Potential and limitations of applying the mean temperature approach to fossil otolith assemblages

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Abstract Evaluation of the impact of climatic changes on the composition of fish assemblages requires quantitative measures that can be compared across space and time. In this respect, the mean temperature of the catch (MTC) approach has been proven to be a very useful tool for monitoring the effect of climate change on fisheries catch. Lack of baseline data and deep-time analogues, however, prevents a more comprehensive evaluation. In this study, we explore the applicability of the mean temperature approach to fossil fish faunas by using otolith assemblage data from the eastern Mediterranean and the northern Adriatic coastal environments corresponding to the last 8000 years (Holocene) and the interval 2.58–1.80 Ma B. P. (Early Pleistocene). The calculated mean temperatures of the otolith assemblage (MTO) range from 13.5 to 17.3 °C. This case study shows that the MTO can successfully capture compositional shifts in marine fish faunas based on variations in their climatic affinity driven by regional climate differences. However, the index is sensitive to methodological choices and thus requires standardized sampling. Even though theoretical and methodological issues prevent direct comparisons between MTO and MTC values, the MTO offers a useful quantitative proxy for reconstructing spatial and temporal trends in the biogeographic affinity of fossil otolith assemblages.

Keywords Mean temperature of the catch · Fossil · Climate change · Baselines · Historical ecology · Conservation paleobiology

Introduction

Fish move to higher latitudes and deeper waters in response to climate change (Chaikin et al. 2022; Last et al. 2011; Parmesan and Yohe 2003), but the absence of baselines that precedes climate warming and other major human pressures prevents us from realizing the full magnitude of these changes. Such pre-industrial baseline datasets are often lacking in most marine ecosystems, but information can be extracted from multiple alternative sources such as historical fishers’ logbooks, museum collections, and the archeological and fossil record (Kidwell 2015; Kosnik and Kowalewski 2016). In particular, the most recent (Holocene and Pleistocene) fossil record...
surface death assemblages (skeletal remains accumulating on the seabed) are proving precious for assessing the pre-human natural variability in the composition of marine faunas, and thus quantifying major shifts in their structure and functioning (e.g., Albano et al. 2021; Kowalewski et al. 2015; Steger et al. 2021; Tomašových et al. 2020; Tomašových and Kidwell 2017). Fossil assemblages, deposited, and buried within sediments (Fig. 1) are time-averaged images of past faunas, and they offer the only direct source of information on how the ecosystem operates in extreme climate states or climatic transitions. On the other hand, death assemblages of skeletal remains (such as fish bones, otoliths, scales, teeth) are recovered from the sediments currently accumulating on the surface of the seabed; Fig. 1) and are also time-averaged over decades to millennia, thereby capturing the communities from the recent past and reflecting active processes. They can, therefore, serve as baselines for comparison with the present-day fauna.

Fish sagittal otoliths (herein simply referred to as “otoliths”), the incremental and aragonitic biomineralisates in the inner ear of teleost fishes, have species-specific morphology that enables species-level identification (Nolf 1985) as well as estimation of important traits such as body size (Edelist 2014). Otolith death and fossil assemblages preserved in marine sediments enable reconstructing long-term changes of fish assemblages. Recent studies on the Holocene and Pleistocene marine fish faunas based on otolith death assemblages forming on the seabed (Agiadi and Albano 2020; Elder et al. 1996; Gaemers and Vorren 1985; Jones and Checkley 2019; Lin et al. 2019, 2018, 2017, 2016; Schwarzhans 2013) or derived from tectonically uplifted marine sediments (Agiadi et al. 2019, 2018; Aguilera and Aguilera 1999; Girone et al. 2006; Girone and Varola 2001; Schwarzhans and Ohe 2019) have shown that the required pre-industrial baseline data

![Fig. 1 Schematic model of the pathways leading to the formation of death and fossil otolith assemblages: Otoliths are input to the seabed through the disintegrated fish skeletons or the feces of their predators, where they suffer taphonomic alteration and mixing due to the action of currents and borrowing animals. The otolith assemblages collected from the uppermost part of the seabed constitute death assemblages. After these otoliths have been buried and are no longer actively mixed — although they may still undergo chemical alteration — they finally form fossil assemblages. Tectonic uplift brings these sediments, and the fossil assemblages within them, to the surface and allows us to study them on land.](image-url)
and past analogues of biotic responses to climate warming are within our reach.

A robust tool for easily monitoring the effect of climate warming on global fisheries is the mean temperature of the catch (MTC) index (Cheung et al. 2013). The MTC is the biomass or abundance-weighted mean temperature of the fisheries catch in a given area, based on the average preferred temperature of the exploited species that was inferred through species-distribution modeling (Cheung et al. 2013). An increase in the value of this index is considered to reflect the shift of species distributions to higher latitudes due to warming, leading to a change in the composition of the catch (Cheung et al. 2013). Although the MTC index completely relies on the availability and quality of fisheries catch data, it has been successfully applied to detect the impact of climate change on marine fisheries around the world (e.g., Dimarchopoulou et al. 2021; Fortibuoni et al. 2015; Gianelli et al. 2019; Leitão et al. 2018; Liang et al. 2018; Maharaj et al. 2018; Pauly and Liang 2020; Stergiou et al. 2016), even using archaeological data (Hillis et al. 2022).

In search of pre-industrial baseline data, we explore the applicability of the mean temperature approach to otolith death and fossil assemblages. We define here the mean temperature of otolith assemblages (MTO), in analogy to the MTC, as the mean inferred temperature preference of the species in an otolith assemblage weighted by their relative abundance. Does the MTO capture regional differences in climatic conditions that are expected to have an impact on the composition of the fish faunas? To address this question for the Mediterranean Sea, we use the otolith assemblage data derived from two areas in the eastern Mediterranean and one in the northern Adriatic Sea (Fig. 2a). The (paleo) environmental conditions at each locality are presented in Table 1, and the species’ abundances in the otolith assemblages are shown in Table 2.

Material and methods

The fossil and death assemblage otolith data derive from two areas in the eastern Mediterranean and one in the northern Adriatic Sea (2.58–1.80 Ma B. P., Early Pleistocene, Quaternary) that have been tectonically uplifted and form today the cliffs and beaches of the northeastern coast of the island of Rhodes (southeastern Aegean, Greece; Cornée et al. 2019). The fossil otoliths were recovered from the sediment by wet-sieving (250-μm mesh), identified and counted. Two localities were sampled: Kritika North (level KN6) and Faliraki South (levels FS2 and FS3; Fig. 2b). The depositional environment is siliciclastic, corresponding to infralittoral–upper circalittoral settings with water depths down to 60 m, various substrata, and mostly subtropical climatic conditions (Table 1; Agiadi et al. 2019; Moissette et al. 2016). However, it is not possible to obtain an improved dating and time-constraint on these deposits, because the necessary stratigraphic evidence (i.e., bioevents, datable volcanic ash layers) are lacking.

Otolith death assemblage material was obtained in 2016 by sampling the surficial sea-bottom sediments along a 10–40-m-depth gradient off the Mediterranean coast of Israel (Fig. 2c). Five replicate Van Veen grab samples were obtained at three stations (SG10, SG30, and S40). The sediment samples were wet-sieved with 0.5-mm and 1-mm mesh, and the otoliths were isolated and identified. A random selection of otoliths from benthic and pelagic species was radiocarbon dated (details available in Agiadi et al. 2021; Agiadi and Albano 2020; and Albano et al. 2020). The otoliths range in post-mortem age from ~8000 years B. P. to the time of sampling, with the median age of 559 years and an inter-quartile range (a common measure of time-averaging, which
Fig. 2 Origin of the otolith fossil and death assemblages. (a) Map of the Mediterranean area indicating the locations of Rhodes Island and the Israeli coast. (b) Simplified geological map of Rhodes Island (modified from Quillévéré et al. 2016) with the locations where the fossiliferous sediments appear and were sampled for this study. (c) Bathymetric map of the Mediterranean coast of Israel with the locations of the four stations where the sea-bottom sediment grab samples were obtained. (d) Map of the northern Adriatic indicating the sampling station location at the coast of Piran, Slovenia.
reflects the degree of temporal mixing of a death assemblage within a sedimentary bed) of 1097 years (Agiadi and Albano 2020). Taphonomic examination revealed no differences in the preservation of otoliths with different shapes or from fishes with different lifestyles (pelagic versus demersal fishes; Agiadi et al. 2021). Given that their median age exceeds 500 years, these Holocene death assemblages can be considered representative of the pre-industrial fish fauna in this area (Agiadi and Albano 2020).

In the northern Adriatic Sea (Gulf of Trieste), otolith death assemblages were recovered from two Van Veen grab samples taken at 22.7-m depth at station Piran 2 (PIR2; Tomašových et al. 2018) located ~4 km north of the coast of Piran, Slovenia (Fig. 2d). The sediment samples were sieved only at 1-mm mesh in this case. The study area was flooded about 9500 years B. P., and the present-day sea level stabilized around 2000–3000 years ago (Amorosi et al. 2008). Today, the area is oligophotic with a skeletal muddy sand substratum, but until the nineteenth century, it was part of a euphotic hard-bottom oyster and *Arca noae* banks zone close to soft-bottom vegetated habitats that dominated the central part of the Gulf of Trieste (Mautner et al. 2018; Tomašových et al. 2018). Precise ages are not available for the otoliths in the grab samples. However, otoliths sampled from a core 20–30 cm below the surface of the seabed have been radiocarbon dated and are up to ~7600 years old (Nawrot et al. 2022). As the sediment at the station is well-mixed by deep-borrowing animals, we consider that the age range of the otoliths captured by the grabs encompasses the last ~7600 years as well.

We considered only otolith assemblages with at least ~50 specimens in the analysis (Fig. 2). From the analyzed samples, we excluded otoliths that were too poorly preserved. We calculated MTO for the entire otolith assemblages and for the pelagic and demersal components separately. In the case of the Holocene death assemblages from the eastern Mediterranean, we calculated MTO with and without the Lessepsian species, i.e. the non-indigenous species that have entered the Mediterranean from the Red Sea since the opening of the Suez Canal in 1869. Finally, the otolith assemblages used to calculate MTO had been obtained by wet-sieving sediment samples using different mesh sizes. In order to check if this difference in sample processing had an effect on the calculated MTO, we calculated the values separately for all otoliths in a given sample and only for those >1 mm. This procedure was only possible for the 30-m-depth station in Israel, which had been sieved with both 0.5- and 1-mm meshes and contained enough otoliths in the larger sieve fraction for a meaningful comparison.

The MTC index is calculated for exploited fishes (Cheung et al. 2013), which generally occupy the euphotic zone. However, death and fossil assemblages capture fishes living in the entire water column that have died and their otoliths were deposited together on the seabed; the composition and species abundances in these accumulations of dead remains are controlled by the species-specific natural mortality and taphonomic processes (Agiadi et al. 2021). This also means that sediments deposited at greater depths include epipelagic fishes, as well as mesopelagic and deep-water fishes, whose inferred preferred temperatures are significantly lower than those of the surface-water fishes of the same area, simply because they live deeper in the water column. Consequently, any meaningful comparison should be made between
| Family          | Species                        | SG10 (>0.5) | SG30 (>0.5) | SG30 (>1) | SG40 (>0.5) | PIR 2 (>1) | FS2 (>0.25) | FS3 (>0.25) | KN6 (>0.25) |
|-----------------|--------------------------------|--------------|--------------|-----------|--------------|-------------|--------------|--------------|--------------|
| Congridae       | *Ariosoma balearicum*          | 19           | 5            | 11        | 1            |             |              |              |              |
| Congridae       | *Conger conger*                | 4            | 2            | 3         | 1            |             |              |              |              |
| Congridae       | *Panturichthys sp.*            | 1            |              | 2         |              |             |              |              |              |
| Engraulidae     | *Engraulis encrasiculus*       | 19           | 135          | 17        | 1            | 1            |              |              |              |
| Clupeidae       | *Sardinia pilchardus*          | 2            |              |           |              |             |              |              |              |
| Clupeidae       | *Sardinella aurita*            | 1            | 2            | 1         |              |             |              |              |              |
| Clupeidae       | *Sardinella maderensis*        | 1            |              | 4         |              |             |              |              |              |
| Clupeidae       | *Sardinella sp.*               |              |              |           |              |             |              |              | 1            |
| Clupeidae       | *Clupeidae indet*              | 1            |              |           |              |             |              |              |              |
| Gobionomatidae  | *Cyclothone braueri*           | 1            |              |           |              |             |              |              |              |
| Phosichthyidae  | *Vinciguerra poweriae*         |              |              |           |              |             |              |              |              |
| Synodontidae    | *Saurida undosquamis*          | 1            |              |           |              |             |              |              |              |
| Myctophidae     | *Ceratoscopelus maderensis*    |              |              |           |              | 1            |              |              |              |
| Myctophidae     | *Diaphus sp.*                  |              | 6            | 6         | 1            |             |              |              |              |
| Bregmacerotidae | *Bregmaceros nectabanus*       |              |              |           |              | 2            |              |              |              |
| Gadidae         | *Phycis blennoides*            |              |              |           |              | 2            |              |              |              |
| Carapidae       | *Carapus acus*                 |              |              |           | 13           | 1            |              |              |              |
| Ophidiidae      | *Ophidion barbatum*            |              |              |           |              | 11           |              |              |              |
| Ophidiidae      | *Ophidion rochi*               | 3            |              | 1         |              |             |              |              |              |
| Bythitidae      | *Grammonus ater*               |              |              |           |              | 1            |              |              |              |
| Apogonidae      | *Apogon imberbis*              | 1            | 2            |           |              |              |              |              |              |
| Apogonidae      | *Apogon sp.*                   | 1            |              | 4         | 12           |              |              |              |              |
| Pomacentridae   | *Chromis chromis*              | 2            |              | 1         | 7            | 19           |              |              |              |
| Gobiidae        | *Amblygobius albimaculatus*    | 1            |              | 2         |              |              |              |              |              |
| Gobiidae        | *Aphia minuta*                 | 1            | 3            | 1         |              |              |              |              |              |
| Gobiidae        | *Callogobius sp.*              |              |              |           | 3            |              |              |              |              |
| Gobiidae        | *Chromogobius zebratus*        | 2            |              | 1         | 10           | 31           |              |              |              |
| Gobiidae        | *Gobiodae indet. A*            | 7            |              |           |              | 1            |              |              |              |
| Gobiidae        | *Gobiodae indet. B*            |              |              |           |              | 18           | 4            |              |              |
| Gobiidae        | *Gobius auratus*               | 2            | 2            | 1         |              |              |              |              |              |
| Gobiidae        | *Gobius bucchichi*             |              | 7            |           |              |              |              |              |              |
| Gobiidae        | *Gobius cobitis*               | 1            | 10           | 5         | 1            |              |              |              |              |
| Gobiidae        | *Gobius couchi*                |              |              |           | 4            |              |              |              |              |
| Family         | Species                      | SG10 (> 0.5) | SG30 (> 0.5) | SG30 (> 1) | SG40 (> 0.5) | PIR 2 (> 1) | FS2 (> 0.25) | FS3 (> 0.25) | KN6 (> 0.25) |
|---------------|------------------------------|--------------|--------------|------------|--------------|-------------|--------------|--------------|--------------|
| Gobiidae      | *Gobius geniporus*           |              |              |            |              |             |              |              |              |
| Gobiidae      | *Gobius niger*               |              |              |            |              |             |              |              |              |
| Gobiidae      | *Gobius paganellus*          | 1            | 4            | 21         | 1            | 28          |              |              |              |
| Gobiidae      | *Gobius sp.A*                | 74           | 12           |            |              |             |              |              |              |
| Gobiidae      | *Gobius sp.B*                |              |              |            |              |             |              |              |              |
| Gobiidae      | *Gobius vittatus*            |              |              |            |              |             |              |              |              |
| Gobiidae      | *Deltentosteus quadrimaculatus* |              |              |            |              |             |              |              |              |
| Gobiidae      | *Lesueurigobius friesii*     | 26           | 1            | 13         |              | 2           |              |              |              |
| Gobiidae      | *Lesueurigobius sanzi*       |              |              |            |              |             |              |              |              |
| Gobiidae      | *Lesueurigobius sp.*         | 7            | 1            |            |              |             |              |              |              |
| Gobiidae      | *Lesueurigobius swerii*      |              |              |            |              |             |              |              |              |
| Gobiidae      | *Oxyurichthys petersii*      | 4            |              |            |              |             |              |              |              |
| Gobiidae      | *Pomatoschistus marmoratus*  | 2            |              |            |              |             |              |              |              |
| Gobiidae      | *Thorogobius macrolepis*     | 6            | 2            | 2          |              |             |              |              |              |
| Gobiidae      | *Zebrus zebrus*              |              |              |            |              |             |              |              |              |
| Atherinidae   | *Atherina sp.*               |              |              |            |              |             |              |              |              |
| Belonidae     | *Tylosurus sp.*              | 1            |              |            |              |             |              |              |              |
| Carangidae    | *Trachurus mediterraneus*    | 1            |              |            |              |             |              |              |              |
| Carangidae    | *Trachurus sp.*              |              |              |            |              |             |              |              |              |
| Citharidae    | *Citharus linguaula*         | 3            |              |            |              |             |              |              |              |
| Scophthalmidae| *Scophthalmus rhombus*       | 1            |              |            |              |             |              |              |              |
| Bothidae      | *Arnoglossus laterna*        | 2            |              |            |              |             |              |              |              |
| Bothidae      | *Arnoglossus rueppelli*      |              |              |            |              |             |              |              |              |
| Bothidae      | *Arnoglossus sp.*            |              |              |            |              |             |              |              |              |
| Soleidae      | *Microchirus ocellatus*       |              |              |            |              |             |              |              |              |
| Soleidae      | *Solea solea*                | 1            |              |            |              |             |              |              |              |
| Cynoglossidae | *Symphurus nigrescens*       |              |              |            |              |             |              |              |              |
| Callionymidae | *Callionymus filamentosus*   |              |              |            |              |             |              |              |              |
| Trachinidae   | *Trachinus draco*            | 1            |              |            |              |             |              |              |              |
| Mullidae      | *Mullus barbatus*            |              |              |            |              |             |              |              |              |
| Mullidae      | *Mullus surmuletus*          |              |              |            |              |             |              |              |              |
| Family          | Species                  | SG10 (> 0.5) | SG30 (> 0.5) | SG30 (> 1) | SG40 (> 0.5) | PIR 2 (> 1) | FS2 (> 0.25) | FS3 (> 0.25) | KN6 (> 0.25) |
|-----------------|--------------------------|--------------|--------------|------------|--------------|-------------|-------------|-------------|-------------|
| Mullidae        | *Upeneus pori*           | 1            |              |            |              |             |             |             |             |
| Serranidae      | *Serranus sp.*           |              |              |            |              |             |             |             |             |
| Haemulidae      | *Pomadasys incisus*      |              |              |            |              |             |             |             |             |
| Cepolidae       | *Cepola macrophthalma*   |              |              |            |              |             |             |             |             |
| Scorpaenidae    | *Scorpaena sp.*          |              |              |            |              |             |             |             |             |
| Triglidae       | *Chelidonichthys lastoviza* |          |              |            |              |             |             |             |             |
| Triglidae       | *Chelidonichthys lucerna* |              |              |            |              |             |             |             |             |
| Sciaenidae      | *Umbrina cirrosa*        |              |              |            |              |             |             |             |             |
| Sparidae        | *Boops boops*            |              |              |            |              |             |             |             |             |
| Sparidae        | *Dentex dentex*          |              |              |            |              |             |             |             |             |
| Sparidae        | *Dentex macrphthalma*    |              |              |            |              |             |             |             |             |
| Sparidae        | *Dentex maroccanus*      |              |              |            |              |             |             |             |             |
| Sparidae        | *Diplodus annularis*     |              |              |            |              |             |             |             |             |
| Sparidae        | *Diplodus sp.*           |              |              |            |              |             |             |             |             |
| Sparidae        | *Pagellus acarne*        |              |              |            |              |             |             |             |             |
| Sparidae        | *Pagellus bogaraveo*     | 1            |              |            |              | 12          | 10          |             |             |
| Sparidae        | *Pagellus erythrinus*    | 1            |              |            |              |             |             |             |             |
| Sparidae        | *Pagellus sp.*           | 1            |              |            |              |             |             |             |             |
| Sparidae        | *Spicara flexuosa*       |              |              |            |              |             |             |             |             |
| Sparidae        | *Spicara maena*          |              |              |            |              |             |             |             |             |
| Sparidae        | *Spicara smaris*         | 2            | 10           | 1           |              | 2           | 4           |             |             |
| Sparidae        | Sparidae indet          | 2            |              | 1           |              |             |             |             |             |
| Sparidae        | Sparidae indet          | 2            |              | 1           |              |             |             |             |             |
| Perciformes indet | Perciformes indet     |              |              |            |              |             |             |             |             |
assemblages from similar water depths. Based on the water depths and the estimated paleodeptths at the sampling sites (Table 1), all the samples in our case study originate from within the euphotic zone.

Our case study is based on the assumption that the fish species in our assemblages exhibited thermal niche conservatism (Ern et al. 2017; Wiens et al. 2010; Wood and McDonald 1997), i.e., they maintained the same temperature preferences as they do today. For the species of the fossil and death assemblages, we obtained the preferred temperature mean values and ranges from Aquamaps (Kaschner et al. 2016; Table 3). Previous studies for the Mediterranean using the MTC index (Keskin and Pauly 2018, 2014; Tsikliras et al. 2015; Tsikliras and Stergiou 2014) obtained the preferred temperatures from Cheung et al. (2013). However, Cheung et al. (2013) did not provide estimated values for all species found in our fossil and death assemblages. The preferred temperatures from Aquamaps differ from those modeled by Cheung et al. (2013). However, Cheung et al. (2013) demonstrated that the species distribution modeling approach used to estimate these preferred temperatures for each species does not affect the relationship between MTC and regional SST changes. For species whose preferred temperatures were unknown or where unidentifiable to species level, we used the values of the phylogenetically closely related species that is most abundant in the corresponding study area (Table 3).

In analogy to MTC, MTO was calculated as:

\[
MTO_a = \frac{\sum_i n_i T_i A_{ri,a}}{\sum_i n_i A_{ri,a}}
\]

where \(a\) is the assemblage, \(T_i\) is the preferred temperature of species \(i\), \(A_{ri,a}\) is the relative abundance of species \(i\) in assemblage \(a\), and \(n\) is the total number of species in assemblage \(a\). We estimated 95% bootstrap confidence intervals around the MTO values using the percentile method by resampling each assemblage with replacement 10,000 times and calculating MTO values for each iteration.

**Results**

The Holocene MTO values for the eastern Mediterranean (Israeli coast) range from 13.6 °C (at 40-m depth) to 17.3 °C (at 10-m depth), which are slightly higher than that from the northern Adriatic (Slovenia coast) of 13.5 °C for the 22.7-m depth (Table 4; Fig. 3). The Early Pleistocene MTO at FS2 and FS3 (13.8 and 14.0 °C, respectively), which correspond to 10–15-m depth, are lower than the Holocene eastern Mediterranean values at similar depths (17.3 °C at SG10). However, the fossil assemblage KN6 corresponding to the deepest level (40–60-m depth) gives an elevated MTO (14.1 °C) compared to both the shallower Pleistocene samples and the Holocene assemblage from the comparable water depth (SG40; 13.6 °C).

Removing the non-indigenous species from the SG30 and SG40 assemblages from Israel decreases the MTO (Table 4; blue in Fig. 3). However, the difference is very small and the MTO values based on native species alone are within 95% confidence intervals for the entire assemblage, suggesting that this reduction is not statistically significant. The MTO for SG30 is primarily driven by the high abundance of the native *Engraulis encrasicolus*, which together with the rarity of non-indigenous species may explain why exclusion of the latter has only a very limited effect on the MTO values. Although *E. encrasicolus* is the most abundant species also at SG40 (Table 2), the relative contribution of the tropical non-indigenous species (*Amblygobius albimaculatus* and *Bregmaceros nectabanus*) is greater at that site, and therefore their exclusion has a slightly higher impact on the MTO value.

Isolating the coarser component (>1 mm) of the SG30 assemblage makes it directly comparable to PIR2, which was only sieved under 1-mm mesh. Otoliths from the 1-mm fraction of SG30 give a significantly higher MTO value compared to the entire assemblage (all specimens >0.5 mm; Fig. 3). This pattern is clearly driven by the exclusion of the dominant *E. encrasicolus* (Table 2), which only appears in the fine fraction, and whose preferred temperature (10.8 °C) is well below the average values for the assemblages. Comparing the >1 mm component of SG30 with PIR2 drastically increases the difference between the MTO values for the eastern Mediterranean and the northern Adriatic otolith death assemblages making them more consistent with the sea surface temperature gradient between the two areas (Fig. 3).
| Species                          | Ecological data from | Annual preferred temperature (°C) | Status       | Lifestyle |
|---------------------------------|----------------------|-----------------------------------|--------------|-----------|
| Ariosoma balearicum             | Ariosoma balearicum  | 26.2                              | Native       | Demersal  |
| Conger conger                   | Conger conger        | 8.7                               | Native       | Demersal  |
| Panturichthys sp.               | Ariosoma balearicum  | 26.2                              | Native       | Demersal  |
| Engraulis encrasicolus          | Engraulis encrasicolus| 10.8                              | Native       | Pelagic   |
| Sardina pilchardus              | Sardina pilchardus   | 10.3                              | Native       | Pelagic   |
| Sardinella aurita               | Sardinella aurita    | 18.8                              | Native       | Pelagic   |
| Sardinella maderensis           | Sardinella maderensis| 21.0                              | Native       | Pelagic   |
| Sardinella sp.                  | Sardinella maderensis| 21.0                              | Native       | Pelagic   |
| Clupeidae indet                 | Sardinella maderensis| 21.0                              | Native       | Pelagic   |
| Cyclothone braueri              | Cyclothone braueri   | 9.3                               | Native       | Pelagic   |
| Vinciguerra poweriae            | Vinciguerra poweriae | 10.6                              | Native       | Pelagic   |
| Saurida undosquamis             | Saurida undosquamis  | 26.0                              | Native       | Demersal  |
| Ceratoscopelus maderensis       | Ceratoscopelus maderensis| 8.6                              | Native       | Pelagic   |
| Diaphus sp.                     | Diaphus rafinesquii  | 10.8                              | Native       | Pelagic   |
| Bregmaceros nectabanus          | Bregmaceros nectabanus| 23.7                              | Non-indigenous| Pelagic |
| Phycis blennoides               | Phycis blennoides    | 9.1                               | Native       | Pelagic   |
| Caranus acus                    | Caranus acus         | 19.4                              | Native       | Demersal  |
| Ophidion barbatum               | Ophidion barbatum    | 13.8                              | Native       | Demersal  |
| Ophidion rochei                 | Ophidion rochei      | 16.5                              | Native       | Demersal  |
| Grammonus ater                  | Grammonus ater       | 18.8                              | Native       | Demersal  |
| Apogon spp.                     | Apogon imberbis      | 16.3                              | Native       | Pelagic   |
| Chromis chromis                 | Chromis chromis      | 20.1                              | Native       | Demersal  |
| Amblygobius albimaculatus       | Amblygobius albimaculatus| 28.4                              | Non-indigenous| Demersal |
| Aphia minuta                    | Aphia minuta         | 10.8                              | Native       | Pelagic   |
| Callogobius sp.                 | Callogobius bifasciatus| 27.4                              | Non-indigenous| Demersal |
| Chromogobius zebratus           | Deltentosteus quadrimaculatus| 15.2                              | Native       | Demersal  |
| Deltentosteus quadrimaculatus   | Deltentosteus quadrimaculatus| 15.2                              | Native       | Demersal  |
| Gobiidae indet. A               | Gobius paganellus    | 17.7                              | Native       | Demersal  |
| Gobiidae indet. B               | Gobius niger         | 10.8                              | Native       | Demersal  |
| Gobius auratus                  | Gobius auratus       | 18.1                              | Native       | Demersal  |
| Gobius buccichii                | Gobius buccichii     | 18.5                              | Native       | Demersal  |
| Gobius cobitis                  | Gobius cobitis       | 18.0                              | Native       | Demersal  |
| Gobius couchi                   | Gobius couchi        | 12.1                              | Native       | Demersal  |
| Gobius geniporus                | Gobius geniporus     | 19.1                              | Native       | Demersal  |
| Gobius niger                    | Gobius niger         | 10.8                              | Native       | Demersal  |
| Gobius paganellus               | Gobius paganellus    | 17.7                              | Native       | Demersal  |
| Gobius vittatus                 | Gobius vittatus      | 18.4                              | Native       | Demersal  |
| Lesueurigobius friesi           | Lesueurigobius friesi| 10.4                              | Native       | Demersal  |
| Lesueurigobius sanzi            | Lesueurigobius sanzi | 17.1                              | Native       | Demersal  |
| Lesueurigobius sp.              | Lesueurigobius friesi| 10.4                              | Native       | Demersal  |
| Lesueurigobius suerii           | Lesueurigobius suerii| 14.7                              | Native       | Demersal  |
| Oxyurichthys petersii           | Oxyurichthys papuensis| 27.9                              | Non-indigenous| Demersal |
| Pomatoschistus marmoratus       | Pomatoschistus marmoratus| 15.1                              | Native       | Demersal  |
| Thorogobius macrolepis          | Gobius niger         | 10.8                              | Native       | Demersal  |
| Zebrus zebrus                   | Zebrus zebrus        | 19.3                              | Native       | Demersal  |
For the death assemblages from the Israeli shelf, the demersal fish MTO, particularly at SG10 (22.4 °C), is much higher than those derived from the pelagic component (12.2 °C at SG10; Fig. 4). This difference is driven by the high abundance of the demersal *Ariosoma balearicum* (Table 2) with a preferred temperature of 26.2 °C, which in fact dominates at SG10. On the other hand, in the very shallow fossil assemblages (FS2 and FS3 at paleodepths of 10–15 m), the MTO values from demersal and pelagic species are similar, whereas in the deepest assemblage (KN6 at paleodepth of 40–60 m), the

| Species                  | Ecological data from | Annual preferred temperature (°C) | Status     | Lifestyle  |
|--------------------------|----------------------|-----------------------------------|------------|------------|
| Atherina sp.             | *Atherina boyeri*     | 18.3                               | Native     | Pelagic    |
| Tylosurus sp.            | *Tylosurus acus*      | 26.5                               | Native     | Demersal   |
| Trachurus spp.           | *Trachurus mediterraneus* | 17.4                              | Native     | Pelagic    |
| Citharus linguatula      | *Citharus linguatula* | 15.2                               | Native     | Demersal   |
| Scophthalmus rhombus     | *Scophthalmus rhombus*| 11.2                               | Native     | Demersal   |
| Arnoglossus laterna      | *Arnoglossus laterna* | 10.8                               | Native     | Demersal   |
| Arnoglossus rupepellii   | *Arnoglossus rupepellii* | 14.2                             | Native     | Demersal   |
| Arnoglossus sp.          | *Arnoglossus laterna* | 10.8                               | Native     | Demersal   |
| Microchirus ocellatus    | *Microchirus ocellatus* | 17.1                              | Native     | Demersal   |
| Solea solea              | *Solea solea*         | 11.4                               | Native     | Demersal   |
| Symphurus nigrescens     | *Symphurus nigrescens*| 13.9                               | Native     | Demersal   |
| Callionymus filamentosus | *Callionymus filamentosus* | 24.0                          | Non-indigenous | Demersal   |
| Trachinus draco          | *Trachinus draco*     | 10.9                               | Native     | Demersal   |
| Mullus barbatus          | *Mullus barbatus*     | 14.2                               | Native     | Demersal   |
| Mullus surmuleatus       | *Mullus surmuleatus*  | 10.2                               | Native     | Demersal   |
| Upeneus pori             | *Upeneus pori*        | 25.6                               | Non-indigenous | Demersal   |
| Serranus sp.             | *Serranus cabrilla*   | 14.4                               | Native     | Demersal   |
| Pomadasys incisus        | *Pomadasys incisus*   | 23.1                               | Native     | Pelagic    |
| Cepola macrophtalma      | *Cepola macrophtalma* | 11.9                               | Native     | Demersal   |
| Scorpaena sp.            | *Scorpaena notata*    | 14.6                               | Native     | Demersal   |
| Chelidonichthys lastoviza| *Chelidonichthys lastoviza* | 11.8                          | Native     | Demersal   |
| Chelidonichthys lucerna  | *Chelidonichthys lucerna* | 9.8                              | Native     | Demersal   |
| Umbrina cirrosa          | *Umbrina cirrosa*     | 18.0                               | Native     | Pelagic    |
| Boops boops              | *Boops boops*         | 17.8                               | Native     | Pelagic    |
| Dentex dentex            | *Dentex dentex*       | 18.1                               | Native     | Pelagic    |
| Dentex macrophtalma      | *Dentex macrophtalma* | 14.9                               | Native     | Pelagic    |
| Dentex maroccanus        | *Dentex maroccanus*   | 13.5                               | Native     | Pelagic    |
| Diplodus spp.            | *Diplodus annularis*  | 18.3                               | Native     | Pelagic    |
| Pagellus acarne          | *Pagellus acarne*     | 14.8                               | Native     | Pelagic    |
| Pagellus bogaaraveo      | *Pagellus bogaaraveo* | 11.2                               | Native     | Pelagic    |
| Pagellus erythrinus      | *Pagellus erythrinus* | 17.2                               | Native     | Pelagic    |
| Pagellus sp.             | *Pagellus bogaaraveo* | 11.2                               | Native     | Pelagic    |
| Perciformes indet        | *Spicara smaris*      | 14.4                               | Native     | Pelagic    |
| Spicara flexuosa         | *Spicara flexuosa*    | 14.5                               | Native     | Pelagic    |
| Spicara maena            | *Spicara maena*       | 14.5                               | Native     | Pelagic    |
| Spicara smaris           | *Spicara smaris*      | 14.4                               | Native     | Pelagic    |
| Sparidae indet           | *Spicara smaris*      | 14.4                               | Native     | Pelagic    |
pelagic species give higher MTO values (Fig. 4), as expected for a site where the difference between surface and bottom water temperature is greater. The same difference between demersal and pelagic MTO is observed in PIR2 as well (Fig. 4), even though this station represents a much shallower water depth. However, the pelagic component at PIR2 comprises only 10 otoliths, many of which could not be identified to species level, so this pattern may be partly driven by sampling bias (Table 2).

**Discussion**

Our results demonstrate that the MTO can successfully capture regional variations in the composition of marine fish faunas related to climate differences, but they also point to several requirements and limitations of this approach. The MTO values calculated here for the Holocene and Pleistocene Mediterranean coastal fish assemblages range from 13.5 to 17.3 °C. As expected, based on the (paleo)climatic framework of the region (Castañeda et al. 2010; Crippa et al. 2016; Essallami et al. 2007; Giunta et al. 2001; Minnett et al. 2019), the highest MTO value corresponds to the shallowest (10-m depth) and southeastern-most site along the Mediterranean coast of Israel, whereas the lowest MTO value is recorded in the colder northern Adriatic Sea. With regard to the fossil otolith assemblages, although it is not possible to

![Fig. 3](image_url)  
**Fig. 3** Mean temperature of the otolith assemblages from the Holocene (the last ~8000 years) of the eastern Mediterranean (SG10, SG30, and SG40), the Holocene (the last ~7600 years) of the northern Adriatic Sea (PIR2), and the Early Pleistocene (2.58–1.8 Ma B. P.) of the eastern Mediterranean (FS2, FS3, and KN6). For SG30, we also calculated the MTO for only the assemblage of otoliths >1 mm. At 30- and 40-m depths of the Israeli coast (SG30 and SG40), where few non-indigenous species appear in the otolith assemblages, we also calculated the MTO for the assemblages without them (marked in blue). Bars indicate 95% bootstrapped confidence intervals. N: number of otolith specimens in the assemblage. Temperature estimates are sea surface temperature averages based on alkenone paleothermometry for each region and time interval (Adriatic Sea in the Holocene: (Giunta et al. 2001; Oldfield et al. 2003); Levantine Sea in the Holocene: (Avnaim-Katav et al. 2019; Castañeda et al. 2010; Essallami et al. 2007); Eastern Mediterranean in the Early Pleistocene (Athanasiou et al. 2017; Burke et al. 2018; Crippa et al. 2016; Lourens et al. 1992).
temporally constrain the Early Pleistocene samples further and directly link the otolith assemblages to specific climatic phases, their MTO range is small (13.8–14.1 °C; Table 4), especially considering the average sea surface temperature in the eastern Mediterranean during this interval (23 °C; Athanasiou et al. 2017; Burke et al. 2018; Crippa et al. 2016; Lourens et al. 1992). It is possible therefore that the observed Early Pleistocene MTO values correspond to the same type of climatic regime, specifically glacial periods. Alternatively, and despite the reconstructed shallow paleodepths of the seabed in the study area (Agiadi et al. 2019), the assemblages include species from deeper environments occasionally visiting the area, specifically mesopelagic myctophids (Table 2), which decreases the MTO.

Furthermore, the MTO is increased by the inclusion of Lessepsian species, as expected since these species are tropical and have very high preferred temperatures (Table 3). The eastern Mediterranean marine fauna is rapidly becoming more tropical due to climate change and the opening of the Suez Canal, which allows warm-water species from the Red Sea to enter into and establish populations in the basin (Edelist et al. 2013), while shifting the distribution of species preferring cooler temperatures to northern latitudes (Givan et al. 2018). In the Mediterranean, MTC based on landings has been found to increase between 1970 and 2010 by 0.56, 1.05, and 0.29 °C per decade in the western, central, and eastern sub-basins, respectively (Tsikliras and Stergiou 2014), by 0.25 °C per decade in the northeast Aegean (Keskin and Pauly 2014), by 1.01 °C, and 1.17 °C per decade for the Aegean and Ionian Seas, respectively (Tsikliras et al. 2015), and by 0.48 °C per decade in the northern part of the Levantine Sea (Keskin and Pauly 2018). These estimates were made without considering the non-indigenous tropical Lessepsian species, although they now constitute a significant proportion of the fish population, especially in the eastern Mediterranean (CIESM 2021; Edelist et al. 2013, 2011) and their inclusion in the calculation would probably have increased the estimated MTC. Although our results show a decrease in MTO when non-indigenous species are excluded from the calculation for the Holocene death assemblages, this decrease is very small due to rarity of Lessepsian species in these assemblages compared to native taxa. Specifically, dominant species, such as E. encrasicolus in the Israeli death assemblages at 30- and 40-m depths, drive the MTO values.
Our results provide also some practical guidelines for future studies relying on the MTO approach. In particular, we have shown that isolating size fractions in individual samples gives drastically different MTO values (Fig. 4). Similarly, mesh size has been shown to affect the estimation of a variety of ecological parameters for both fossil (e.g., Bush et al. 2007) and living assemblages, including surveys of fish communities (e.g., Bethke et al. 1999; Godø and Walsh 1992; Millar and Walsh 1992). This means that comparing death and fossil otolith assemblages based on MTO cannot be done without standardizing sample processing, specifically sieve size.

Additionally, the bathymetry of the study area influences the MTO values. This becomes obvious by the differences in MTO of pelagic versus demersal fishes, especially in the deepest assemblages (Table 4; Fig. 4). Pelagic assemblages give MTO values closer to the mean annual sea surface temperatures in the Holocene assemblages, particularly in the shallower sampling stations (Fig. 4). However, MTO based on pelagic species shows a decreasing trend along the Israeli depth gradient: the MTO at 10-m depth is 17.3 °C, but only 13.6 °C at 40-m depth (Table 4), while the sea surface temperature for this area is estimated at 24 °C on average (Avnaim-Katav et al. 2019; Castañeda et al. 2010; Essallami et al. 2007). We hypothesize that this trend is caused by the inclusion of pelagic species living in deeper levels of the water column in the assemblages from the deeper stations.

A potential limitation of MTO comes from a basic paleoecological assumption of niche conservatism. Fish show thermal plasticity when faced with gradual seawater temperature change (Crozier and Hutchings 2014; Loisel et al. 2019; Ryu et al. 2020), and therefore may be expected to have shown somewhat different temperature preferences between long-term climate perturbations over geological timescales, such as the glacial and interglacial stages. Although the assumption that fish species maintained the same traits in the geological past as today is a good starting point in paleoecological research (Eduardo et al. 2018; El-Sayed et al. 2021), it may not hold true, and this should be considered when using MTO. Nevertheless, MTO, as MTC, accepts that fish species’ first respond to climate change by shifting their distribution, rather than change their temperature preferences, and indeed this seemed to be the case as well during the Pleistocene climatic perturbation in the eastern Mediterranean (Agiadi et al. 2018). Moreover, long-term thermal niche conservatism during major climatic shifts has been demonstrated for a number of other taxa (e.g., Antell et al. 2021; Saupe et al. 2014). Therefore, at least for this case study, we consider the assumption safe.

There are significant differences between MTO and MTC, which prevent their direct comparison. The MTO captures the preserved part of an entire fish assemblage (Fig. 1), whereas MTC derives exclusively from the exploited component of fish assemblages. Therefore, MTO is affected by mortality and taphonomic processes, whereas MTC is influenced by fisheries targets and practices. Secondly, the catch composition reflects the snapshot of the exploited part of a modern assemblage that lives at the time of capture in the fishing ground or survey area, and MTC is calculated by summing up the catches over a relatively short period of time (e.g., yearly). On the other hand, death and fossil assemblages are time-averaged over much longer periods of time, usually exceeding the life span of the included fish species. Therefore, they represent accumulations of remains of individuals that died naturally typically over a period of decades to millennia (Albano et al. 2020; Nawrot et al. 2022). In addition, the sampling methodologies differ between living and death/fossil assemblages, making them incomparable at first instance. For example, a common method of fishing/surveying living fish assemblages is by net trawling, whereby the size of the captured fishes depends on the shape and dimensions of the net. Death/fossil assemblages are obtained by wet-sieving sediment samples of a given volume that corresponds to a limited surface area of the seabed. The mesh size of the sieve is usually 1 mm or smaller, so even the smallest species and otoliths of juvenile specimens are caught, but large fish individuals tend to be rare in death and fossil otolith assemblages. Finally, the MTC and MTO represent very different spatial scales, as the MTC is typically based on catch data encompassing large marine ecosystems or entire marine basins, while death/fossil otolith assemblages capture the composition of a local fish community. Thus, both the temporal and the spatial resolutions of the catch data and otolith assemblages differ by orders of magnitude. Therefore, MTO and MTC values should not be directly compared, but may be used independently to derive spatial and temporal trends, which are comparable.
The mean temperatures calculated from otolith death and fossil assemblages from the Eastern Mediterranean and northern Adriatic coasts reflect relatively well the regional differences in climate that would be expected to impact fish faunal composition. Thus, MTO represents a promising new proxy for tracking shifts in climatic affinity of fossil fish assemblages over large spatial and temporal scales. We highlight, however, that certain conditions must be met in such analyses: (a) sampling design should target specific questions (such as detecting fish stock changes at specific depths and through time in response to climate); (b) sample processing should be standardized; (c) a precise chronological framework is necessary to derive the most information out of such studies.

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Data availability All the data related to this paper are presented in the tables.

Declarations

Ethical approval This is a study based on fossils. No ethical approval is required.

Conflict of interest The authors declare no competing interests.

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References

Agiadi K, Albano PG (2020) Holocene fish assemblages provide baseline data for the rapidly changing eastern Mediterranean. The Holocene 30:1438–1450. https://doi.org/10.1177/0959683620932969

Agiadi K, Gireoud A, Koskeridou E, Moissette P, Cornée J-J, Quillévére F (2018) Pleistocene marine fish invasions and paleoenvironmental reconstructions in the eastern Mediterranean. Quat Sci Rev 196:80–99. https://doi.org/10.1016/j.quascirev.2018.07.037

Agiadi K, Vasileiou G, Koskeridou E, Moissette P, Cornée J-J (2019) Coastal fish otoliths from the early Pleistocene of Rhodes (eastern Mediterranean). Geobios 55:1–15. https://doi.org/10.1016/j.geobios.2019.06.006

Agiadi K, Azzarone M, Hua Q, Kaufman D, Thivaiou D, Albano PG (2021) The taphonomic clock in fish otoliths. Paleobiology. https://doi.org/10.1017/pab.2021.30

Aguilera O, Aguilera D (1999) Bathymetric distribution of Miocene to Pliocene Caribbean Teleostean fishes from the coast of Panama and Costa Rica. Bull Am Paleontol 357:251–269

Albano PG, Hua Q, Kaufman D, Tomašových A, Zuschin M, Agiadi K (2020) Radiocarbon dating supports bivalve-fish age coupling along a bathymetric gradient in high-resolution paleoenvironmental studies. Geology 48:589–593. https://doi.org/10.1130/G47210.1

Albano PG, Steger J, Bošnjak M, Dunne B, Guíjarro Z, Turapova E, Hua Q, Kaufman DS, Rilov G, Zuschin M (2021) Native biodiversity collapse in the eastern Mediterranean. Proc r Soc B Biol Sci 288:20202469. https://doi.org/10.1098/rspb.2020.2469

Amorosi A, Fontana A, Antonioli F, Primon S, Bondesan A (2008) Post-LGM sedimentation and Holocene shoreline evolution in the NW Adriatic coastal area. GeoActa 7:41–67

Antell GS, Fenton IS, Valdes PJ, Sause EE (2021) Thermal niches of planktonic foraminifera are static throughout glacial-interglacial climate change. Proc Natl Acad Sci 118:e2017105118. https://doi.org/10.1073/pnas.2017105118

Athanasiou M, Bouloubassi I, Gogou A, Klein V, Dimiza MD, Parinos C, Skampa E, Triantaphyllou MV (2017) Sea surface temperatures and environmental conditions during the “warm Pliocene” interval (~4.1–3.2 Ma) in the Eastern Mediterranean (Cyprus). Glob Planet Change 150:46–57. https://doi.org/10.1016/j.gloplacha.2017.01.008

Avnaim-Katav S, Almogi-Labin A, Schneider-Mor A, Crouvi O, Burke AA, Kremenetski KV, MacDonald GM (2019) A multi-proxy shallow marine record for Mid-to-Late Holocene climate variability, Thera eruptions and cultural change in the Eastern Mediterranean. Quat Sci Rev 204:133–148. https://doi.org/10.1016/j.quascirev.2018.12.001

Becker J, Lourens LI, Hilgen FJ, van der Laan E, Kouwenhoven TJ, Reichart G-J (2005) Late Pliocene climate variability on Milankovitch to millennial time scales: a high-resolution study of MIS100 from the Mediterranean. Palaeogeogr Palaeoclimatol Palaeoecol 228:338–360. https://doi.org/10.1016/j.palaeo.2005.06.020
Bethke E, Arrhenius F, Cardinale M, Håkansson N (1999) Comparison of the selectivity of three pelagic sampling trawls in a hydroacoustic survey. Fish Res 44:15–23. https://doi.org/10.1016/S0165-7865(99)00054-5

Burke KD, Williams JW, Chandler MA, Haywood AM, Lunt DJ, Otto-Bliesner BL (2018) Pliocene and Eocene provide best analogs for near-future climates. Proc Natl Acad Sci. 201809600. https://doi.org/10.1073/pnas.1809600115

Bush AM, Kowalewski M, Hoffmeister AP, Bambach RK, Daley GM (2007) Potential paleoecological biases from size-filtering of fossils: strategies for sieving. Palaios 22:612–622. https://doi.org/10.2110/pal.2006.p06-002r

Castañeda IS, Scheufuß E, Pätzold J, Sinninghe Damsté JS, Weldeab S, Schouten S (2010) Millenium-scale sea surface temperature changes in the eastern Mediterranean (Nile River Delta region) over the last 27,000 years. Paleoceanography 25. https://doi.org/10.1029/2009PA001740

Chaitkin S, Dubiner S, Belmaker J (2022) Cold-water species deepen to escape warm water temperatures. Glob Ecol Biogeogr. https://doi.org/10.1111/geb.13414

Cheung WWL, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. Nature 497:365. https://doi.org/10.1038/nature12156

CIESM (2021) Atlas of Exotic Fishes, 2nd ed

Cornée J-J, Quillévéré P, Fietzke J, López-Otálvaro GE, Melinte-Dobrinescu M, Philippin M, van Hisenberg DJJ, Agiadi K, Koskeridou E, Münch P (2019) Tectonic motion in oblique subduction forearcs: insights from the revisited Middle and Upper Pleistocene deposits of Rhodes, Greece. J Geol Soc 176:78–96. https://doi.org/10.1144/jgs2018-090

Crippa G, Angelini L, Bottini C, Erba E, Frigerio C, Hennissen JAI, Leng MJ, Petrizzo MR, Raffi I, Raineri G, Stephenson MH (2016) Seasonality fluctuations recorded in fossil bivalves during the early Pleistocene: implications for climate change. Palaeogeogr Palaeoclimatol Palaeoecol 446:234–251. https://doi.org/10.1016/j.palaeo.2016.01.029

Crozier LG, Hutchings JA (2014) Plastic and evolutionary responses to climate change in fish. Evol Appl 7:68–87. https://doi.org/10.1111/eva.12135

Dietz GP, Flessa KW (2011) Conservation paleobiology: putting the dead to work. Trends Ecol Evol 26:30–37. https://doi.org/10.1016/j.tree.2010.09.010

Dimarchopoulou D, Makino M, Prayoga MR, Zeller D, Vianna GMS, Humphries AT (2021) Responses in fisheries catch data to a warming ocean along a latitudinal gradient in the western Pacific Ocean. Environ Biol Fishes. https://doi.org/10.1007/s10641-021-01162-z

Edelst J (2014) New length–weight relationships and Lmax values for fishes from the Southeastern Mediterranean Sea. J Appl Ichthyol 30:521–526. https://doi.org/10.1111/j.1439-0426.2012.02060.x

Edelst J, Sonin O, Golani D, Rilov G, Spanier E (2011) Spatialtemporal patterns of catch and discards of the Israeli Mediterranean trawl fishery in the early 1990s: ecological and conservation perspectives. Sci Mar 75:641–652. https://doi.org/10.3989/scimar.2011.175n4641

Edelst J, Rilov G, Golani D, Carlton JT, Spanier E (2013) Restructuring the sea: profound shifts in the world’s most invaded marine ecosystem. Divers Distrib 19:69–77. https://doi.org/10.10111/dii.12002

Eduardo AA, Martinez PA, Gouveia SF, da Silva Santos F, de Aragão WS, Morales-Barbero J, Kerber L, Liparini A (2018) Extending the paleontology–biogeography reciprocity with SDMs: exploring models and data in reducing fossil taxonomic uncertainty. PLOS ONE 13:e0194725. https://doi.org/10.1371/journal.pone.0194725

Elder KL, Jones GA, Bolz G (1996) Distribution of otoliths in surficial sediments of the U.S. Atlantic Continental Shelf and slope and potential for reconstructing Holocene fish stocks. Paleoceanography 11:359–367. https://doi.org/10.1029/96PA00042

El-Sayed S, Friedman M, Anan T, Faris MA, Sallam H (2021) Diverse marine fish assemblages inhabited the paleotropics during the Paleocene-Eocene thermal maximum. Geology 49:993–998. https://doi.org/10.1130/G48549.1

Ern R, Johansen JL, Rummer JL, Esbaugh AJ (2017) Effects of hypoxia and ocean acidification on the upper thermal niche boundaries of coral reef fishes. Biol Lett 13:20170135. https://doi.org/10.1098/rsbl.2017.0135

Essallam L, Sicre MA, Kallel N, Labeyrie L, Siani G (2007) Hydrological changes in the Mediterranean Sea over the last 30,000 years. Geochem Geophys Geosystems. 8. https://doi.org/10.1029/2007GC001587

Fortibuoni T, Aldighieri F, Giovanardi O, Panov F, Zucchetta M (2015) Climate impact on Italian fisheries (Mediterranean Sea). Reg Environ Change 15:931–937. https://doi.org/10.1007/s10113-015-0781-6

Gaemers PAM, Vorren TO (1985) Otolith stratigraphy of Late Weichselian and Holocene sediments of Malangsdjupet, off northern Norway. Nor Geol Tidsskr 65:187–199

Gianelli I, Ortega L, Marín Y, Piola AR, Defeo O (2019) Evidence of ocean warming in Uruguay’s fisheries landings: the mean temperature of the catch approach. Mar Ecol Prog Ser 625:115–125. https://doi.org/10.3354/meps13035

Girone A, Varola A (2001) Fish otoliths from the middle Pleistocene deposits of Montalbano Jonico (Southern Italy). Boll Della Soc Paleontol Ital 40:431–443

Girone A, Nolf D, Cappetta H (2006) Pleistocene fish otoliths from the Mediterranean Basin: a synthesis. Geobiology 39:651–671. https://doi.org/10.1016/j.geobi.2005.05.004

Giunta S, Emeis K-C, Negri A (2001) Sea surface temperatures reconstruction of the last 16,000 years in the eastern Mediterranean Sea. Riv. Ital. Paleontol. Stratigr. 107. https://doi.org/10.13130/2039-4942/5447

Givan O, Edelst D, Sonin O, Belmaker J (2018) Thermal affinicity as the dominant factor changing Mediterranean fish abundances. Glob Change Biol 24:e80–e89. https://doi.org/10.1111/gcb.13835

Gods OR, Walsh SJ (1992) Escapement of fish during bottom trawl sampling — implications for resource assessment. Fish. Res. Fishing Gear Selectivity 13:281–292. https://doi.org/10.1016/0165-7836(92)90082-5

Herbert TD, Ng G, Cleaveland Peterson L (2015) Evolution of Mediterranean sea surface temperatures 3.5–1.5 Ma: regional and hemispheric influences. Earth Planet Sci Lett 409:307–318. https://doi.org/10.1016/j.epsl.2014.10.006

Hillis D, McKechnie I, Gustas R, Pauly D, Cheung WWL, Salomon AK (2022) A paleothermometer of ancient indigenous fisheries reveals increases in mean temperature of the catch over five millennia. Environ Biol Fishes (in press)
Jones WA, Checkley DM (2019) Mesopelagic fishes dominate otolith record of past two millennia in the Santa Barbara Basin. Nat Commun 10:4564. https://doi.org/10.1038/s41467-019-12600-z

Kaschner K, Kerner-Reyes K, Garlao C, Rius-Barile J, Rees T, Froese R (2016) AquaMaps: predicted range maps for aquatic species [WWW Document]. URL www.aquamaps.org. Accessed 01.10.2021

Keskin Ç, Pauly D (2018) Reconciling trends of mean trophic index and mean temperature of the catch in the Eastern Mediterranean and Black Seas. Mediterr Mar Sci. 19, 79–83. https://doi.org/10.1080/11101128.2018.0160951

Keskin Ç, Pauly D (2014) Changes in the “mean temperature of the catch”: application of a new concept to the North-eastern Aegean Sea. Acta Adriat 55:213–218

Kidwell SM (2015) Biology in the Anthropocene: challenges and insights from young fossil records. Proc Natl Acad Sci 112:4922–4929. https://doi.org/10.1073/pnas.1403660112

Kosnik MA, Kowalewski M (2016) Understanding modern extinctions in marine ecosystems: the role of palaeoecological data. Biol Lett 12:20150951. https://doi.org/10.1098/rsbl.2015.0951

Kowalewski M, Wittmer JM, Dexter TA, Amorosi A, Scarponi D (2015) Differential responses of marine communities to natural and anthropogenic changes. Proc. R. Soc. Lond. B Biol Sci. 282, 20142990. https://doi.org/10.1098/rspb.2014.2990

Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Glob Ecol Biogeogr 20:58–72. https://doi.org/10.1111/j.1466-8238.2010.00575.x

Leitão F, Maharaj RR, Vieira VMNCS, Teodósio A, Cheung WWL (2018) The effect of regional sea surface temperature rise on fisheries along the Portuguese Iberian Atlantic coast. Aquat Conserv Mar Freshw Ecosyst 28:1351–1359. https://doi.org/10.1002/aqc.2947

Liang C, Xiao W, Pauly D (2018) Impacts of ocean warming on China’s fisheries catches: an application of “mean temperature of the catch” concept. Front Mar Sci 5:26. https://doi.org/10.3389/fmars.2018.00026

Lin C-H, Girone A, Nolf D (2016) Fish otolith assemblages from Recent NE Atlantic sea bottoms: a comparative study of palaeoecology. Palaeoecogr Palaeoclimatol Palaeoecol 446:98–107. https://doi.org/10.1016/j.palaeo.2016.01.022

Lin C-H, Taviani M, Angeletti L, Girone A, Nolf D (2017) Fish otoliths in superficial sediments of the Mediterranean Sea. Palaeoecogr Palaeoclimatol Palaeoecol 471:134–143. https://doi.org/10.1016/j.palaeo.2016.12.050

Lin C-H, Gracia BD, Pierotti MER, Andrews AH, Griswold K, O’Dea A (2019) Reconstructing reef fish communities using fish otoliths in coral reef sediments. PLoS ONE 14:e0218413. https://doi.org/10.1371/journal.pone.0218413

Lin C-H, Chiang Y-P, Tuset VM, Lombarte A, Girone A (2018) Late Quaternary to Recent diversity of fish otoliths from the Red Sea, central Mediterranean, and NE Atlantic sea bottoms. Geobios. https://doi.org/10.1016/j.geobios.2018.06.002

Loisel A, Isla A, Daufresne M (2019) Variation of thermal plasticity in growth and reproduction patterns: importance of ancestral and developmental temperatures. J Therm Biol 84:460–468. https://doi.org/10.1016/j.jtherbio.2019.07.029

Lourens LJ, Hilgen FJ, Gudjonsson L, Zachariasse WJ (1992) Late Pliocene to early Pleistocene astronomically forced sea surface productivity and temperature variations in the Mediterranean. Mar Micropal 19:49–78. https://doi.org/10.1016/0377-8398(92)90021-B

Maharaj RR, Lam WY, Pauly D, Cheung WWL (2018) Regional variability in the sensitivity of Caribbean reef fish assemblages to ocean warming. Mar Ecol Prog Ser 590:201–209. https://doi.org/10.3354/meps12462

Mautner A-K, Gallmetzer I, Haselmair A, Schnedl S-M, Tomášových A, Zuschin M (2018) Holocene ecosystem shifts and human-induced loss of Arca and Ostrea shell beds in the north-eastern Adriatic Sea. Mar Pollut Bull 126:19–30. https://doi.org/10.1016/j.marpolbul.2017.10.084

Millar RB, Walsh SJ (1992) Analysis of trawl selectivity studies with an application to trouser trawls. Fish. Res., Fishing Gear Selectivity 13, 205–220. https://doi.org/10.1016/0165-7836(92)90077-7

Minnett PJ, Alvera-Azcárate A, Chin TM, Corlett GK, Gentemann CL, Karagali I, Li X, Marsouin A, Marullo S, Maturi E, Santoleri R, Saux Picart S, Steele M, Vazquez-Cuervo J (2019) Half a century of satellite remote sensing of sea-surface temperature. Remote Sens Environ 233:111366. https://doi.org/10.1016/j.rse.2019.111366

Moissette P, Koskeridou E, Drinia H, Cornée J-J (2016) Facies associations in warm-temperate siliciclastic deposits: insights from early Pleistocene eastern Mediterranean (Rhodes, Greece). Geol Mag 153:61–83. https://doi.org/10.1017/S0016065215000230

Nawrot R, Berensmeier M, Gallmetzer I, Haselmair A, Tomášových A, Zuschin M (2022) Multiple phyla, one time resolution? Similar time averaging in benthic foraminifera, mollusk, echinod, crustacean and otolith fossil assemblages. Geology.

Nolf D (1985) Otolith Piscum, Handbook of paleoichthyology. G. Fischer Verlag, Stuttgart

Oldfield F, Asioli A, Accorsi CA, Mercuri AM, Juggins S, Langone L, Rolph T, Trincardi F, Wolff G, Gibbs Z, Vigliotti S, Maturi E, Santoleri R, Saux Picart S, Steele M, Gentemann CL, Karagali I, Li X, Marsouin A, Marullo S, Maturi E, Santoleri R, Saux Picart S, Steele M, Vazquez-Cuervo J (2019) Half a century of satellite remote sensing of sea-surface temperature. Remote Sens Environ 233:111366. https://doi.org/10.1016/j.rse.2019.111366

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42. https://doi.org/10.1038/nature01286

Pauly D, Cheung WWL, Zuschin M (2020) The fisheries of the South China Sea: major trends since 1950. Mar Policy 121:103584. https://doi.org/10.1016/j.marpol.2019.103584

Quillévéré F, Cornée J-J, Moissette P, López-Otálvaro GE, van Baak C, Münch P, Melinte-Dobrinescu MC, Krijgsman W (2016) Chronostratigraphy of uplifted Quaternary hemipelagic deposits from the Dodecanese Island of Rhodes (Greece). Quat Res 86:79–94. https://doi.org/10.1016/j.qures.2016.05.002
Ryu T, Veilleux HD, Munday PL, Jung I, Donelson JM, Ravasi T (2020) An epigenetic signature for within-generational plasticity of a reef fish to ocean warming. Front Mar Sci 7:284. https://doi.org/10.3389/fmars.2020.00284

Saupe EE, Hendricks JR, Portell RW, Dowsett HJ, Haywood A, Hunter SJ, Liebermann BS (2014) Macroevolutionary consequences of profound climate change on niche evolution in marine molluscs over the past three million years. Proc r Soc B Biol Sci 281:20141995. https://doi.org/10.1098/rspb.2014.1995

Schwarzhans W (2013) Otoliths from dredges in the Gulf of Guinea and off the Azores - an actuo-paleontological case study. Palaeo Ichthyol 13:7–40

Schwarzhans W, Ohe F (2019) Lanternfish otoliths (Teleostei, Myctophidae) from the Pliocene and Pleistocene of Japan. Riv. Ital. Paleontol. Stratigr. 125. https://doi.org/10.13130/2039-4942/11670

Steger J, Bošnjak M, Belmaker J, Galil BS, Zuschin M, Albano PG (2021) Non-indigenous molluscs in the Eastern Mediterranean have distinct traits and cannot replace historic ecosystem functioning. Glob Ecol Biogeogr. https://doi.org/10.1111/geb.13415

Stergiou KI, Somarakis S, Triantafyllou G, Tsiaras KP, Gianoulaki M, Petithakis G, Machias A, Tsikliras AC (2016) Trends in productivity and biomass yields in the Mediterranean Sea large marine ecosystem during climate change. Environ. Dev., Thematic Issue - Ecosystem Based Management of Large Marine Ecosystems 17, 57–74. https://doi.org/10.1016/j.envdev.2015.09.001

Tomašových A, Kidwell SM (2017) Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. Proc r Soc B Biol Sci 284:20170328. https://doi.org/10.1098/rspb.2017.0328

Tomašových A, Gallmetzer I, Haselmair A, Kaufman DS, Mavrić B, Zuschin M (2018) A decline in molluscan carbonate production driven by the loss of vegetated habitats encoded in the Holocene sedimentary record of the Gulf of Trieste. Sedimentology 66:781–807. https://doi.org/10.1111/sed.12516

Tomašových A, Albano PG, Fuxsi T, Gallmetzer I, Haselmair A, Kowalewski M, Nawrot R, Nerlović V, Scarponi D, Zuschin M (2020) Ecological regime shift preserved in the Anthropocene stratigraphic record. Proc r Soc B Biol Sci 287:20200695. https://doi.org/10.1098/rspb.2020.0695

Tsikliras AC, Stergiou KI (2014) Mean temperature of the catch increases quickly in the Mediterranean Sea. Mar Ecol Prog Ser 515:281–284. https://doi.org/10.3354/meps11005

Tsikliras AC, Peristeraki P, Tserpes G, Stergiou KI (2015) Mean temperature of the catch (MTC) in the Greek Seas based on landings and survey data. Front Mar Sci 2:23. https://doi.org/10.3389/fmars.2015.00023

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecol Lett 13:1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Wood CM, McDonald DG (1997) Global warming: implications for freshwater and marine fish. Cambridge University Press

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