



# Environmental and anthropogenic impacts on key Mediterranean Sea fishes and molluscs from the late Pleistocene until the Industrial Revolution

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## Abstract

Historical baselines are essential for evaluating the cumulative impacts on modern marine ecosystems, particularly in regions such as the Mediterranean, where human activities have been intensive for millennia, and climate change is accelerating. However, quantitative evidence of historical impacts remains fragmented. In this study, we investigate changes in the presence, abundance and body size (BS) of the Atlantic bluefin tuna (*Thunnus thynnus*), gilthead sea bream (*Sparus aurata*), banded-dye murex (*Hexaplex trunculus*) and turbate monodont (*Phorcus turbinatus*) across the Mediterranean Sea from 130 000 years Before Present until the Industrial Revolution (1850 AD), using geological, archaeological, and historical records. Our results reveal significant temporal shifts in the abundance and BS of the banded-dye murex, Atlantic bluefin tuna, and gilthead sea bream. Environmental factors, particularly seawater temperature, were the primary drivers of abundance and size in Atlantic bluefin tuna in the past. Human activities, especially exploitation, influenced the abundance of banded-dye murex and Atlantic bluefin tuna, as well as the BS of gilthead sea bream. These findings underscore the importance of integrating long-term ecological data to understand better the interplay between climate, human pressures, and ecosystem dynamics.

**Keywords** Atlantic bluefin tuna, Gilthead sea bream, Banded-dye murex, Turbate monodont, Environmental variability, Overexploitation, Holocene

## Introduction

Marine ecosystems are major components of the Earth system, supporting biodiversity, human societies, and economies (Halpern et al. 2008). However, they are increasingly under threat. Understanding how multiple stressors affect marine biota requires long-term ecological records, yet high-resolution temporal data remain scarce (Dietl et al. 2015). While most ecological studies rely on short-term datasets (Jackson 1997, Dayton et al. 1998), geological, archaeological, and historical records offer valuable insights into long-term ecosystem responses to environmental and anthropogenic pressures (Jackson Jeremy et al. 2001, Lotze et al. 2006, 2011 Fortibuoni et al. 2010, Bas et al. 2019, 2023, Agiadi and Albano 2020, Agiadi et al. 2023, 2024, Porz et al. 2024).

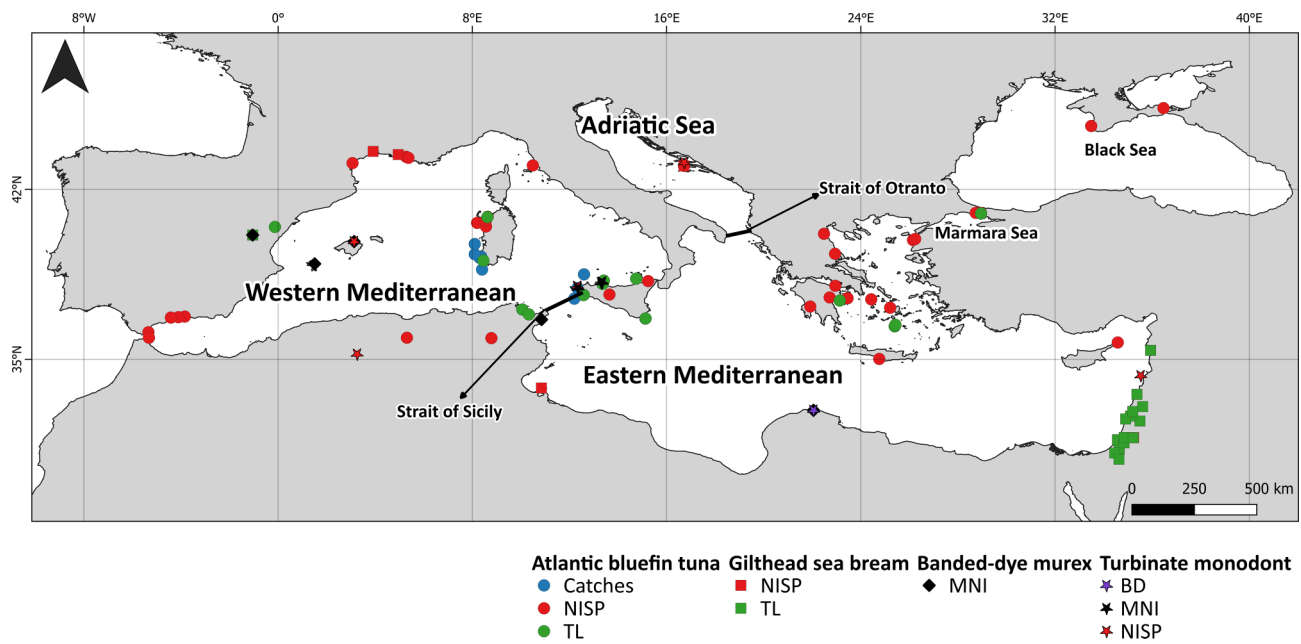
The Mediterranean Sea is a global biodiversity hotspot (IUCN-MED 2009, Coll et al. 2010), hosting various emblematic species, such as the Atlantic bluefin tuna (*Thunnus thynnus*) (Linnaeus, 1758) (MacKenzie et al. 2009) and the Mediterranean monk seal (*Monachus monachus* Hermann, 1779) (Reijnders et al. 1997), which is at present classified as Vulnerable in the IUCN Red List. Past changes in climate and ocean connectivity have shaped

the Mediterranean ecosystems, influencing species distributional changes, including range shifts and biological invasions (Agiadi et al. 2011, 2018, 2024). Since the Industrial Revolution, the Mediterranean has warmed faster than the global average (IPCC 2022, Artana et al. 2026) with profound consequences for marine biodiversity and ecosystems functioning (Garrahou et al. 2009, Smale et al. 2019, Trisos et al. 2020, Ouled-Cheikh et al. 2022).

Marine resources have supported Mediterranean societies for millennia (Madariaga 1964, Mehvar et al. 2018). Shellfish exploitation dates back to the lower Paleolithic (e.g. ~300 ka B.P.; c. 300 kyrs ago, de Lumley 1966), and by the Bronze Age (5–3 ka BP; c. 3300–1200 AD), extensive fisheries and trade networks were established (e.g. Van Neer et al. 2004, Guy et al. 2018, Zohar and Artzy 2019), intensifying throughout the Classical period (Sáez Romero 2014, Mylona 2018). In this context, a previous work identified that several key marine species were either extensively exploited and/or affected by past environmental changes (Leal et al. 2025a). Long-term exploitation, combined with environmental variability, has contributed to the reshaping of marine ecosystems (Lotze et al. 2006, 2011). Today, habitat loss, degradation, and overexploitation continue to alter species productivity, fitness, and distribu-

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**Figure 1** Map of the Mediterranean Sea showing the subregions (Western Mediterranean, Eastern Mediterranean, and Adriatic Sea) and their natural divisions (Strait of Otranto and Strait of Sicily), with the data locations (Table S1). Variables used include the Number of Identified Specimens (NISP), Minimum Number of Individuals (MNI), Catches, Total Length (TL), and Basal Diameter (BD).

tion, with cascading effects on ecosystem structure and functioning (Halpern et al. 2008, Coll et al. 2010, 2012, Planque et al. 2010, Howarth et al. 2014, Artana et al. 2026).

In this study, we examine how environmental variability and human activities have influenced commercially relevant species in the Mediterranean Sea over the past 130 kyrs until the Industrial Revolution. Using regional data (Leal et al. 2025a) we analyse Atlantic bluefin tuna (*T. thynnus*), gilthead sea bream (*Sparus aurata*), banded-dye murex (*Hexaplex trunculus*) and turbinate monodont (*Phorcus turbinatus*), testing whether: (i) temperature oscillations from the late Pleistocene to the late Holocene (LH; Cacho et al. 2002, 2006, Marchal et al. 2002, Rohling et al. 2002, Schmiedl et al. 2010) influenced species abundance and body size (BS); and (ii) human exploitation compounded these effects over time.

## Materials and methods

### Study area

The Mediterranean Sea is a semienclosed basin (3 000 000 km<sup>2</sup>, maximum depth ~5300 m (Robinson and Golnaraghi 1994). For analytical purposes, we divided the basin into three subregions: Western, Eastern, and Adriatic, defined by the straits of Sicily and Otranto (Millot and Taupier-Letage 2005, Rio et al. 2007, Robinson et al. 2009) (Fig. 1). In the past, sea-level fluctuations altered the connection between the Mediterranean, Marmara, and Black seas, whose phases of isolation and reconnection differed markedly from present-day conditions (Yanko-Hombach et al. 2007, Yanchilina et al. 2017). Although the initial search terms (Leal et al. 2025a) did not explicitly include the Black or Marmara seas, we retrieved a few records of Atlantic bluefin tuna from both seas. Given the species' high mobility, we decided to include these records in the analyses of the Eastern Mediterranean.

### Species and temporal framework

Species data were available at both spatial and temporal scales across the Mediterranean subregions, whereas catch data were available only for Atlantic bluefin tuna.

We adopted the temporal divisions defined by the International Commission on Stratigraphy (ICS; Cohen et al. 2025): upper stage of the Pleistocene (late Pleistocene; 129 000–11 700 years before 2000 AD), Greenlandian [early Holocene (EH); 11 700–8236 years before 2000 AD], Northgrippian (MH; 8236–4250 years before 2000 AD), and Meghalayan (LH; 4250 years before 2000 AD—present). Each period is characterized by major climatic events (e.g. glacial-interglacial cycles, Lionello et al. 2023) and societal transitions (e.g. from hunter-gatherers to sedentary communities, Isern et al. 2014, Valla 2018) (see Table S2 for detailed information on each environmental and cultural event). The late Pleistocene includes the last interglacial (130–116 kyrs BP; c. 128 000–114 000 BC; Kukla et al. 2002) and the Younger Dryas (14 749–13 646 years BP; c. 12 800–11 700 BC; Benjamin et al. 2017). The Holocene features notable temperature fluctuations, such as the Medieval Warm Period (MWP; 1050–650 BP; c. 850–1200 AD) and the Little Ice Age (LIA; 650–100 years BP; c. 1200–1850 AD) (Cisneros et al. 2016).

Mediterranean fisheries evolved significantly between the preindustrial (130 kyrs–1850 AD) and the postindustrial era (1850 AD—present day). During the preindustrial era, fishing practices were predominantly manual and artisanal (e.g. harpoons, gillnets, and traps; Ruas 2005, Roberts et al. 2011, Horden and Purcell 2013, Pedergrana et al. 2021), while the onset of industrial fishing (1880 AD) introduced mechanized fishing and steam-powered trawlers that greatly increased fishing efficiency (Gabriel et al. 2005, Anticamara et al. 2011). Although our primary analyses focus on the preindustrial era, we decided to include postindustrial developments in fishing gear to contextualize its technological evolution,

which may have contributed to the fluctuations observed in Atlantic bluefin tuna catches (FAO 2022).

## Database

The database compiled by Leal et al. (2025b) was developed through a systematic review following the PRISMA methodology (Page et al. 2021), integrating peer-reviewed and secondary literature with geological, archaeological, and historical sources (Table S3).

Presence and abundance data were quantified using two zooarchaeological metrics: the NISP (Grayson 1984) and Minimum Number of Individuals (MNI; Lyman 1994). NISP is a fundamental direct count of bone fragments (including teeth and identifiable fragments) categorized by taxon and skeletal elements, whereas MNI is an estimate of the lowest number of individual animals present in an assemblage that is calculated based on the most frequently occurring, paired, or distinct skeletal element. Both metrics are widely used in zooarchaeology, but are subject to taphonomic biases, due to differences in the preservation of skeletal remains between settings, along with recovery biases (e.g. small bones often missed presieving standardization), and sampling effort variation (Stiner 1994, Van Neer et al. 2004).

The review also incorporated over 1200 entries of Atlantic bluefin tuna catch data from Italian tuna traps (1700–1936; Addis et al. 2008, Longo and Clark 2012, Polanco-Martínez et al. 2018), which serve as long-term proxies for abundance (Ravier 2001). Historical abundance trends were analysed in relation to Sea Surface Temperature (SST; Jalali et al. 2016), human civilizations, and fishing technologies. The catch data analysed in this study derive from seven fixed tuna traps that operated in Sardinia and Sicily (Italy), whose structural design and fishing methodology were similar across the timeframe studied (Addis et al. 2008, Longo and Clark 2012, Ganzedo et al. 2016). The reported changes were limited to material substitutions (e.g. cotton nets and iron anchors), with no significant modifications to the trap structure or operating settings.

While most of the Atlantic bluefin tuna catch data comes from Italian tuna traps, the SST data for the same period (1700–1936 AD) were the closest available from the Gulf of Lion. While this region is known as a cold spot in the Mediterranean Sea (Shaltout and Omstedt 2014), it represents one of the few continuous and well-documented historical SST reconstructions available for the Western Mediterranean over the 1700–1936 period. Moreover, despite mean-state variations within subregions, paleoclimate studies show that multidecadal to centennial SST anomalies are generally coherent throughout the Western Mediterranean (e.g. Cisneros et al. 2016). Consequently, the Gulf of Lion SST record is used here as a regional indicator of Western Mediterranean thermal variability, rather than a direct measure of local temperature at the fishing sites. BS data were derived from multiple sources: (i) TL for Atlantic bluefin tuna from Andrews et al. (2022, 2023a, 2023b, 2023c) ( $n = 68$ ); (ii) TL for gilthead sea bream from Western archaeological sites (Fernández-López De Pablo and Gabriel 2016) and Eastern sites (Guy et al. 2018, Fuller et al. 2020) ( $n_{\text{Western and Eastern}} = 154$ ); and (iii) BD of the turbinat monodont from Haua Fteah cave, Libya (Hunt et al. 2011, Prendergast et al. 2016) ( $n_{\text{mean}} = 14$ ;  $n_{\text{maximum}} = 57$ ). These data inherently have biases; therefore, ecological interpretations must be cautious and framed as indicative of relative past implications upon species rather than definitive.

However, the same data and the analytical approach taken in this study provide valuable insights into past environmental and anthropogenic impacts in the Mediterranean Sea.

## Data analyses

Normality and homoscedasticity were tested using the Shapiro–Wilk and Levene’s tests, respectively (*car* R package; Fox and Weisberg 2019). For NISP and MNI, nonparametric tests were applied: the Mann–Whitney *U* test for two-group comparisons and the Kruskal–Wallis test for multigroup comparisons, followed by post hoc pairwise Wilcoxon tests. For TL, a two-sample *t*-test for Western Mediterranean tuna and a Mann–Whitney *U* test for the Eastern Mediterranean tuna. For the gilthead sea bream, ANOVA with a Tukey’s HSD post hoc test was used to compare three periods. For BD, ANOVA (mean values) and Welch ANOVA (maximum values) were applied to multiperiod comparisons. Catch data trends were analysed using the Mann–Kendall (MK) test (*trend* R package; Pohlert 2023). This is a nonparametric test that assumes independent observations without serial autocorrelation and no seasonality (Gilbert 1987). Catch trends analysed on the trap-level data revealed serial autocorrelation (ACF lag-1 = 0.88; Ljung-Box  $P < 2e^{-16}$ ), and were addressed via modified MK (*modifiedmk* R package; Patakamuri and O’Brien 2017). Data classification was performed using Jenks’ natural breaks method (Jenks 1977) (*classInt* R package; Bivand 2006). Interperiod differences were assessed with Kruskal–Wallis and pairwise Wilcoxon tests. A significance threshold of  $P \leq .05$  was applied, with Bonferroni correction. Maps were produced in QGIS 3.34.13, and statistical analyses in R 4.4.3 (R Core Team 2025).

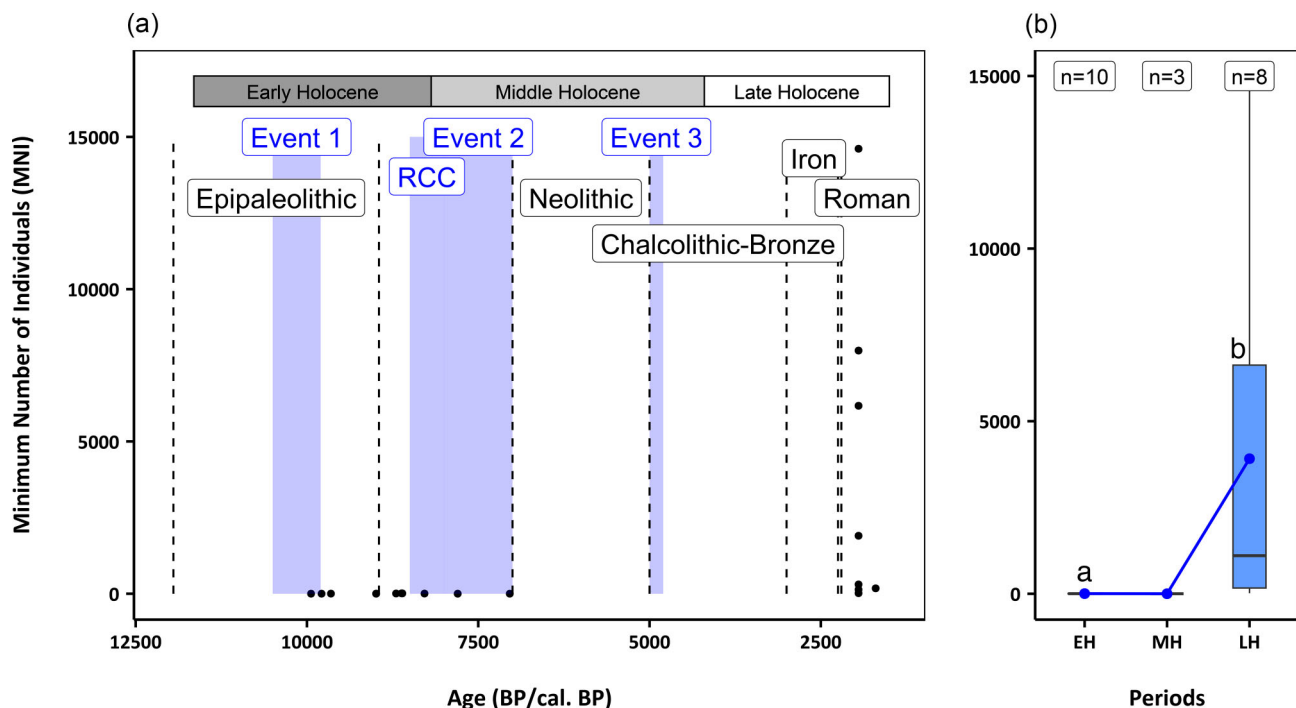
The Supplementary Materials include additional statistical outputs, including nonsignificant results, such as those concerning the turbinat monodont. They also provide figures representing the data dispersion across temporal phases and subregions, tables summarizing the locations of sampling sites, and the sample sizes per species and variables obtained through the systematic review. This additional information supports the methodological framework presented in the main text.

## Results

### Presence and abundance of targeted species

NISP data for gilthead sea bream and Atlantic bluefin tuna span the entire temporal framework. However, comparisons between periods within each region revealed no statistically significant differences (Table S4.1; Figs. S5.1B–S5.4B). Among molluscs, only the turbinat monodont presented sufficient data for temporal analysis across the Mediterranean Sea, but no significant differences were detected across periods (Table S4.1; Figs. S5.5B and S5.6B).

MNI data for turbinat monodont were available for both the Western and Eastern Mediterranean, yet no significant differences were found between periods (Table S4.2, Figs. S5.7 and S5.8). In contrast, banded-dye murex showed significant temporal variation in the MNI in the Western Mediterranean ( $H_2 = 15.792$ ;  $P = .0004$ , Fig. 2a), particularly between the early and LH ( $P = .0013$ ; Fig. 2b; Table S4.2).



**Figure 2** Distribution of MNI for banded-dye murex in the Western Mediterranean. (a) Temporal distribution of records, including major climatic events and anthropogenic periods. Holocene Events 1 (10 500–9800 yr BP), 2 (8000–7000 yr BP) and 3 (5000–4800 yr BP) refer to cooling episodes (Lionello et al. 2023); (b) Boxplots of MNI data by geological period: EH, middle Holocene (MH), and LH. Mean values and standard deviation are also indicated. Letters denote statistically significant differences. Sample sizes ( $n$ ) are shown above each boxplot.

## Catch records

Catch data (annual totals) were available only for Atlantic bluefin tuna from 250 to 14 years BP, corresponding to the period between 1700 and 1936 AD (Fig. 3). Recorded values ranged from 0 to approximately 12 500 individuals per year along the coasts of Sardinia and Sicily in the Western Mediterranean (Fig. 1). Two major peaks were observed: around 200 years BP (~1750 AD) during the LIA with ~10 000 individuals, and between 75 and 45 years BP (1875–1905 AD), following the Industrial Revolution (1850 AD) (~12 000 individuals).

While a significant declining trend was detected in trap-level catches between 250 and 14 years BP ( $S = -3.98e^5$ ;  $\tau = -0.239$ ;  $P < 2.2e^{-16}$ ), annual aggregates showed no monotonic trend (standard MK:  $S = 605$ ,  $\tau = 0.021$ ,  $P = .62$ ; modified MK:  $P = .84$ ). Interperiod differences were significant ( $H_5 = 407.55$ ;  $P < 2.2e^{-16}$ ; Tables S4.3 and S6; Figure S6).

## Body size

In the Western Mediterranean, a significant increase in the TL of Atlantic bluefin tuna was found between the MWP and the LIA ( $t_{15,141} = 2.967$ ;  $P = .01$ ; Figs. 4 and S7.1; Table S4.4).

In the Eastern Mediterranean, TL of Atlantic bluefin tuna also showed significant increases between the Roman Period (2500–1050 years BP) and the MWP (1050–650 years BP), as well as within the MWP itself ( $W = 8$ ;  $P = .01035$ ) (Figs. 5 and S7.2; Table S4.4).

For gilthead sea bream, TL data were available for the Eastern Mediterranean (Fig. 6). Pairwise comparisons ( $F = 10.28$ ;  $P = 7.54e^{-5}$ ) revealed significant reductions in TL between the

early and LH ( $P = .0061$ ), the middle and LH ( $P = .0010$ ; Fig. 6b), and between the Bronze and Iron Ages and the Byzantine Period ( $H_2 = 8.501$ ;  $P = .014$ , Table S4.4 and Figure S7.3).

For the turbinate monodont, BD data were available for the Eastern Mediterranean, including both mean and maximum values. No significant differences were found between the geological periods, for either metric (Table S4.5; Figs S7.4 and S7.5).

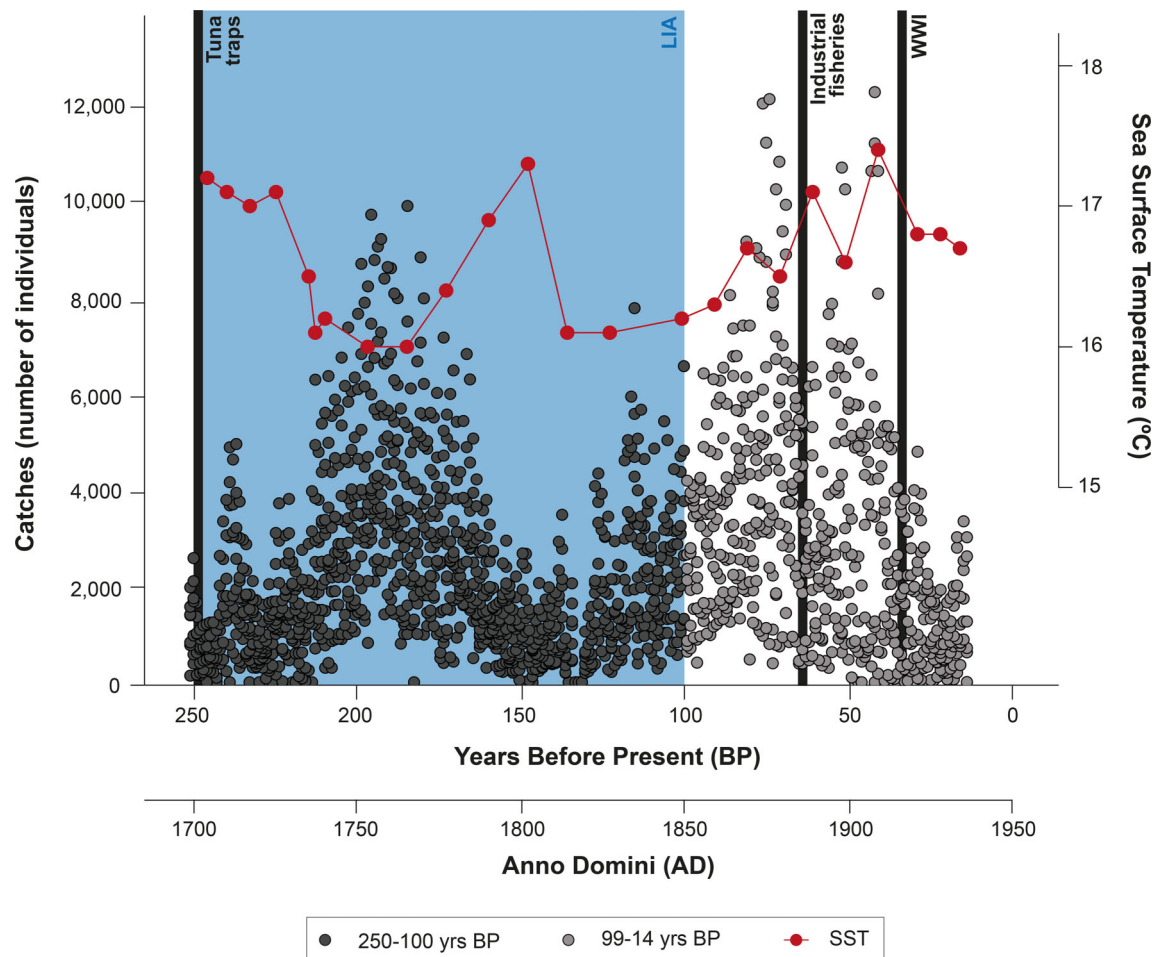
## Discussion

### Environmental driven changes in Atlantic bluefin tuna

Atlantic bluefin tuna is a highly migratory species that travels between cold feeding grounds in the North Atlantic and warm spawning areas in the Mediterranean Sea (Mather et al. 1995, Block et al. 2001, 2005, Rooker et al. 2007). Climatic changes influence its growth, reproduction, population size, mortality, and migration patterns (Pepin 1991, Graham and Dickson 2004).

Our data show a peak in tuna catches during the late LIA. This pattern is temporally consistent with cooler conditions (Cisneros et al. 2016, Margaritelli et al. 2020) and enhanced nutrient availability and primary productivity in the North Atlantic (Pourmand et al. 2007), resulting in a greater number of mature individuals entering the Mediterranean. Additionally, tuna migration may have shifted toward the basin during the LIA, likely due to increased climatic instability and extreme events, leading to higher recruitment in the Western Mediterranean and greater concentration of schools near historical tuna traps (Ravier and Fromentin 2004,





**Figure 3** Atlantic bluefin tuna catch records from the LH (250–14 years BP; 1700–1936 AD), based on tuna traps from the Western Mediterranean Sea ( $n = 1225$ ). Preindustrial catches (250–100 years BP; 1700–1850 AD) and postindustrial catches (99–14 years BP; 1851–1936 AD) are represented. Reconstructed SST from the Gulf of Lions (Jalali et al. 2016) is indicated and used here as a regional indicator of Western Mediterranean thermal variability during the study period. LIA period is also indicated. Vertical lines indicate the use of tuna traps, the onset of industrial fisheries (70 BP; 1880 AD; von Brandt 1972, Gabriel et al. 2005), and WWI (World War I). Note: tuna trap technology remained largely unchanged until the 1960s (Doumenge 1998).

Ganzedo et al. 2009). Considering the 6–7 year lag between hatching and recruitment (Zorita et al. 2005), the increased landings observed in the later stages of the LIA could reflect changes in distribution and behavior rather than an overall increase in population size. Although trap structure and the way it was operated remained similar across tuna traps and through time, the lack of detailed quantitative data on fishing effort prevents distinguishing the effects of potential changes in fishing effort. Thus, these interpretations should be considered as tentative and subject to refinement as new evidence becomes available. Temperature also plays a key role in shaping plankton dynamics, influencing both production and distribution (e.g. McGowan et al. 1998, Beaugrand et al. 2002). Our results suggest that cooler conditions during the late LIA could have enhanced trophic productivity, increased tuna availability, and potentially catch rates in the Western Mediterranean. Similar patterns have been observed for Pacific bluefin tuna, where SST is a stronger driver of recruitment than spawning stock biomass, likely due to its influence on juvenile habitat suitability (Muhling et al. 2018). Temperature-driven changes in plankton propagate through the food web, altering prey availabil-

ity and influencing tuna migration (Mather et al. 1995, Ravier and Fromentin 2004).

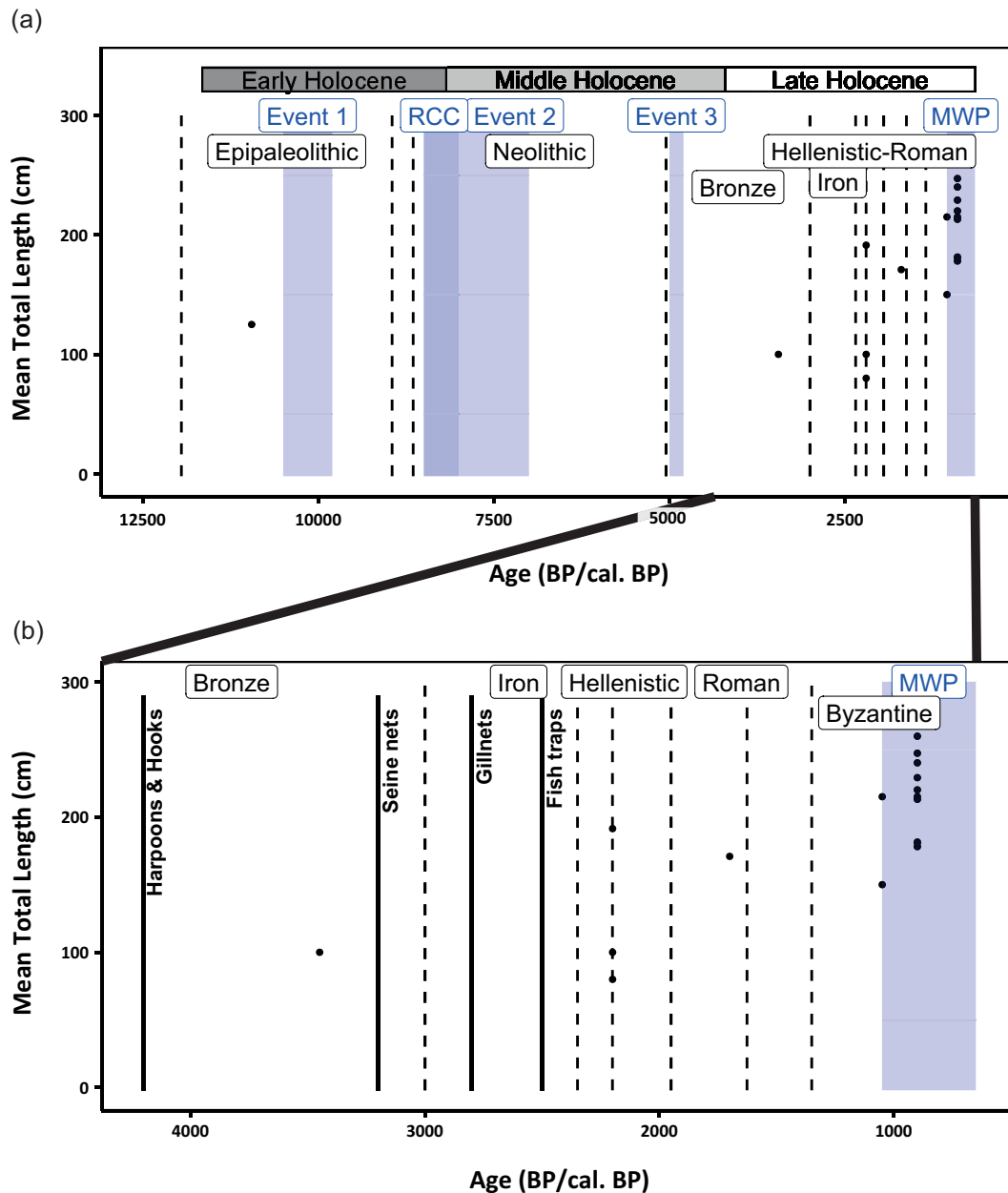
We also observed an increase in TL of Atlantic bluefin tuna during the late LIA. The size estimates are based on archaeological vertebrae measurements, which were analysed using a standardized approach to estimate fork length (FL) across all samples by the same author (Andrews et al. 2021, 2022, 2023a, 2023b, 2023c). To ensure comparability among species and periods, we converted FL to TL using length–length regressions, thereby improving interperiod comparisons of BS estimates. The observed increase in TL is in line with cooler conditions, improved feeding opportunities, and altered migration patterns that may have concentrated larger individuals in the region. This aligns with the species’ recruitment lag (Santamaria et al. 2009), explaining the delayed increase in adult abundance and TL. However, fixed tuna traps may exhibit inherent size selectivity, potentially underrepresenting smaller individuals or influencing the maximum size retained; hence, tuna traps’ size selectivity cannot be excluded as a contributing factor to observed size trends.



Although warmer conditions can enhance consumer–resource interactions (Allen et al. 2005, López-Urrutia et al. 2006, O’Connor 2009), the increase in TL under cooler SST suggests indirect effects, such as enhanced trophic productivity or greater adult retention, played a key role. The species’ broad dietary niche (Olesen and Jordano 2002, Pardo et al. 2025) likely supported adaptation to shifting prey fields, while cooler, more productive conditions may have improved larval growth and survival (García et al. 2006, Catalán et al. 2011, Reglero et al. 2018, Trueman et al. 2023). Consistent with other Mediterranean fish (Hattab et al. 2021), larger BZs under colder temperatures indicate that long-lived top predators like the Atlantic bluefin tuna (Santamaria et al. 2009) may deviate from general patterns due to their complex ecological responses (Fromentin and Powers 2005).

Although absolute changes cannot be fully separated from varying harvesting effort and detectability across historical periods, this study provides valuable insights into long-term trends in species abundance and BS in the Mediterranean Sea linked to human exploitation, supported by historical and ethnographic records of traditional practices (Galili et al. 2013, De Nicolò 2018, Lucchetti et al. 2023).

According to our results, the harvesting of the banded-dye murex was higher in the LH, particularly in the Roman Period (Oliver 2015), than in the other two geological periods. Although the overall sample size is limited ( $n < 30$ ), due to site preservation, taphonomic processes, and recovery protocols—which constrain

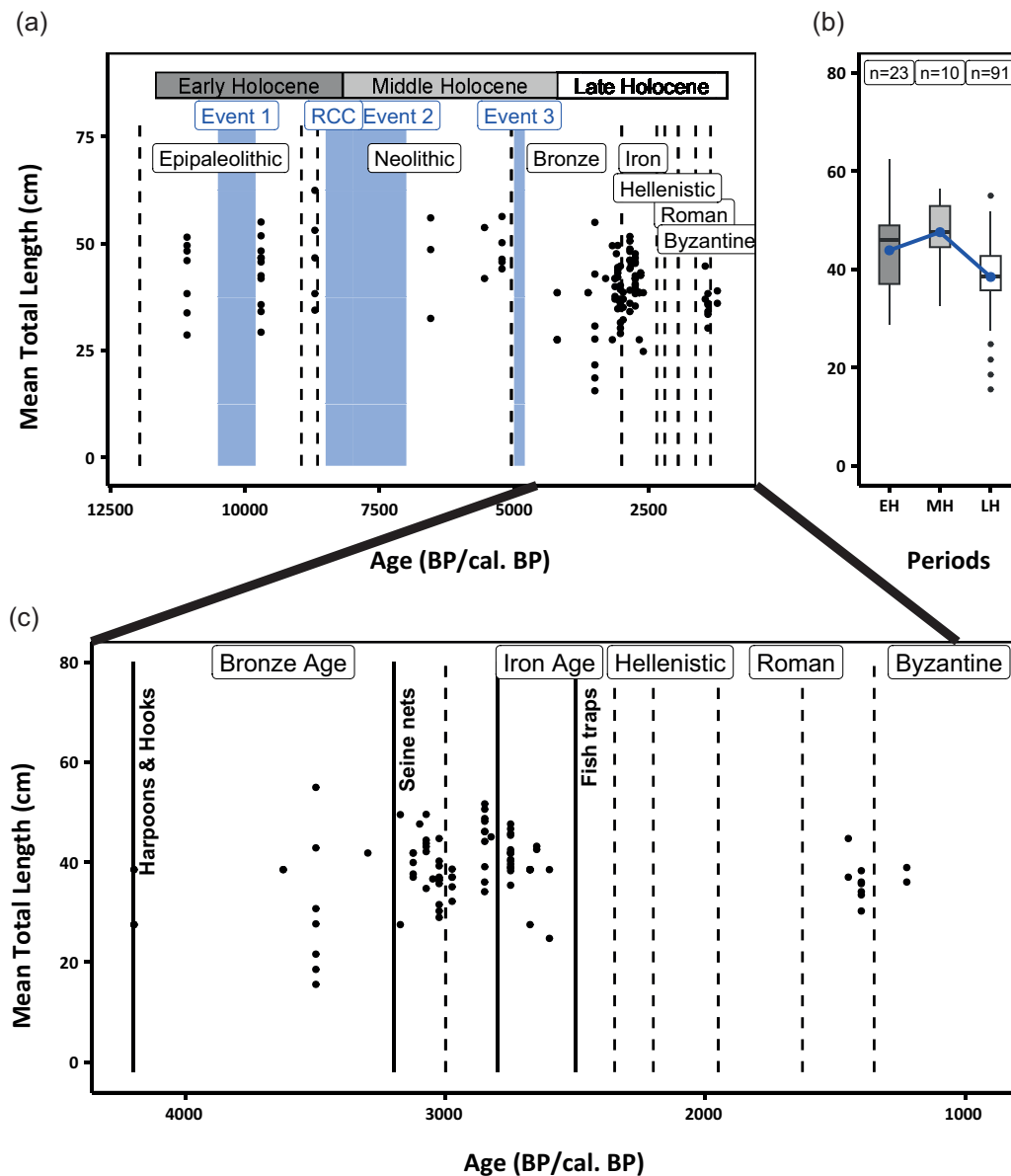


**Figure 5** Distribution of TL data for Atlantic bluefin tuna in the Eastern Mediterranean ( $n = 27$ ). (a) Temporal distribution of records, including major climatic events and anthropogenic periods. Holocene Events 1 (10 500–9800 yr BP), 2 (8000–7000 yr BP) and 3 (5000–4800 yr BP) refer to cooling episodes (Lionello et al. 2023); (b) LH distribution of records, with vertical lines indicating the main fishing technologies used during the period.

the statistical robustness of the analyses—the results provide meaningful evidence of differential harvesting pressure across time and may partly reflect differences in detectability. This is a shallow-shelf species that lives between 1 and 100 m (Fischer et al. 1987, Terlizzi et al. 1999), which made it easily accessible to early communities (Bonanno et al. 2016, Fernández-López De Pablo and Gabriel 2016) and later enabled large-scale exploitation for purple dye production (Michel and McGovern 1987, Oliver 2015). Shellfish provided a stable, year-round food resource, supporting coastal populations during periods of environmental stress or resource scarcity (Erlandson 1988, Colonese et al. 2011). However, this accessibility could have also made them vulnerable to over-exploitation, especially with the rise of industrial dye production

(Michel and McGovern 1987, Erlandson et al. 2008, Oliver 2015). These dynamics potentially illustrate the duality of shellfish as both resilient resources and indicators of human-induced ecosystem change.

The long-term decline in Atlantic bluefin tuna abundance likely reflects sustained fishing pressure (Polanco-Martínez et al. 2018; this study). Traditional tuna traps, once considered sustainable (De la Serna et al. 2012, Longo 2012), were gradually replaced by industrial technologies (e.g. iron anchors, steel cables; Lentini 2001), and steam-powered gears; Joseph 2003), which enabled large-scale exploitation and contributed to the stock collapse (Andrews et al. 2022). Removing top predators can destabilize food webs through top-down effects (Pauly et al. 1998, Scheffer et al.



**Figure 6** Distribution of TL data for gilthead sea bream in the Eastern Mediterranean ( $n = 91$ ). (a) Temporal distribution of records, including major climatic events and anthropogenic periods. Holocene Events 1 (10 500–9800 yr BP), 2 (8000–7000 yr BP), and 3 (5000–4800 yr BP) refer to cooling episodes (Lionello et al. 2023); (b) Boxplots of TL data for each geological period: EH, MH, and LH. Mean values and standard deviation are also indicated. Letters denote statistically significant differences. Sample sizes ( $n$ ) are shown above each boxplot; (c) LH distribution of records, with vertical lines indicating the main fishing technologies used during the period.

2005). Although direct evidence of trophic cascades involving tuna in the Mediterranean Sea is limited, isotopic and archaeological data suggest shifts in its trophic ecology during historical periods (Andrews et al. 2022, 2023c), altering predator-prey dynamics. Ecopath models from the Catalan Sea confirm these findings, showing food web restructuring following the loss of top and intermediate trophic-level species (Forrestal et al. 2012), consistent with broader patterns in the Mediterranean (Stergiou et al. 2009) and the North Sea (Mariani et al. 2017).

Although this work did not yield significant results for the turbinate monodont, its inclusion remains relevant for understanding its long-term importance in the Mediterranean coastal

setting. The absence of significant trends in past abundance and size patterns may be linked to limited sample sizes across periods and subregions, or it may reflect relatively stable exploitation processes over time. Archaeological evidence highlights the historical importance of this species as a subsistence resource among hunter-gatherer communities (Colonese et al. 2018), and it has been widely used to reconstruct shellfish exploitation seasonal patterns in past communities (Branscombe et al. 2021). Even in the absence of detectable long-term biological change, the turbinate monodont provides valuable insights into historical coastal resource use in the Mediterranean Sea.



## Changes in body size

Overexploitation may have contributed to the reduction in BS of gilthead sea bream from the early to the LH, particularly between the Bronze and Iron Age and the Byzantine Period. In contrast, Atlantic bluefin tuna results showed the opposite trend, with increasing BSs from the Roman Period through the MWP and the LIA.

Historical records show declining tuna landings in the Gulf of Cadiz between the mid-sixteenth and eighteenth centuries (Sarmiento 1757), likely due to juvenile overfishing and habitat degradation (García 2006). However, tuna BS increased during the MWP and LIA, possibly reflecting demographic shifts in the individuals reaching the fishing grounds. Local depletion of juveniles and smaller individuals could have led to a higher contribution of larger, transient individuals displaced from other Mediterranean areas, which were then caught in these tuna traps. Similar long-term effects have been documented in Baltic cod, with larger individuals in the Neolithic (~4500 yrs BP) compared to modern specimens (Limburg et al. 2008). From the Iron Age onward, the adoption of fish traps (Mylona 2021) and later industrial gears, such as purse seines, marked a shift to large-scale fisheries, likely influencing tuna BS across the basin.

Gilthead sea bream showed signs of increased fishing pressure in the Eastern Mediterranean during the LH, especially from the Bronze Age to the Byzantine period, with a marked decline in BS (Guy et al. 2018; this study). Similar trends have been observed in other sparids, such as *Archosargus probatocephalus*, under long-term fishing pressure (Guiry et al. 2021). Zooarchaeological records from Orkney (Scotland) also reveal offshore overfishing of large cod between the eleventh and thirteenth centuries, followed by declines in abundance and size (Harland and Barrett 2012). The shift to industrial-scale, less selective fishing gear (Galili et al. 2013) likely reinforced these reductions. Size-selective harvesting can alter trophic interactions and reduce ecosystem resilience (Shackell et al. 2010, García et al. 2012), underscoring the long-term ecological consequences of sustained exploitation.

## Limitations

While this study provides valuable insights, several limitations must be acknowledged. Our analyses focused on data-rich, historically and economically relevant species, potentially overlooking less-studied taxa and broader ecosystem dynamics. Data scarcity, particularly in the Adriatic Sea, reflects the uneven availability of published records (Leal et al. 2025a). Most data originate from coastal archaeological sites, which may bias the representation of past exploitation patterns (Leal et al. 2025a, Galili and Rosen 2008). Additional constraints include variability in dating, BS measurements, and taphonomic preservation, which limit the accuracy of past population reconstructions and interperiod comparability (Agiadi et al. 2024a, 2024b). Moreover, uncertainty regarding the fishing gear used, temporal variation in catch intensity, and differences in gear selectivity may have influenced the size and age composition of the catches recorded in the archaeological and historical records. Changes in fishing technology and effort through time could have affected the observed trends independently of anthropogenic and environmental drivers (Harley et al. 2001). The exclusion of non-peer-reviewed sources, such as log-

books or diaries, introduces further biases (Agiadi et al. 2024a). Despite these limitations, our study advances the understanding of how environmental variability and human activities have shaped key Mediterranean marine species over long timescales. Emerging techniques, such as ancient (aDNA) and sedimentary ancient DNA (sedaDNA), offer promising avenues for higher resolution reconstructions of paleoecological conditions and ecosystem dynamics (De Schepper et al. 2019, Monk et al. 2021, Kjær et al. 2022).

## Conclusions

This study underscores the importance of adopting long-term perspectives to explore changes in the marine ecosystem. Our findings suggest that both environmental and human factors may have influenced Atlantic bluefin tuna, while banded-dye murex and gilthead sea bream exhibit trends consistent with sustained exploitation. However, the absence of resolved data on fishing and gathering effort and catch intensity limits our ability to disentangle the relative contribution of anthropogenic and environmental drivers. Although no significant long-term trends were detected for the turbinate monodont, its documented role in coastal subsistence strategies among historical communities reinforces the importance of incorporating archaeological evidence when assessing past human–environment interactions. Rather than establishing direct causation through our results, this study highlights the importance of integrating paleoecological, archaeological, and historical records to reconstruct high-resolution temporal datasets while explicitly acknowledging their inherent caveats. Understanding these historical ecosystem dynamics helps the ongoing discussion regarding the interpretation of “shifting baselines” (Pauly et al. 1998). This integrative framework provides a foundation for future research aiming to refine historical high-resolution datasets and inform adaptive management of Mediterranean marine ecosystems.

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## Author contributions

Daniela Leal (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Funding acquisition [lead], Methodology [equal], Writing—original draft [equal]), Konstantina Agiadi (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Supervision [equal], Writing—review & editing [equal]), Marta Coll (Funding acquisition [equal], Methodology [equal], Writing—review & editing [equal]), Maria Bas (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Supervision [equal], Writing—review & editing [equal]).

## Supplementary material

Supplementary material is available at [ICES Journal of Marine Science](#) online.

## Conflicts of interests

The authors declare that there are no conflicts of interest.

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## Data availability

All data produced for this work are available within the manuscript and in the Supplementary material.

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