaşkin M.; Bakar Siddig A.; Emre Öncü Ö.; Öztaşkin G.K.; Chrószcz A.                           | Animal exploitation at the Olympos, southwestern Anatolia: Zooarchaeological analysis   | 2022 | 10.1016/j.jasrep.2022.103487      |
| Polanco-Martínez J.M.; Caballero-Alfonso .M.; Ganzedo U.; Castro-Hernández J.J.   | A reconstructed database of historic bluefin tuna captures in the Gibraltar Strait and Western Mediterranean  | 2018 | 10.1016/j.dib.2017.11.028         |
| Prendergast A.L.; Stevens R.E.; O'Connell T.C.; Fadlalak A.; Touati M.; al-Mzeine A.; Schöne B.R.; Hunt C.O.; Barker G.         | Changing patterns of eastern Mediterranean shellfish exploitation in the Late Glacial and Early Holocene: Oxygen isotope evidence from gastropod in Epipaleolithic to Neolithic human | 2016 | 10.1016/j.quaint.2015.09.035      |

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Libya

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| <p>Puncher G.N.; Cariani A.; Cilli E.; Massari F.; Leone A.; Morales-Muñiz A.; Onar V.; Toker N.Y.; Bernal Casasola D.; Moens T.; Tinti F.</p>   | <p>Comparison and optimization of genetic tools used for the identification of ancient fish remains recovered from archaeological excavations and museum collections in the Mediterranean region</p> | <p>2019</p> | <p>10.1002/oa.2765</p>         |
| <p>Salmona J.; Dayon J.; Lecompte E.; Karamanlidis A.A.; Aguilar A.; Fernandez De Larrinoa P.; Pires R.; Mo G.; Panou A.; Agnesi S.; Borrell A.; Danyer E.; Öztürk B.; Tonay A.M.; Anestis A.K.; González L.M.; Dendrinis P.; Gaubert P.</p> | <p>The antique genetic plight of the Mediterranean monk seal (<i>Monachus monachus</i>)</p>  | <p>2022</p> | <p>10.1098/rspb.2022.0846</p>  |
| <p>Sanchez, W; Yanes, Y; Linstädter, J; Hutterer, R</p>  | <p>Chronology, time averaging, and oxygen isotope composition of harvested marine mollusk assemblages from Ifri Oudadane, northeast Morocco</p>  | <p>2022</p> | <p>10.1017/qua.2021.60</p>     |
| <p>Stringer C.B.; Finlayson J.C.; Barton R.N.E.; Fernández-Jalvo Y.; Cáceres I.; Sabin R.C.; Rhodes E.J.; Currant A.P.; Rodríguez-Vidal J.; Giles-Pacheco F.; Riquelme-Cantal J.A.</p>   | <p>Neanderthal exploitation of marine mammals in Gibraltar</p>   | <p>2008</p> | <p>10.1073/pnas.0805474105</p> |
| <p>Trixl S.; Ben Tahar S.; Ritter S.; Peters J.</p>  | <p>Wool sheep and purple snails—Long-term continuity of animal exploitation in ancient Meninx (Jerba/Tunisia)</p>  | <p>2020</p> | <p>10.1002/oa.2911</p>         |

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|---|---|------|---|
| Tütken T.; Weber M.; Zohar I.;<br>Helmy H.; Bourgon N.; Lernau<br>O.; Jochum K.P.; Sisma-<br>Ventura G. | Strontium and Oxygen Isotope Analyses<br>Reveal Late Cretaceous Shark Teeth in Iron<br>Age Strata in the Southern Levant                            | 2020 | 10.3389/fevo<br>.2020.57003<br>2          |
| Yaltirak C.; Sakinç M.; Aksu<br>A.E.; Hiscott R.N.; Galleb B.;<br>Ulgen U.B.                            | Late Pleistocene uplift history along the<br>southwestern Marmara Sea determined<br>from raised coastal deposits and global<br>sea-level variations | 2002 | 10.1016/S00<br>25-<br>3227(02)003<br>51-1 |

#### S4. Explanation of the modifications made to the database

The columns and cells coloured in grey were submitted to modifications done by the authors of this work:

1. When the authors of the publication in question presented the coordinates in different ways than decimal degrees, a transformation was applied using <https://www.fcc.gov/media/radio/dms-decimal>;
2. When the authors only reported the location's name of where the data comes from and not the exact coordinates, then the coordinates used were added according to the name provided;
3. If the authors only reported a broad area from where the records came from, then the respective coordinates were selected as a midpoint within the area reported;
4. Relative abundance expressed in percentage was converted to decimal for the later analyses;
  - 4.1. In the cases where relative abundance is presented for NISP and MNI, the MNI one was chosen, because it refers to individuals;
5. To standardize the length measurements for each species/family/genus into only one type of measure, conversions based on length-length relationships were applied to several fishes:
  - 5.1. *Thunnus thynnus*: Fishbase data on parameters a and b, from FL to TL:  $a=0.0$  and  $b=1.075$  unsexed individuals (Binohlan et al., 2011);
  - 5.2. *Sparus aurata*: Fishbase data on parameters a and b, from FL to TL:  $a=0.0$  and  $b=1.100$  unsexed individuals (Binohlan et al., 2011);
  - 5.3. *Sparus aurata*: to transform SL to TL, I used a linear relation described by Kara et al. (2020) in which  $SL=0.8238TL-0.2876$  and because the relation is linear this way and vice versa,  $TL=(SL+0,2876)/0,8238$
  - 5.4. Clupeidae: Fishbase data on parameters a and b, from FL to SL:  $a=0.0$  and  $b\sim 0.882$  unsexed individuals. The b parameter is the mean of the b values for *Engraulis*

*encrasicolus* (a=0, b=0.911), *Sardinella aurita* (a=0 or 1.93, b=0.934 or 0.760) e *Sardinella maderensis* (a=0, b=0.923) (Binohlan et al., 2011);

5.5. *Diplodus* spp.: to transform FL to SL, I used the regression equations described by Moutopoulos & Stergiou (2002) for *Diplodus annularis* (SL = 0.21 + 0.87FL), *Diplodus sargus* (SL = - 0.71 + 0.93FL) and *Diplodus vulgaris* (SL = - 0.18 + 0.92FL) and then I made an average of these to infer for *Diplodus* spp.;

5.6. *Thunnus* spp.: I searched to see which species of this genus inhabit the Atlantic and Mediterranean waters and then I took the values from Fishbase to transform from FL to TL → *Thunnus alalunga* (a=0 and 0, b=1.083 and 1.095), *Thunnus albacares* (a=8.831, 7.903, 0, 3.989, 0, b=0.967, 1.045, 1.058, 1.071, 1.108) and *Thunnus thynnus* (a=0, b=1.075) all for unsexed individuals (Binohlan et al., 2011);

6. The separation between types of assemblage was done based on the information that was in the corresponding article. The two main categories were either natural or archaeological. However, in article nº67, which was a review paper, the authors did not specify from which category the data came, so the adopted term was "Archaeological/Natural". In the article nº45, the authors used raw data, which came from natural assemblages, but also reconstructed ones from a model. Therefore, the adopted term was "Natural/Reconstructed".

7. Regarding the age columns, several steps were adopted to ensure the correspondence between relative and absolute age:

7.1. If the authors reported the relative age, then that designation remains. However, if the authors report the absolute age and not the relative one, that information was complemented with the respective one from the period timetable concerning the region of the Mediterranean (Western, Eastern or Adriatic);

7.2. Alternatively, if the authors reported the relative age, but not the absolute age, that information was complemented with Table S1 according to the regions and respective periods:

- 7.2.1. If a period was not completely described in the timetable, adjustments were made based on the information from the paper and the cultural periods for the remaining regions;
- 7.3. If the authors reported the absolute age in BC/AD or BCE/CE, these were transformed into BP, using the “rcarbon” package from R (Crema & Bevan, 2021). However, if the authors reported in cal. BP, these were accepted;
- 7.4. Ages expressed in cal. BC/AD were transformed into cal. BP using an equation from Stuiver & Pearson (1993).
- 7.5. If the age intervals reported by the authors had gaps, then for the analyses the designated period was then decided conservatively, with the most extreme ages being reported;
- 7.6. When the ages were reported as parts of centuries, such as “late century”, I included the second half to ensure a conservative age. In the same way, the early century is the first half of the century, and the mid-century is the middle of the century.

## S5. List of climatic and cultural events

**Table S5** – 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 1 <sup>st</sup> 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 2 <sup>nd</sup> cooling event (Event 2) | 8,000 - 7,000                  | Lionello et al. (2023) |
|                                | Holocene 3 <sup>rd</sup> 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)          |
|                                | 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)          |                        |

|          |  |               |                           |
|----------|--|---------------|---------------------------|
| Cultural | 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)     |

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## S6. Table of the Sampling units from the scientific articles

**Table S6** – List of location’s number, location’s name, country and respective reference for every sampling unit used in this work.

| Location Number | Location Name                      | Country | Reference  |
|-----------------|------------------------------------|---------|--|
| 1               | Between Portoscuso and Isola Piana | Italy   | Addis et al., 2008   |
| 2               | SG10                               | Israel  | Agiadi & Albano, 2020  |
| 3               | SG20                               | Israel  | Agiadi & Albano, 2020  |
| 4               | SG30                               | Israel  | Agiadi & Albano, 2020  |
| 5               | SG40                               | Israel  | Agiadi & Albano, 2020  |
| 6               | Pedras de Fogu                     | Italy   | Andrews et al., 2022; Andrews, Di Natale, et al., 2023; Andrews, Pampoulie, et al., 2023   |
| 7               | Mazara del Vallo                   | Italy   | Andrews et al., 2022; Andrews, Di Natale, et al., 2023; Andrews, Pampoulie, et al., 2023   |
| 8               | Yenikapi                           | Turkey  | Puncher et al., 2019; Andrews et al., 2021; Andrews et al., 2022; Andrews, Di Natale, et al., 2023; Andrews, Pampoulie, et al., 2023; Andrews, Orton, et al., 2023 |

|    |                      |           |  |
|----|----------------------|-----------|--|
| 9  | Palermo              | Italy     | Andrews, Di Natale, et al., 2023   |
| 10 | Portopalo            | Italy     | Andrews et al., 2022;<br>Andrews, Di Natale, et al., 2023  |
| 11 | Gorham's Cave        | Gibraltar | Stringer et al., 2008;<br>Morales-Pérez et al., 2019;<br>Andrews et al., 2022;                   |
| 12 | Nerja Cave           | Spain     | Tortosa et al., 2002;<br>Pardo et al., 2016;<br>Morales-Pérez et al., 2019; Andrews et al., 2022 |
| 13 | Franchthi Cave       | Greece    | Andrews et al., 2022   |
| 14 | Maroulas             | Greece    | Andrews et al., 2022   |
| 15 | Vela Spila           | Croatia   | Rainsford et al., 2014;<br>Branscombe et al., 2020; Andrews et al., 2022                         |
| 16 | Cape Andreas Kastros | Cyprus    | Andrews et al., 2022   |
| 17 | Grotte du Cap Ragnon | France    | Andrews et al., 2022   |
| 18 | Lerna                | Greece    | Andrews et al., 2022   |
| 19 | Saliagos Cave        | Greece    | Andrews et al., 2022   |
| 20 | Pefkakia, Volos      | Greece    | Andrews et al., 2022   |
| 21 | Besik Tepe           | Turkey    | Andrews et al., 2022   |
| 22 | Perachora            | Greece    | Andrews et al., 2022   |

|    |                  |         |                      |
|----|------------------|---------|----------------------|
| 23 | Troy             | Turkey  | Andrews et al., 2022 |
| 24 | Kommos           | Greece  | Andrews et al., 2022 |
| 25 | Akrotiri         | Greece  | Andrews et al., 2022 |
| 26 | Koukounaries     | Greece  | Andrews et al., 2022 |
| 27 | Cova Fosca       | Spain   | Andrews et al., 2022 |
| 28 | Utica            | Tunisia | Andrews et al., 2022 |
| 29 | Carthage         | Tunisia | Andrews et al., 2022 |
| 30 | Althiburos       | Tunisia | Andrews et al., 2022 |
| 31 | Chersonesos      | Ukraine | Andrews et al., 2022 |
| 32 | Pilarou Cave     | Greece  | Andrews et al., 2022 |
| 33 | Messene          | Greece  | Andrews et al., 2022 |
| 34 | Pantikapaion     | Ukraine | Andrews et al., 2022 |
| 35 | Sant'Antioco     | Italy   | Andrews et al., 2022 |
| 36 | Kalaureia        | Greece  | Andrews et al., 2022 |
| 37 | Milazzo          | Italy   | Andrews et al., 2022 |
| 38 | Cerro del Mar    | Spain   | Andrews et al., 2022 |
| 39 | Populonia        | Italy   | Andrews et al., 2022 |
| 40 | Dion             | Greece  | Andrews et al., 2022 |
| 41 | Teatro<br>Romano | Spain   | Andrews et al., 2022 |
| 42 | Santa Filitica   | Italy   | Andrews et al., 2022 |
| 43 | Sant'Imbenia     | Italy   | Andrews et al., 2022 |
| 44 | Gruissan         | France  | Andrews et al., 2022 |
| 45 | Balat            | Turkey  | Andrews et al., 2022 |
| 46 | Bathonea         | Turkey  | Andrews et al., 2022 |

|    |                        |         |   |
|----|------------------------|---------|---|
| 47 | Casale San Pietro      | Italy   | Andrews et al., 2022                                |
| 48 | San Antonio            | Italy   | Andrews,<br>Pampoulie, et al.,<br>2023              |
| 49 | Corso dei Mille        | Italy   | Andrews et al., 2022                                |
| 50 | Monteleone             | Italy   | Andrews et al., 2022                                |
| 51 | Cappuccine             | Italy   | Andrews et al., 2022                                |
| 52 | Sassari                | Italy   | Andrews et al., 2022                                |
| 53 | Leca Harbour           | France  | Andrews et al., 2022                                |
| 54 | Kruze basilica         | Ukraine | Biard et al., 2017                                  |
| 55 | Ksâr 'Akil rockshelter | Lebanon | Bosch et al., 2015;<br>Bosch et al., 2018           |
| 56 | Qorba                  | Tunisia | Chakroun &<br>Zaghib-Turki, 2016                    |
| 57 | Grotta d'Oriente       | Italy   | Colonese et al.,<br>2018; Lo Presti et al.,<br>2019 |
| 58 | El Collado             | Spain   | De Pablo & Gabriel,<br>2016                         |
| 59 | Tell Tweini            | Syria   | Linseele et al., 2019;<br>Fuller et al., 2020       |
| 60 | Sidon                  | Lebanon | Fuller et al., 2020                                 |
| 61 | Hatoula                | Israel  | Guy et al., 2018                                    |
| 62 | Ashkelon<br>Afridar    | Israel  | Guy et al., 2018                                    |
| 63 | Gilat                  | Israel  | Guy et al., 2018;<br>Tütken et al., 2020            |

|    |                 |        |                  |
|----|-----------------|--------|------------------|
| 64 | Ashkelon Barnea | Israel | Guy et al., 2018 |
| 65 | Lachish         | Israel | Guy et al., 2018 |
| 66 | Tel Rehov       | Israel | Guy et al., 2018 |
| 67 | Ashkelon        | Israel | Guy et al., 2018 |
| 68 | Tel Dor         | Israel | Guy et al., 2018 |
| 69 | Tel Miqne       | Israel | Guy et al., 2018 |
| 70 | Jerusalem       | Israel | Guy et al., 2018 |
| 71 | Tel Tananim     | Israel | Guy et al., 2018 |
| 72 | Halutsa         | Israel | Guy et al., 2018 |
| 73 | Shivta          | Israel | Guy et al., 2018 |

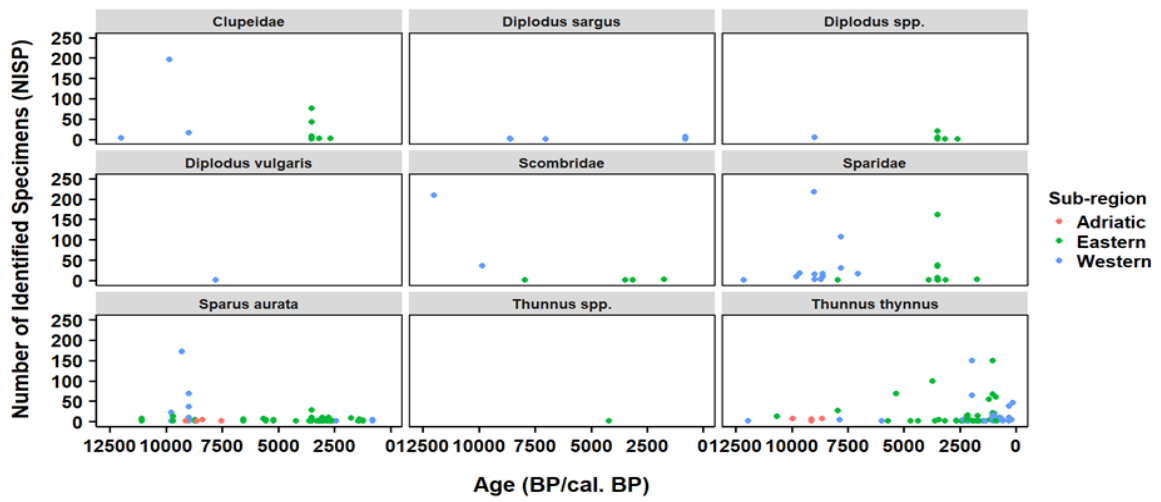
|    |                         |           |  |
|----|-------------------------|-----------|--|
| 74 | Tamra                   | Israel    | Guy et al., 2018   |
| 75 | Haua Fteah              | Lybia     | Hunt et al., 2011;<br>Prendergast et al.,<br>2016        |
| 76 | CP1592                  | Lybia     | Hunt et al., 2011  |
| 77 | CP1585                  | Lybia     | Hunt et al., 2011  |
| 78 | Grotta di Punta Capperi | Italy     | Lo Presti et al., 2019                                   |
| 79 | Grotta Schiacciata      | Italy     | Lo Presti et al., 2019                                   |
| 80 | Grotta del Genovese     | Italy     | Lo Presti et al., 2019                                   |
| 81 | Formica                 | Italy     | Longo & Clark, 2012;<br>Ganzedo et al., 2016             |
| 82 | Favignana               | Italy     | Longo & Clark, 2012                                      |
| 83 | Paseo de las Palmeras   | Ceuta     | López-Sáez et al., 2023                                  |
| 84 | Puerta Califal          | Ceuta     | López-Sáez et al., 2023                                  |
| 85 | Adriatic Sea            |           | Lotze et al., 2010                                       |
| 86 | Ifri Armas              | Morocco   | Lucarini et al., 2020                                    |
| 87 | Grotta delle Incisioni  | Italy     | Mannino et al., 2011                                     |
| 88 | Grotta Niscemi          | Italy     | Mannino et al., 2011                                     |
| 89 | Grotta Addaura Caprara  | Italy     | Mannino et al., 2011                                     |
| 90 | Grotta della Molara     | Italy     | Mannino et al., 2011                                     |
| 91 | Lattara                 | France    | Mercier et al., 2012                                     |
| 92 | Fos-sur-Mer             | France    | Mion et al., 2022  |
| 93 | Vanguard Cave           | Gibraltar | Stringer et al., 2008;<br>Morales-Pérez et al.,<br>2019; |

|     |                         |         |   |
|-----|-------------------------|---------|---|
| 94  | Grotta Di S. Agostino   | Italy   | Morales-Pérez et al.,<br>2019   |
| 95  | Grotta Romanelli        | Italy   | Morales-Pérez et al.,<br>2019   |
| 96  | Grotta di Cala Genovesi | Italy   | Morales-Pérez et al.,<br>2019   |
| 97  | Grotta dell'Uzzo        | Italy   | Mannino et al., 2007;<br>Mannino et al., 2015;<br>Morales-Pérez et al.,<br>2019 |
| 98  | Araguina-Sennola        | France  | Morales-Pérez et al.,<br>2019   |
| 99  | Zafrín                  | Morocco | Morales-Pérez et al.,<br>2019   |
| 100 | Aléria                  | France  | Mouchi et al., 2021   |
| 101 | Pollentia               | Spain   | Oliver, 2015  |
| 102 | Antalya                 | Turkey  | Onar et al., 2022   |
| 103 | Saline                  | Italy   | Ganzedo et al., 2016  |
| 104 | Isola Piana             | Italy   | Addis et al., 2008;<br>Ganzedo et al., 2016                                     |
| 105 | Porto Scuso             | Italy   | Addis et al., 2008;<br>Ganzedo et al., 2016                                     |
| 106 | Porto Paglia            | Italy   | Ganzedo et al., 2016  |
| 107 | Bonagia                 | Italy   | Ganzedo et al., 2016  |
| 108 | San Giuliano            | Italy   | Ganzedo et al., 2016  |
| 109 | Ifri Oudadane           | Morocco | Sánchez et al., 2021  |
| 110 | Meninx                  | Tunisia | Trixl et al., 2020  |

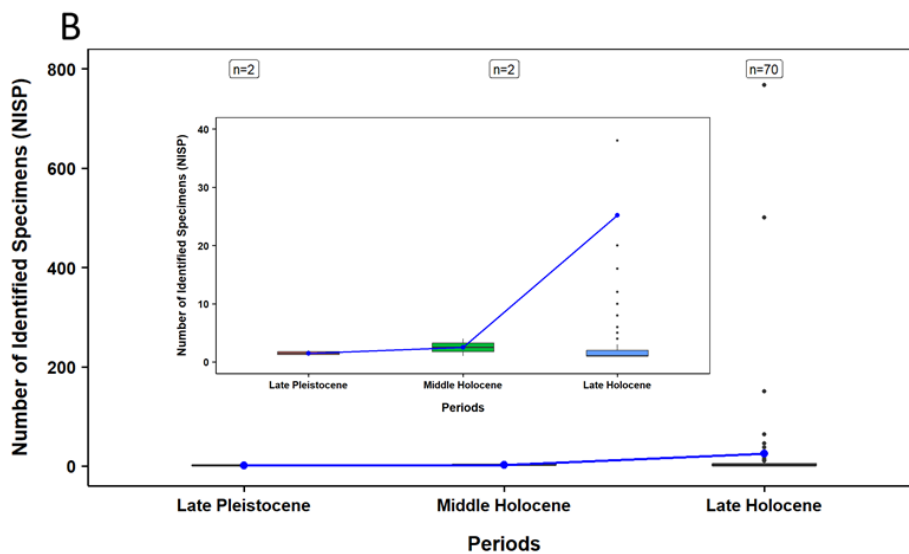
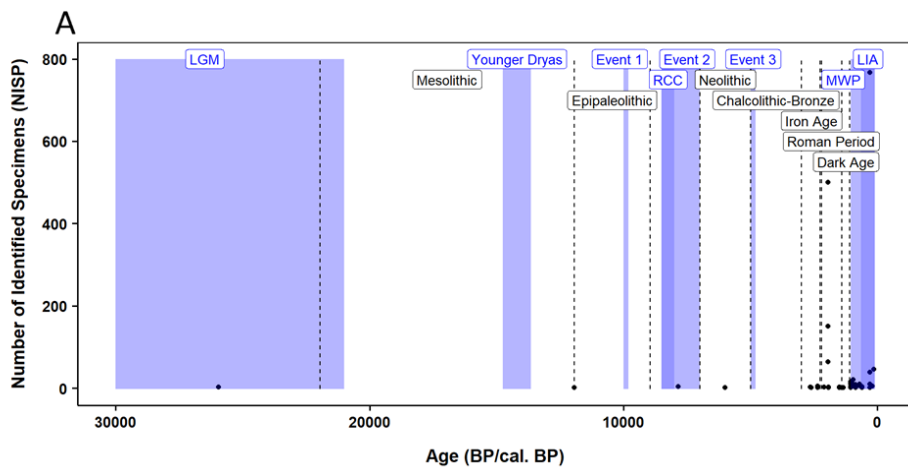
|     |                     |        |                             |
|-----|---------------------|--------|-----------------------------|
| 111 | City of David       | Israel | Tütken et al., 2020         |
| 112 | Gaziköy             | Turkey | Yaltırak et al., 2002       |
| 113 | Cala Olivera        | Spain  | Giner & Ribas, 2008         |
| 114 | Youra               | Greece | Vika & Theodoropoulou, 2012 |
| 115 | Archontiko          | Greece | Vika & Theodoropoulou, 2012 |
| 116 | Toumba              | Greece | Vika & Theodoropoulou, 2012 |
| 117 | Karabournaki        | Greece | Vika & Theodoropoulou, 2012 |
| 118 | Ceuta               | Spain  | Andrews et al., 2022        |
| 119 | Titán Wreck         | France | Andrews et al., 2022        |
| 120 | Sant'Antonino       | Italy  | Andrews et al., 2022        |
| 121 | Cave of the Cyclops | Greece | Trantalidou, 2011           |

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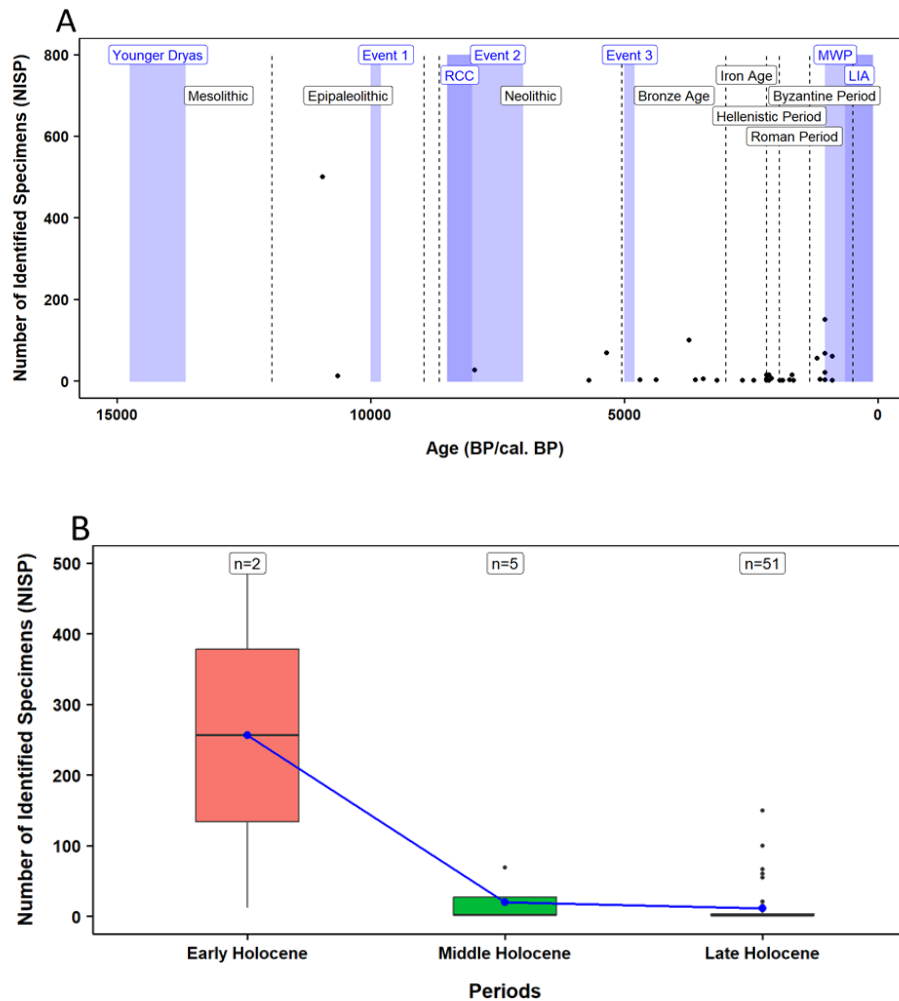
## S7. NISP distribution



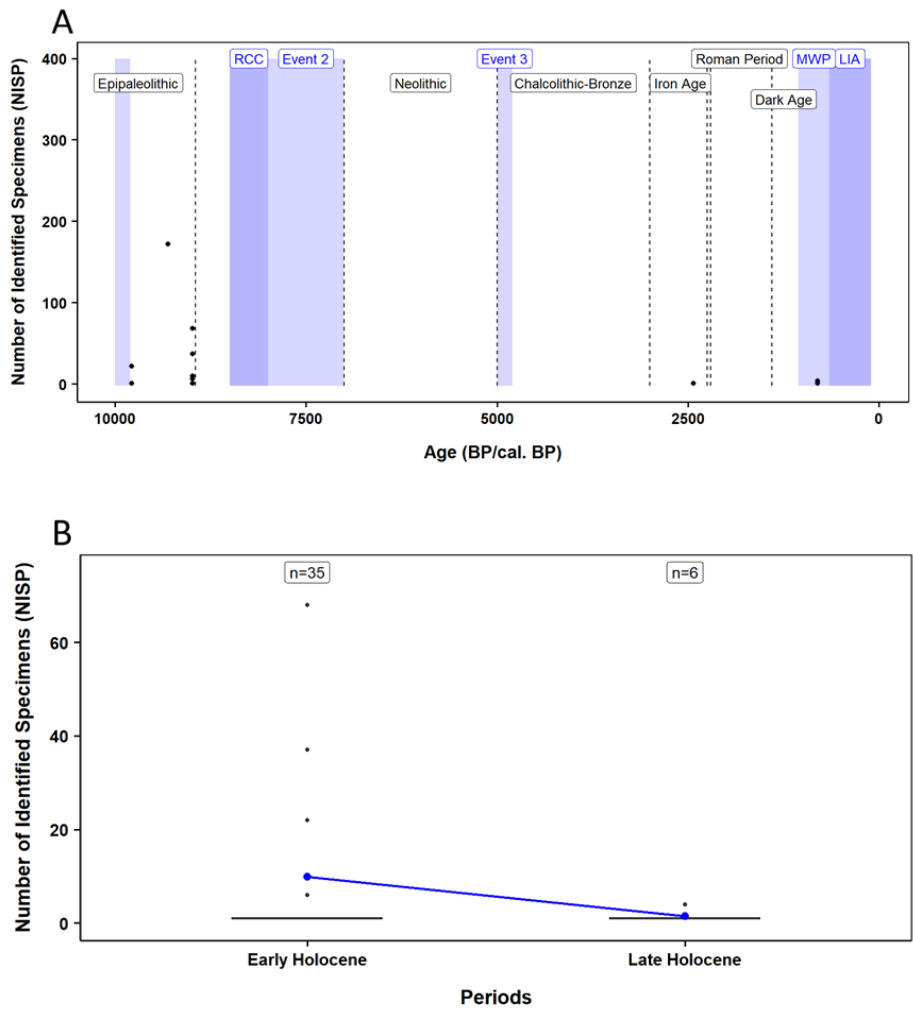
**Figure S7.1** - Distribution of data for NISP for fishes. Colours separate the data for each sub-region of the Mediterranean Sea.



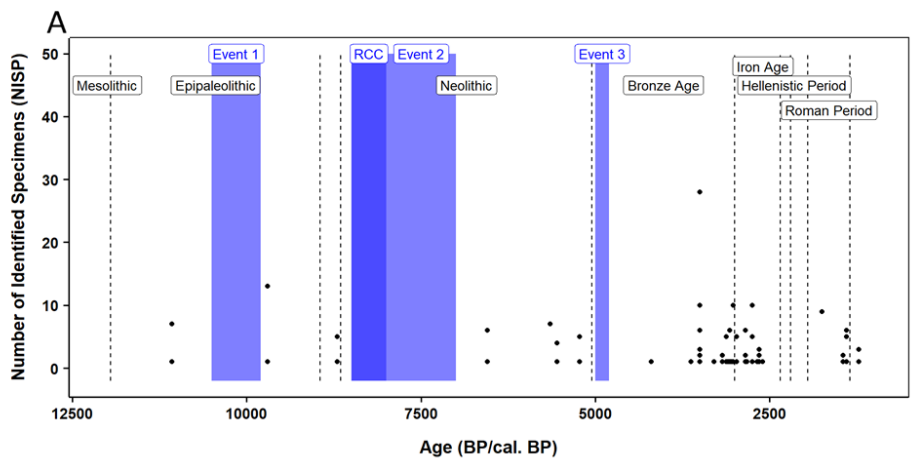
**Figure S7.1.1** - Distribution of data for NISP on *Thunnus thynnus* in the Western sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above. The plot inside the second figure is a zoom-in of the data, for better visualization of the increase in NISP values towards the Late Holocene (no outliers were excluded).

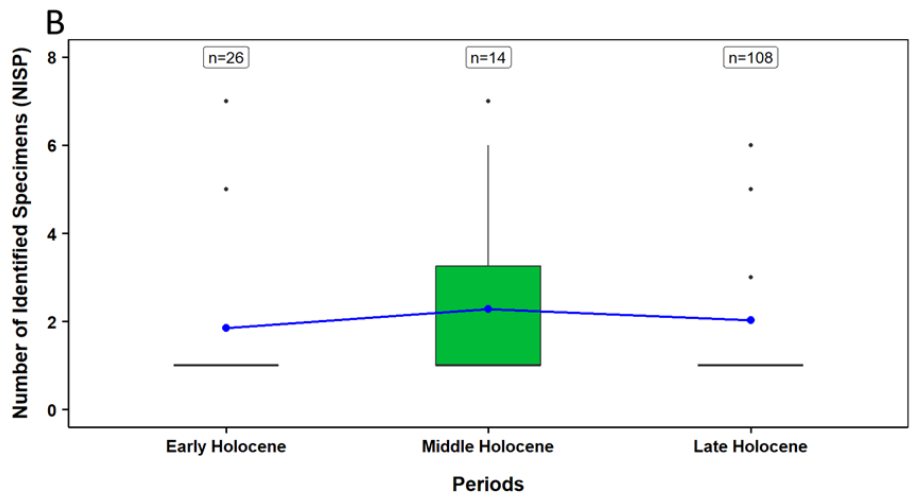


**Figure S7.1.2** - Distribution of data for NISP on *Thunnus thynnus* in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

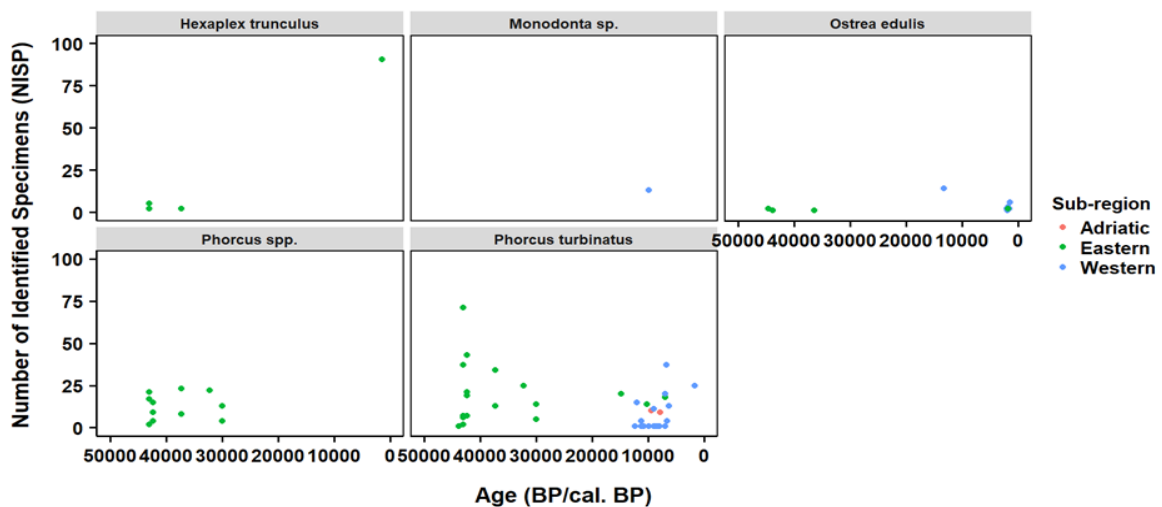


**Figure S7.1.3** - Distribution of data for NISP on *Sparus aurata* in the Western sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

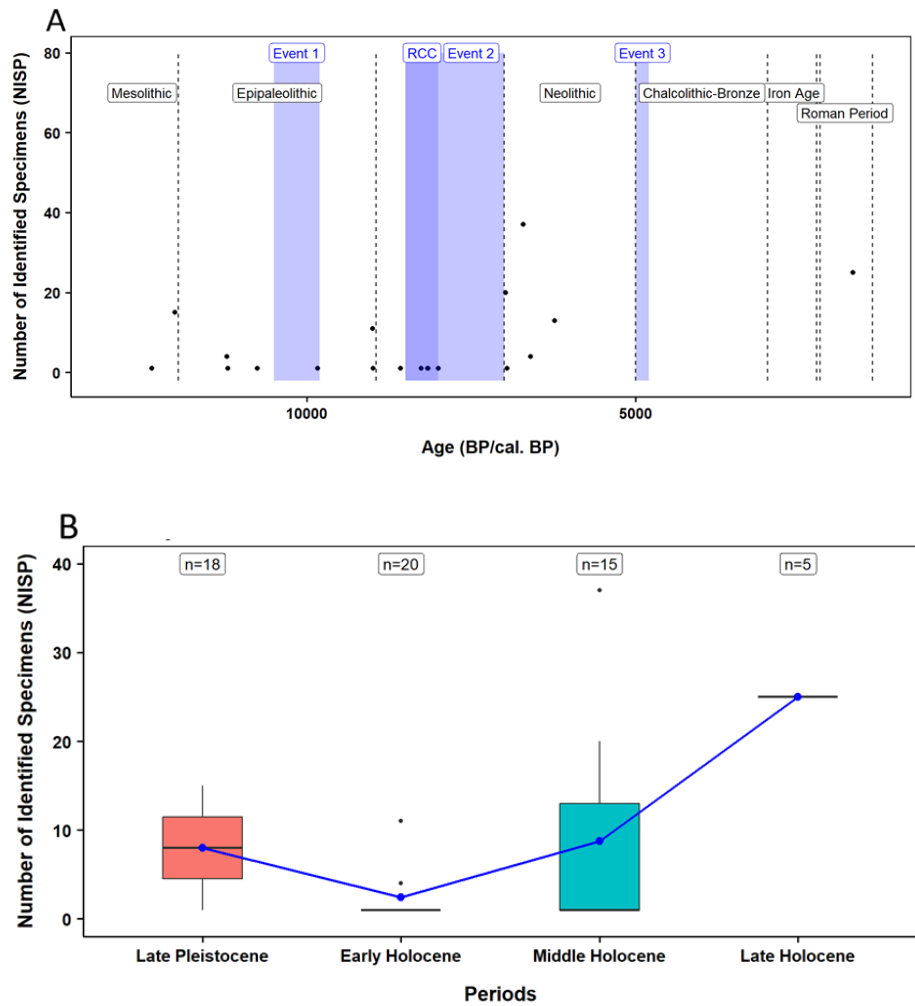




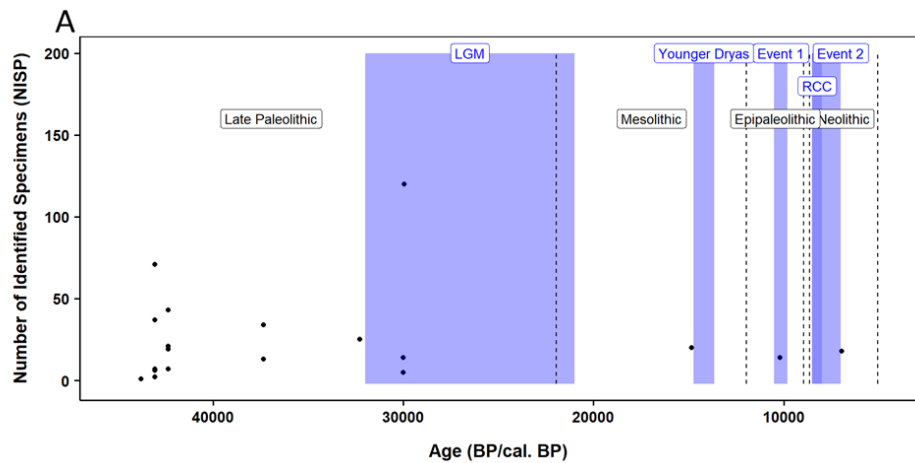
**Figure S7.1.4** - Distribution of data for NISP on *Sparus aurata* in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

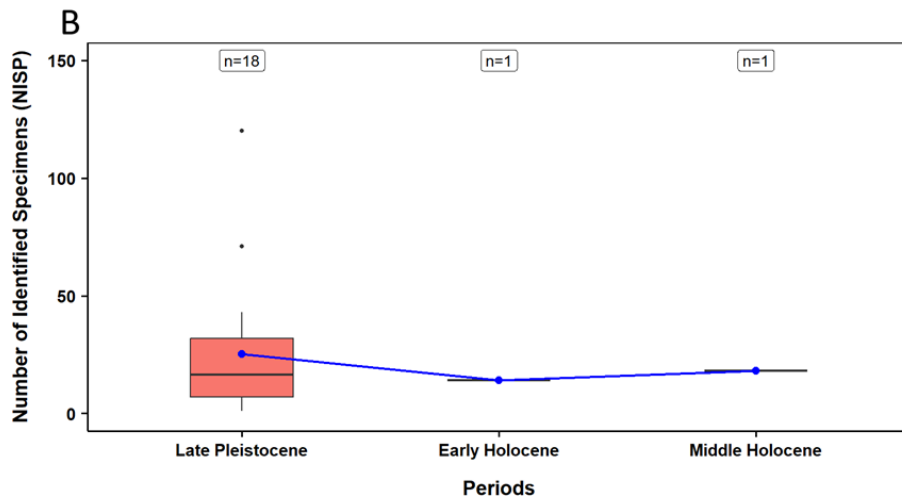


**Figure S7.2** - Distribution of data for NISP for molluscs. Colours separate the data for each sub-region of the Mediterranean Sea.

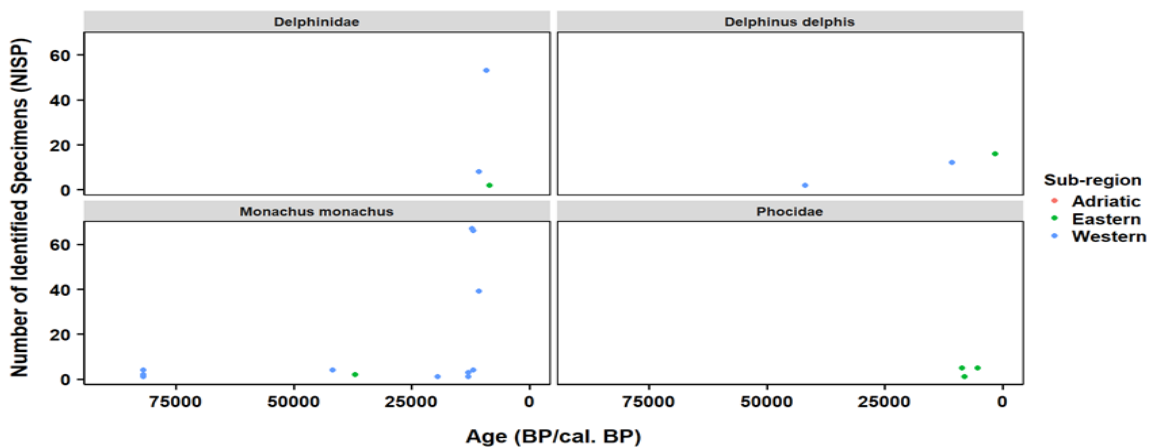


**Figure S7.2.1** - Distribution of data for NISP on *Phorcus turbinatus* in the Western sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.



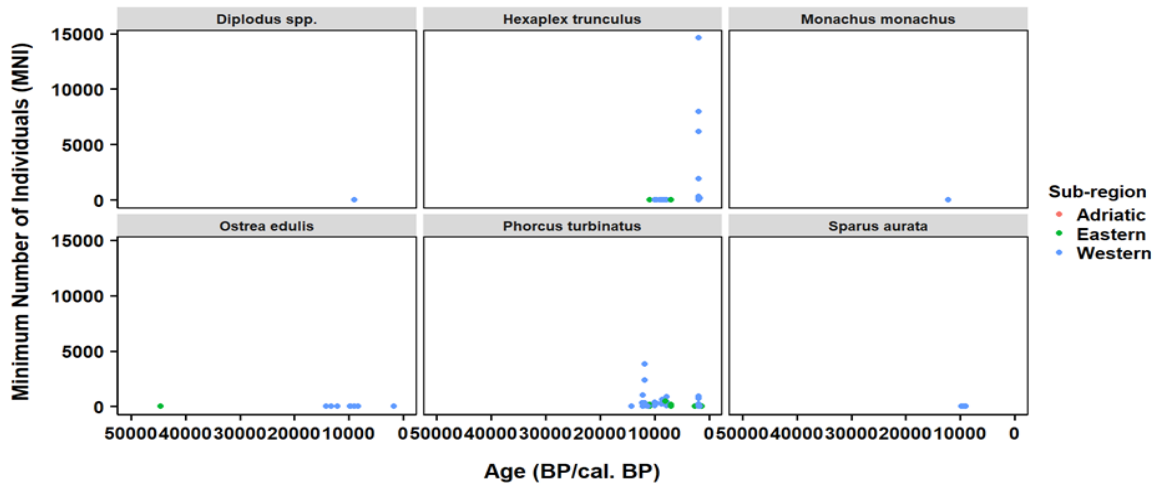


**Figure S7.2.2** - Distribution of data for NISP on *Phorcus turbinatus* in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

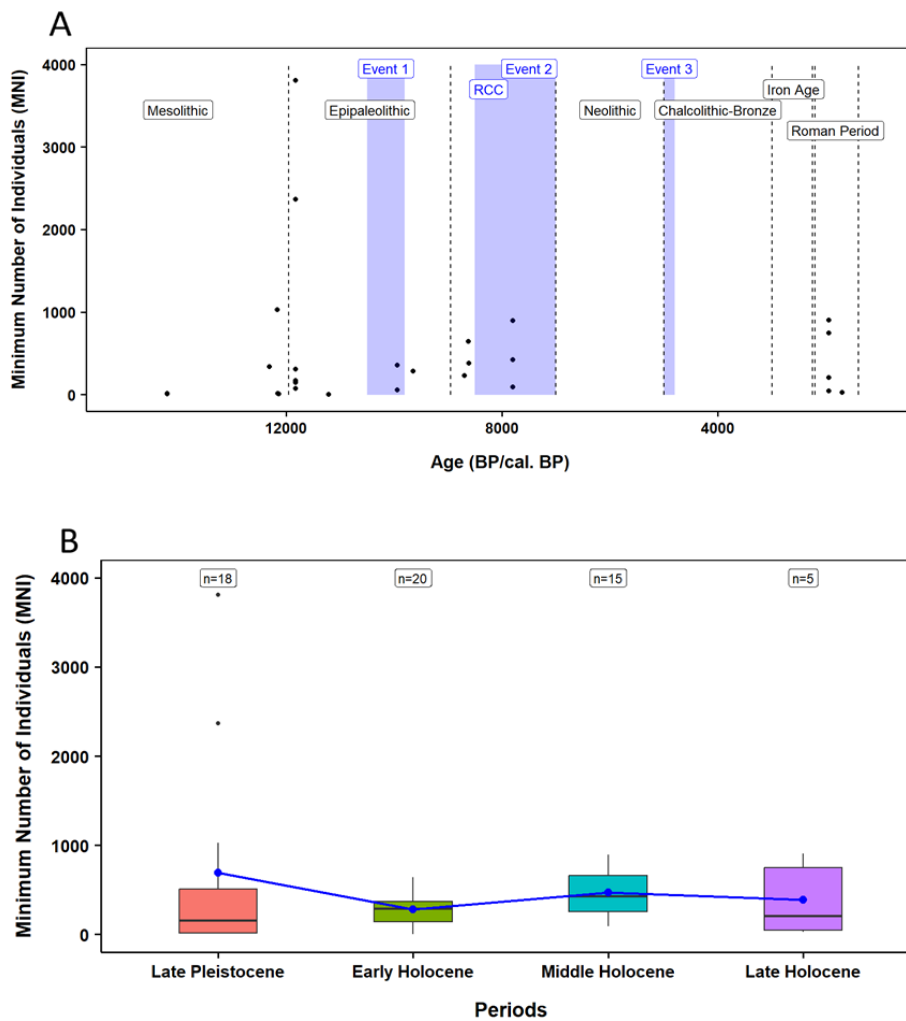


**Figure S7.3** - Distribution of data for NISP for marine mammals. Colours separate the data for each sub-region of the Mediterranean Sea.

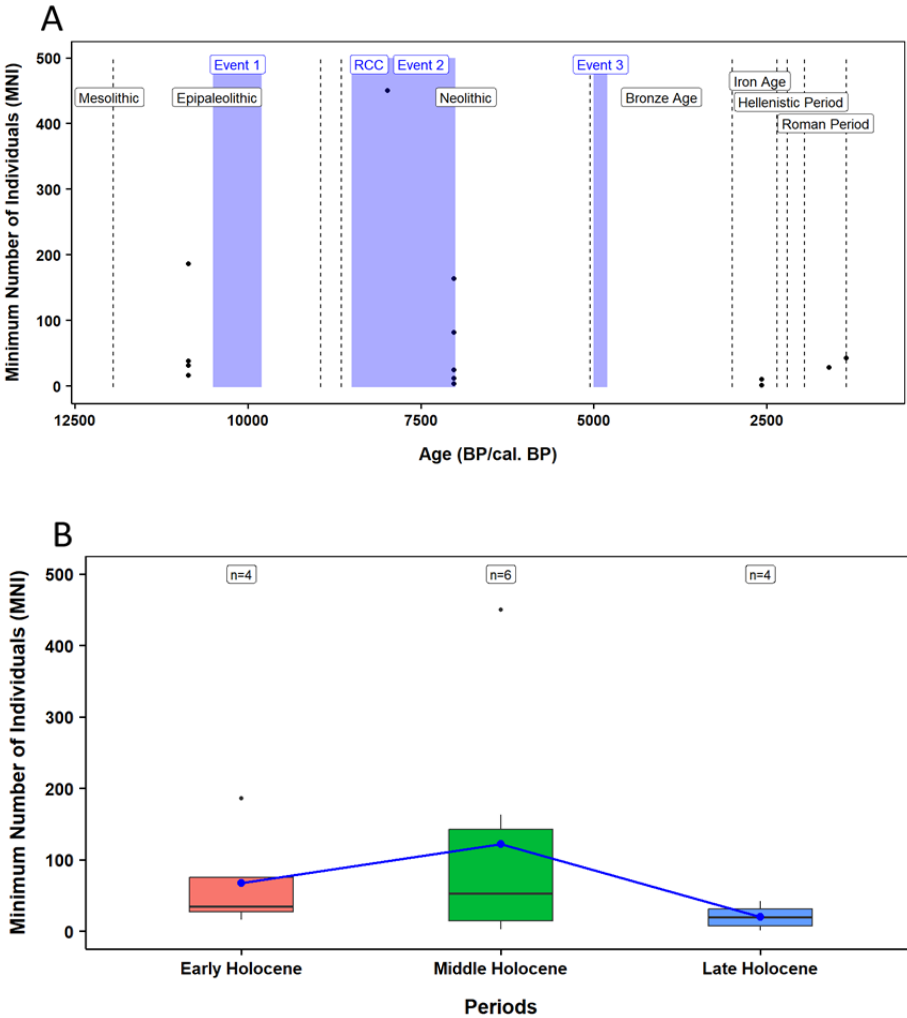
## S8. MNI distribution



**Figure S8.1** – MNI species distribution data. Colours separate the data for each sub-region of the Mediterranean Sea.

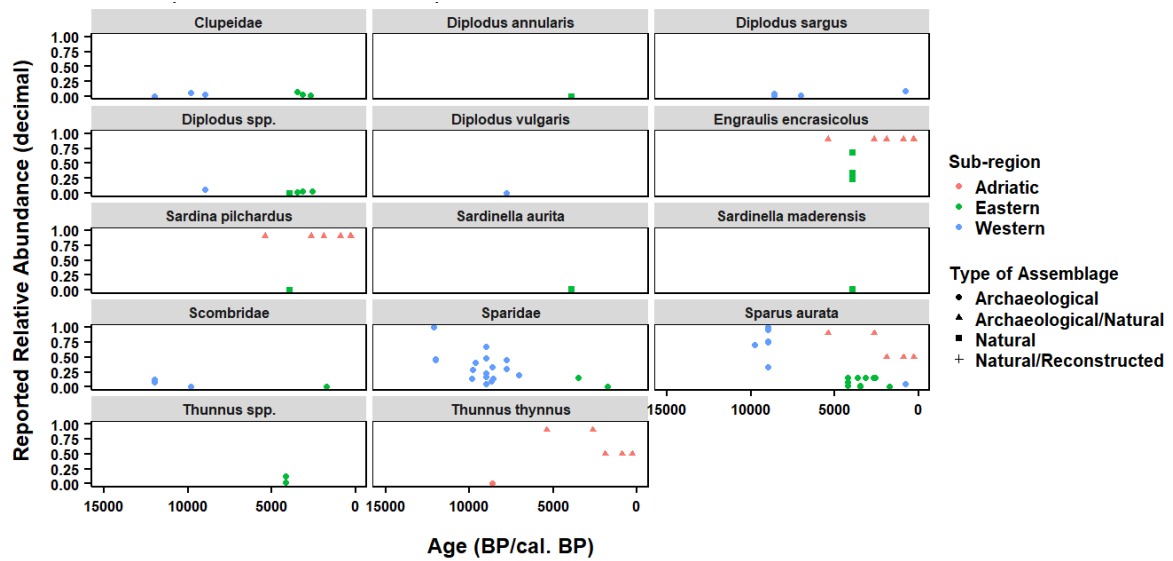


**Figure S8.1.1** - Distribution of data for MNI on *Phorcus turbinatus* in the Western sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

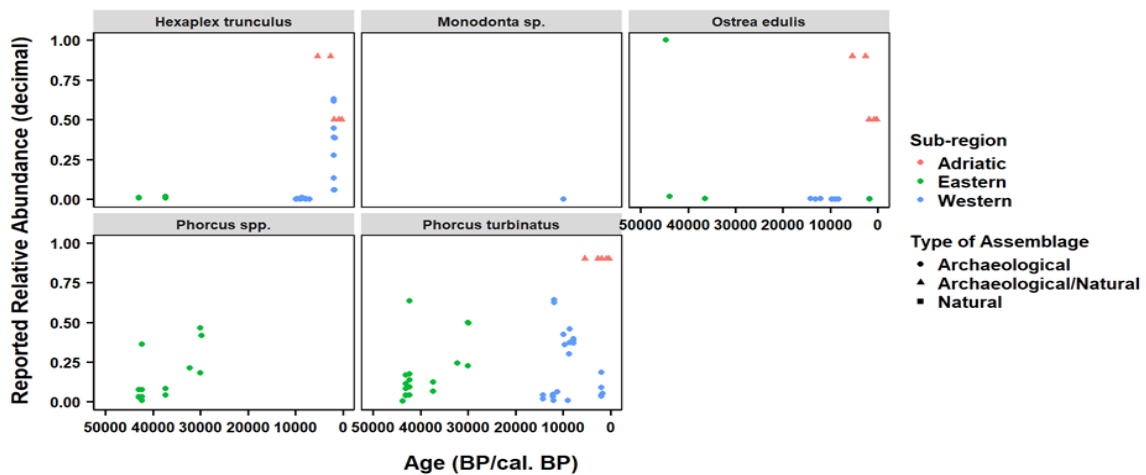


**Figure S8.1.2** - Distribution of data for MNI on *Phorcus turbinatus* in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

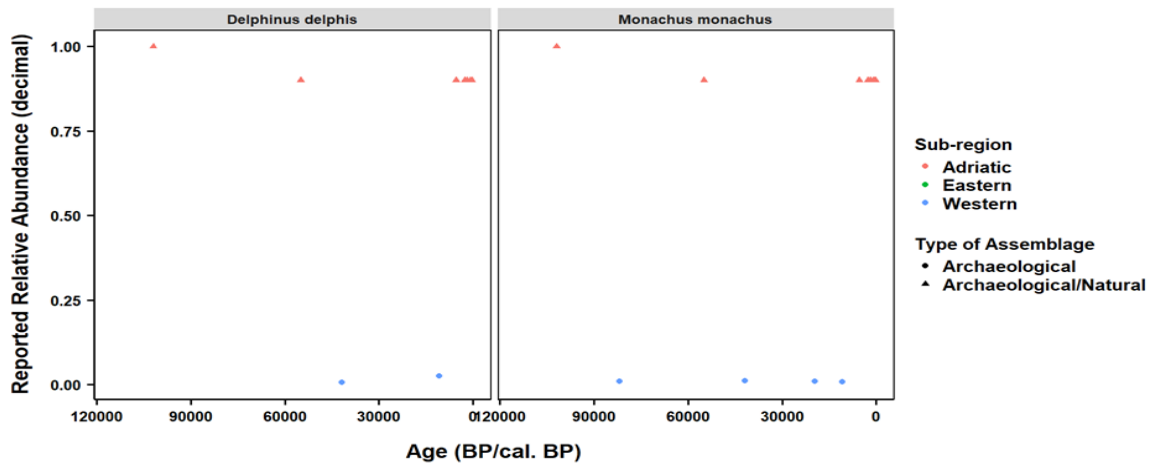
## S9. Reported Relative Abundance (RRA)



**Figure S9.1** – Distribution of data for Reported Relative Abundance (RRA) for fishes. The colours separate the data for each sub-region of the Mediterranean Sea, while the shape of each point dictates the type of assemblage from where the data came from.

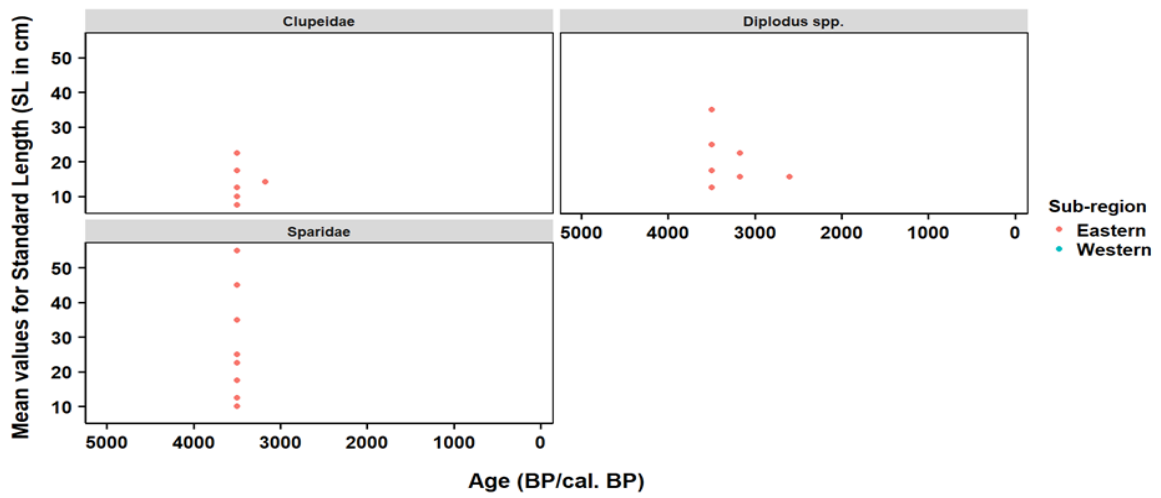


**Figure S9.2** – Distribution of data for Reported Relative Abundance (RRA) for molluscs. The colours separate the data for each sub-region of the Mediterranean Sea, while the shape of each point dictates the type of assemblage from where the data came from.

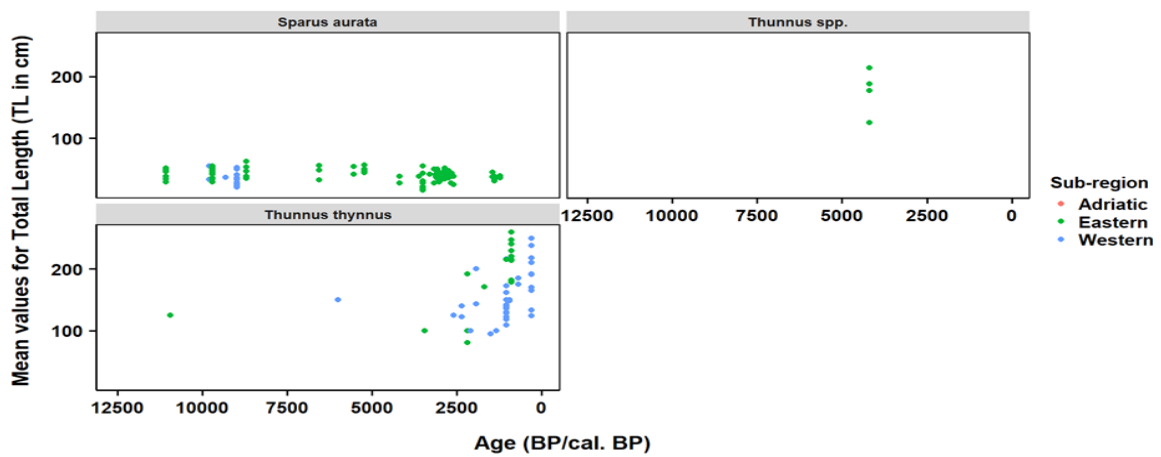


**Figure S9.3** – Distribution of data for Reported Relative Abundance (RRA) for marine mammals. The colours separate the data for each sub-region of the Mediterranean Sea, while the shape of each point dictates the type of assemblage from where the data came from.

### S10. Fishes' standard and total length

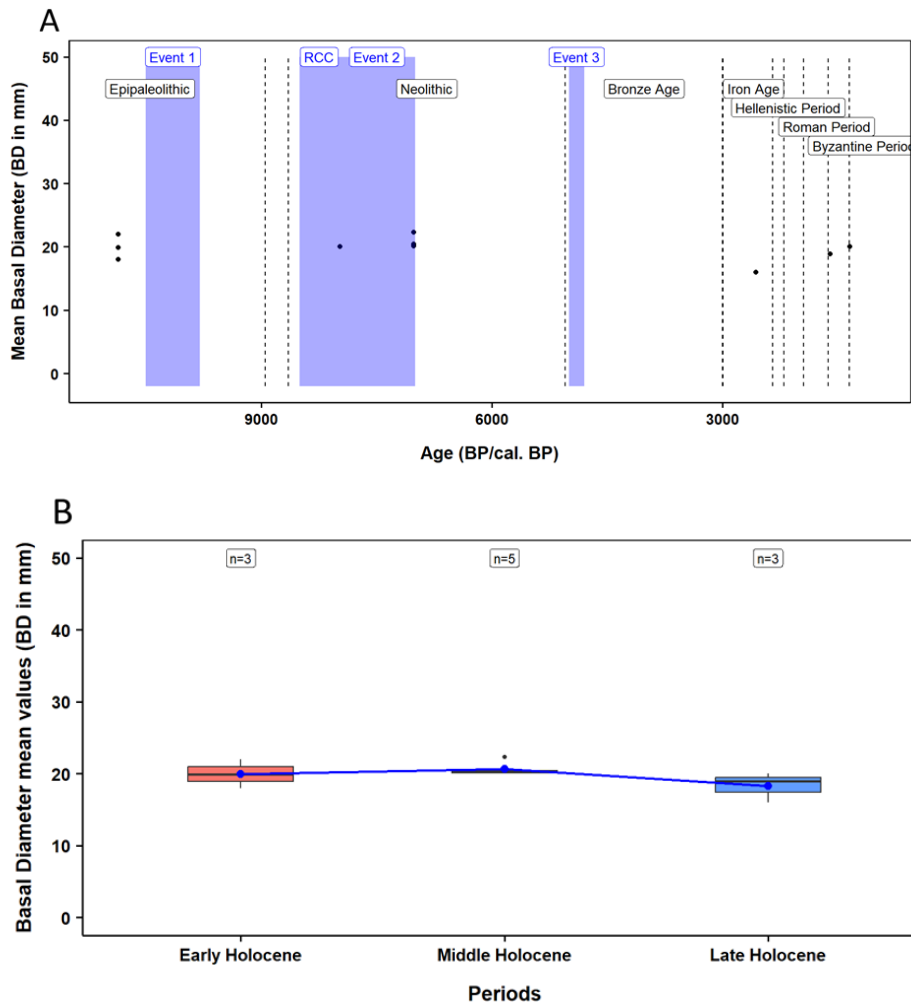


**Figure S10.1** – Fishes distribution of data for Standard Length (SL). The colour indicates that the data comes from the Eastern Mediterranean Sea.

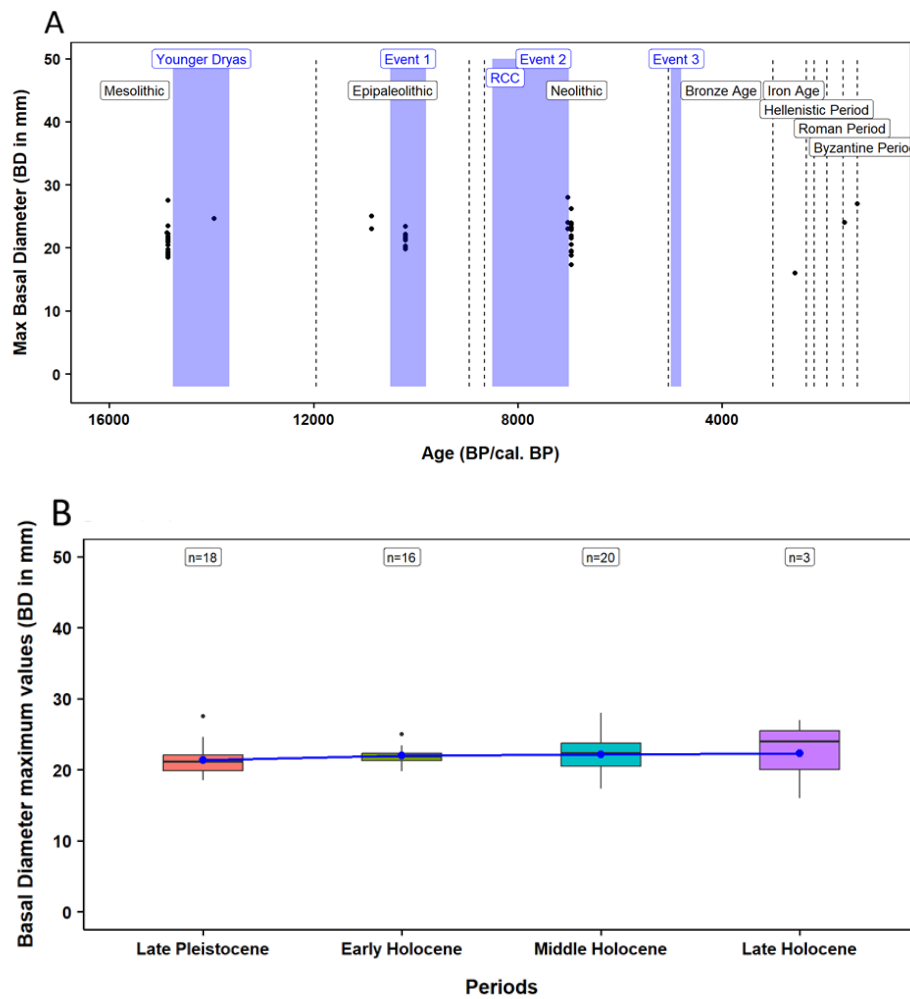


**Figure S10.2** – Fishes distribution of data for Total Length (TL). The colour indicates from which sub-basin of the Mediterranean Sea the data comes.

## S11. Molluscs basal diameter (BD)

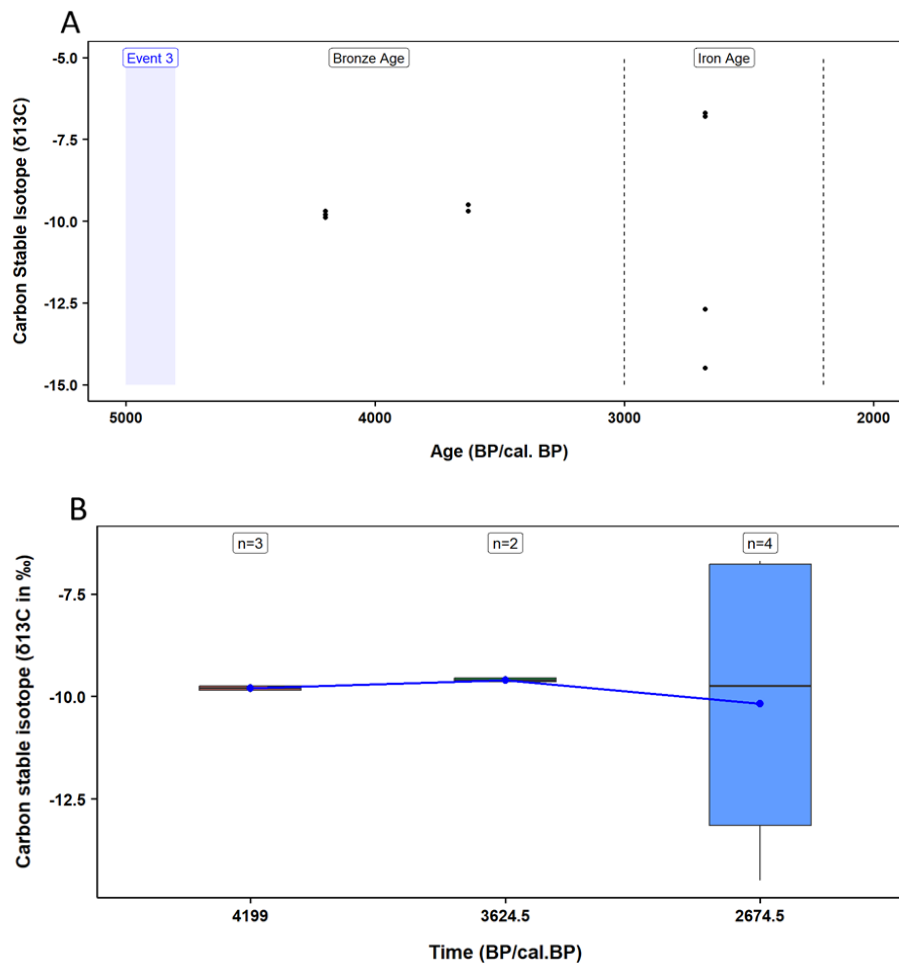


**Figure S11.1** - Distribution of data for mean BD on *Phorcus turbinatus* in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

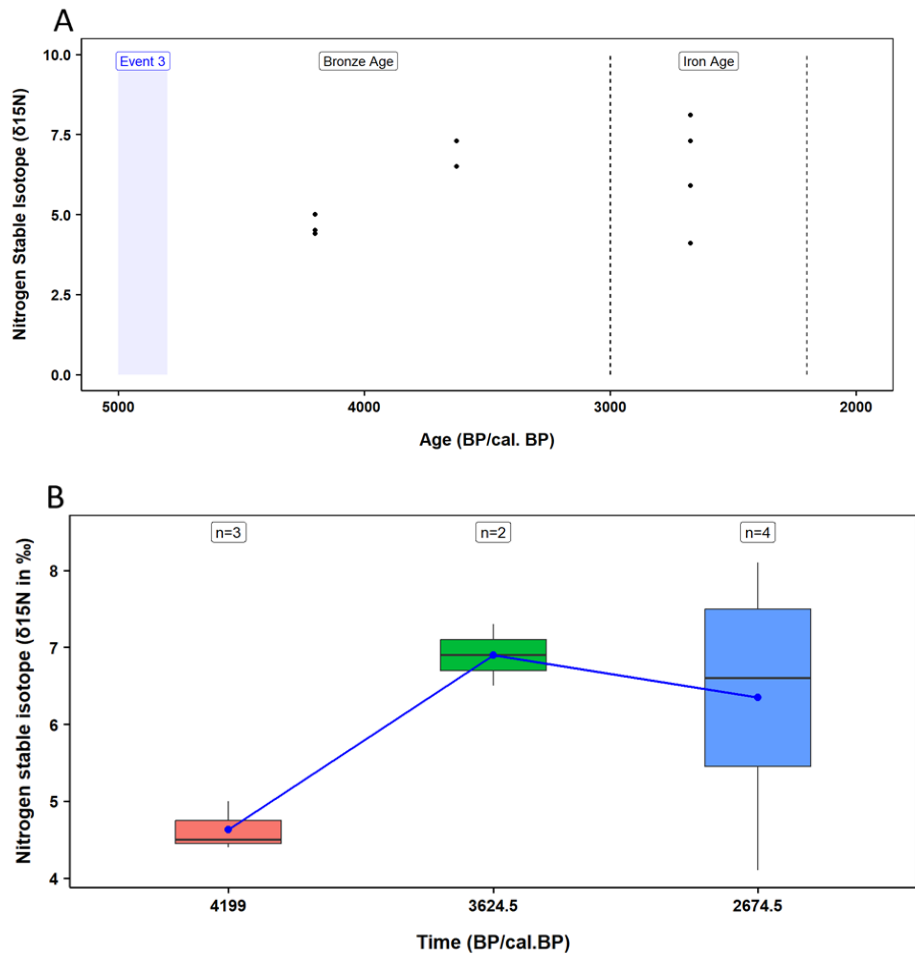


**Figure S11.2** - Distribution of data for maximum values of BD on *Phorcus turbinatus* in the Eastern sub-region. (A) Distribution of records in time with corresponding major climatic (in blue rectangles) and anthropogenic events (in black dashed lines); (B) Boxplots with the data for each geologic period. The blue dots are the mean values for each period and the bars are the standard deviation. The number of points (n) included in each box plot is indicated above.

## S12. *Sparus aurata* stable isotopic data



**Figure S12.1** – Distribution of data for the  $\delta^{13}\text{C}$  of *Sparus aurata* from the Eastern sub-region. (A) The  $\delta^{13}\text{C}$  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 points (n) included in each box plot is indicated above.



**Figure S12.2** – Distribution of data for the  $\delta^{15}\text{N}$  of *Sparus aurata* from the Eastern sub-region. (A) The  $\delta^{15}\text{N}$  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 points (n) included in each box plot is indicated above.

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