

Research



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Author for correspondence:

Konstantina Agiadi

e-mail: konstantina.agiadi@univie.ac.at

Palaeontological evidence for community-level decrease in mesopelagic fish size during Pleistocene climate warming in the eastern Mediterranean

Konstantina Agiadi¹, Frédéric Quillévéré², Rafał Nawrot¹, Theo Sommeville^{1,3}, Marta Coll⁴, Efterpi Koskeridou⁵, Jan Fietzke⁶ and Martin Zuschin¹

¹Department of Palaeontology, University of Vienna, Josef-Holaubek-Platz 2, UZA II, 1090, Vienna, Austria

²Université Claude Bernard Lyon 1, ENS de Lyon, CNRS, UMR 5276 LGL-TPE, 69622 Villeurbanne, France

³IMBRSea Program, Ghent University - Marine Biology Research Group, Krijgslaan 281/58, 9000 Ghent, Belgium

⁴Institute of Marine Sciences (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003, Barcelona, Spain

⁵Department of Historical Geology and Paleontology, National and Kapodistrian University of Athens, Panepistimioupolis, 15784, Athens, Greece

⁶GEOMAR, Helmholtz Centre for Ocean Research Kiel, Wischhofstrasse 1-3, 24148 Kiel, Germany

¹KA, 0000-0001-8073-559X; FQ, 0000-0002-6248-0447; RN, 0000-0002-5774-7311;

MC, 0000-0001-6235-5868; JF, 0000-0002-5530-7208; MZ, 0000-0002-5235-0198

Mesopelagic fishes are an important element of marine food webs, a huge, still mostly untapped food resource and great contributors to the biological carbon pump, whose future under climate change scenarios is unknown. The shrinking of commercial fishes within decades has been an alarming observation, but its causes remain contended. Here, we investigate the effect of warming climate on mesopelagic fish size in the eastern Mediterranean Sea during a glacial–interglacial–glacial transition of the Middle Pleistocene (marine isotope stages 20–18; 814–712 kyr B.P.), which included a 4°C increase in global seawater temperature. Our results based on fossil otoliths show that the median size of lanternfishes, one of the most abundant groups of mesopelagic fishes in fossil and modern assemblages, declined by approximately 35% with climate warming at the community level. However, individual mesopelagic species showed different and often opposing trends in size across the studied time interval, suggesting that climate warming in the interglacial resulted in an ecological shift toward increased relative abundance of smaller sized mesopelagic fishes due to geographical and/or bathymetric distribution range shifts, and the size-dependent effects of warming.

1. Introduction

Climate change affects fish size, fitness, abundance and distribution [1–3] with devastating anticipated socioeconomic impacts [4]. Within the euphotic zone, where most human activities take place and seawater temperature is directly regulated by local climatic conditions, average fish size has been predicted to decrease by 14–24% by the year 2050 [5]. Climate change is expected to have a significant impact on the mesopelagic zone as well (i.e. the part of the water column in the world's oceans between 200 and 1000 m), by rapidly displacing isotherms [6]: models predict a resulting expansion and shallowing of the deep scattering layers of the ocean water column, where most mesopelagic organisms live, leading to homogenization of their community composition and changes in mesopelagic biomass [7], and these predictions are so far confirmed by observations [8]. Fishes are a dominant component of the mesopelagic communities with an estimated biomass of 2–19.5 Gt, approximately 100 times greater than that of the total global annual fishery catches [9,10]. Mesopelagic fishes are an

important component of the ecosystem today and in the past [11–15], having a significant contribution to the biological carbon pump [16] through their light-controlled diel vertical migrations [17]. They usually occupy the mesopelagic realm during daytime and migrate to surface waters at night to feed, functioning as a trophic link between primary consumers and megafauna [18,19]. In fact, they help maintain ecosystem stability under environmental change [20], and their nighttime movement upwards into surface waters in order to feed while avoiding predators leads to a downward flux of organic carbon from the productive euphotic zone into the deeper parts of the ocean [21–23]. Due to this function, any adverse effects of climate warming on mesopelagic fishes directly impacts the oceans' ability to sequester carbon from the atmosphere to the deeper parts of the ocean. Moreover, due to the current state of global food security, they are an important potential food resource [9,24,25]. Indeed, mesopelagic fishes are a rich, targeted food resource, with 2.68 Mt of reported catches between 1950 and 2018 globally, even without proper exploitation efforts [24], and much higher estimated total biomass [26].

Body size is a key biological trait, which plays a significant role in controlling the structure and functioning of marine ecosystems [27], and it is strongly affected by ambient water temperature [28,29]. Evaluating and predicting the long-term effects of climate change on the size structure of modern fish assemblages is challenging, because these effects are difficult to disentangle from the impacts of other anthropogenic stressors like size-selective harvesting [30,31]. Moreover, fishery and scientific survey data rarely encompass more than a few decades and are often biased towards commercially important species. The fossil record provides a rich archive of major environmental perturbations of the geological past and their palaeoecological consequences, allowing us to track biotic responses to natural climatic shifts on timescales well beyond the limits of ecological monitoring [32]. Here, we quantify the effect of the Pleistocene climatic variability on the size structure of the eastern Mediterranean mesopelagic fish assemblages across the time interval 814–712 kyr B.P. corresponding to the marine isotope stages (MIS) 20–18: MIS 20 glacial (814–761 kyr B.P.), MIS 19 interglacial (761–757 kyr B.P.) and MIS 18 glacial (757–712 kyr B.P.; [33,34]). Our study is based on fossil otoliths from a unique hemipelagic sedimentary succession of this age exposed on the island of Rhodes in the eastern Mediterranean.

By contrast to present-day ecosystems, Pleistocene marine ecosystems were affected by the severe climatic oscillations of the glacial and interglacial periods, which can be used as analogues of current and forecasted climate warming situations without the confounding effects of the multiple anthropogenic stressors impacting present-day ecosystems. The Early–Middle Pleistocene Transition encompasses our target time interval MIS 20–18 and was characterized by important changes in Earth's climate, when the duration of climate oscillations increased, leading to the growth of the Northern Hemisphere ice-sheets during glacial periods and a shift to the modern climatic regime with stronger climatic fluctuations [33,35]. The interval MIS 20–18 involved a global sea surface temperature increase of about 4°C [36,37], also expressed in the Mediterranean [38,39], which took place over a few thousand years (MIS 20–19 deglaciation 786–789 kyr B.P.; [40,41]) and is in line with the IPCC-predicted mean surface temperature increase under the high

greenhouse gas emissions scenario that is expected to disrupt the marine food-web structure irreversibly [1,42–44]. In the eastern Mediterranean, previous studies have shown that the mesopelagic fish fauna was indeed affected by the Pleistocene climatic perturbations: North Atlantic and Arctic fish species, whose geographical distribution included the eastern Mediterranean during glacial periods after 1.5 Ma B.P., became extirpated by the subsequent interglacials [11]. Although the timescale over which the MIS 20–19 Pleistocene deglaciation took place was longer than the modern unprecedented climate change by one order of magnitude [40,41], the MIS 20–18 interval allows the potential long-term impact of a climate change on marine ecosystems to be evaluated and thus constrains the range of the possible future biotic responses on the ongoing warming.

We reconstructed changes in body size and composition of Pleistocene mesopelagic fish assemblages using fossil otoliths. Fish otoliths are aragonitic incremental biomineralizates with species-specific morphology [45] that are commonly preserved as fossils in marine sediments, and whose assemblages faithfully record past fish faunas [14,46,47]. Otolith size correlates with fish size through species-specific functions [48]. In rare cases, during periods of starvation and negative somatic growth, otolith growth may continue and then become decoupled from fish growth: for this reason, otolith growth is considered to represent the average fish growth [49]. Here, we used otolith length–fish length or otolith width–fish length, and fish length–weight functions derived from present-day fishes to estimate Pleistocene fish sizes during MIS 20, 19 and 18. Changes in average size at the scale of entire assemblages can result from processes occurring at different levels of biological organization: from the individual to the community [28,29]. We consider decoupling between otolith growth and somatic growth [49] to be either: (a) significant enough to cause the local extinction of the fish, (b) insignificant at our timescale, or (c) significant to cause a change in the taxon abundance but not extinction. In the case of (a) and (b), body size changes would not be observable in our assemblages. In order to consider case (c), in addition to body size changes, we also tracked changes in the relative abundances of the taxa in our assemblages to evaluate the relative importance of size shifts within the population and of changes in community composition in driving the observed body size patterns.

2. Material and methods

The samples were obtained on the island of Rhodes in the south-eastern Aegean Sea, in the eastern Mediterranean (figure 1). Rhodes is part of the Hellenic forearc and has experienced intense vertical tectonic movements during the past 2 Myr, leading to the deposition at bathyal depths and recent uplift of Early and Middle Pleistocene hemipelagic sediments, now exposed onshore along its eastern coast [50–53]. The occurrence of such Pleistocene deep-water sediments accessible on land is unique for the eastern Mediterranean, providing a reference point for studying the Early and Middle Pleistocene climates in this region [50]: there are no other deep-sea sediments covering this time interval cropping out across the region [52,54–56]. We sampled three marl levels, LR15–19, LR19–27, and LR > 27, of the Lindos Bay Formation in the lower part of Lardos section on Rhodes (N 37°17'48", E 27°8'4") corresponding to MIS 20, MIS 19 and MIS 18, respectively [57]. These sediments had been deposited continuously with an average sedimentation rate of 1.9 cm kyr⁻¹ [57] and show uniform lithologies. The

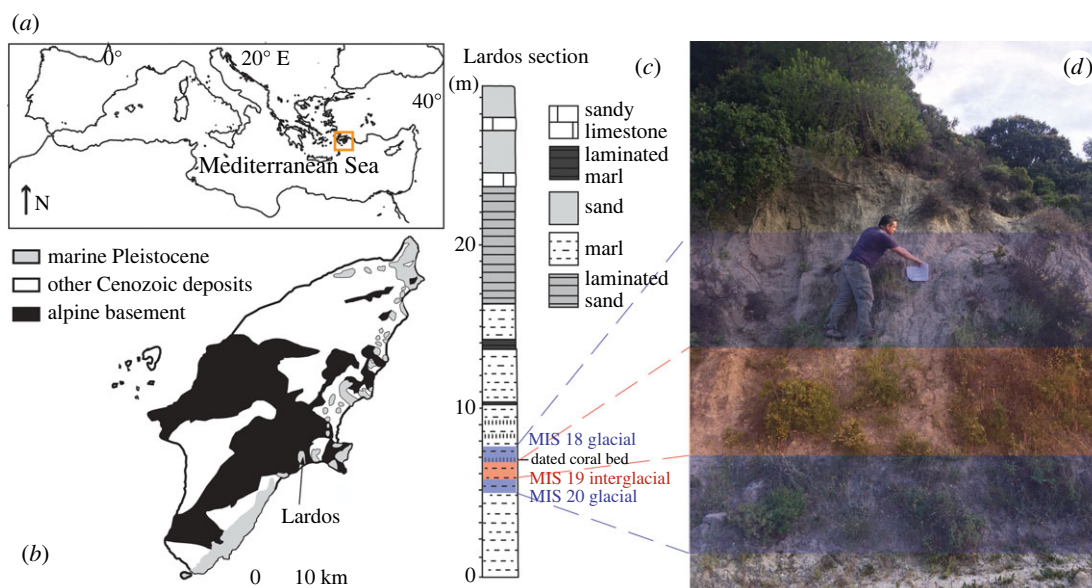


Figure 1. Sampling location. (a) Map of the Mediterranean Sea; (b) simplified geologic map of Rhodes, showing the location of the studied Lardos section (modified after [50]); (c) lithological column of the Lardos section, indicating the studied MIS 20–18 interval; and (d) photograph of the sampled part of the outcrop. (Online version in colour.)

palaeodepth in the study area exceeded 200 m for both MIS 20 and MIS 19, but became slightly shallower during MIS 18, as indicated by the greater abundance of goby otoliths [11]. The sediment samples were diluted in water, sieved with a 250- μm mesh sieve and then dried in an oven. The sagittal otoliths (henceforth referred to simply as ‘otoliths’) were handpicked from the residues and identified based on the morphological characteristics [45] and through comparison with modern and fossil material from the Mediterranean [11,12,58,59].

Each otolith was photographed, and its length and width were measured (electronic supplementary material, figure S1; [60]) using the microscope ZEISS SteREO Discovery V20 and the software ZEN (ZEISS Efficient Navigation). Since most of the identified species are extant, we estimated their weight using modern empirical otolith length/width–fish length (electronic supplementary material, table S1; [60]) and the fish length–weight functions developed based on fish shape [61,62]. The climatic-zone affinity and the habitat (pelagic or demersal) of the identified species were obtained from AquaMaps [63] and Fishbase [64], respectively (electronic supplementary material, table S2; [60]). Climatic affinities were assigned based on the biome classification scheme of Sarmiento *et al.* [65]: warm-affinity taxa presently occupy the permanently stratified subtropical gyre biome and upwelling biomes, and cold-affinity taxa are distributed in the seasonally mixed subtropical gyre biome and the subpolar biome.

We examined changes in the frequency distributions of the otolith length, and fish lengths and weights across the three time intervals for the entire assemblages. To depict the main drivers of these patterns, we traced shifts in median fish weight and relative abundances within the most abundance species, individual families and climatic-affinity groups. As the size-frequency distributions were strongly right-skewed, all analyses were performed on log-transformed data.

In order to test whether any differences in the body size of the fishes between the glacials and the interglacial were statistically significant, we used a non-parametric Kruskal–Wallis test, followed by a pairwise Wilcoxon test with a-posteriori Bonferroni correction to compare median weight between the three assemblages and estimate 95% confidence intervals around this parameter using a bootstrap procedure with 10 000 iterations. To test for differences in otolith preservation that could affect the interpretation of our results, we quantified and statistically

compared the otolith preservation state following a previously presented approach [66]. Specimens that could not be identified at least to family level were included in the otolith preservation analysis, but excluded from size calculations. All analyses were performed in R (v. 4.1.2) [67].

3. Results

We identified and estimated the fish length and weight from the length or width of 1960 otoliths from the three time intervals: 655 otoliths (97.05% of the assemblage) from MIS 20, 1022 otoliths (98.46%) from MIS 19 and 283 otoliths (93.40%) from MIS 18 (electronic supplementary material, table S3; [60]). The otolith length ranges from 0.38 to 8.69 mm (median of 1.40 mm), and the otolith width ranges from 0.41 to 4.68 mm (median of 1.34 mm).

Overall, the fish in the three assemblages are small, with a median length of 3.22 cm (ranging from 0.82 to 10.07 cm) and a median weight of 0.27 g (ranging from 0.002 to 106.13 g) (figure 2 and electronic supplementary material, figure S3; electronic supplementary material, table S3; [60]). The small size of the fish is expected, given the nature of the otolith fossil record and the sampling method [68]. The transition from the MIS 20 glacial to the MIS 19 interglacial is associated with 36% decrease in the assemblage-level median fish weight (from 0.36 g to 0.23 g), followed by 73% increase in the subsequent MIS 18 glacial period (to 0.40 g), and these changes are statistically significant: Kruskal–Wallis test $\chi^2 = 65.104$, d.f. = 2, $p < 0.001$; pairwise Wilcoxon test: $p < 0.001$ for both MIS 20–MIS 19 and MIS 19–MIS 18 (figure 2; electronic supplementary material, table S3; [60]).

At the genus and species level, lanternfishes’ sizes show contrasting trends (figure 3; electronic supplementary material, table S4; [60]). Considering the most abundant myctophid taxa in the assemblages (electronic supplementary material, figure S2; [60]), the subtropical *Lobianchia dofleini*, the only representative of its genus, has similar median size throughout the studied interval with only a slight increase during MIS 19, as does the temperate *Hygophum benoiti*. However, the abundance

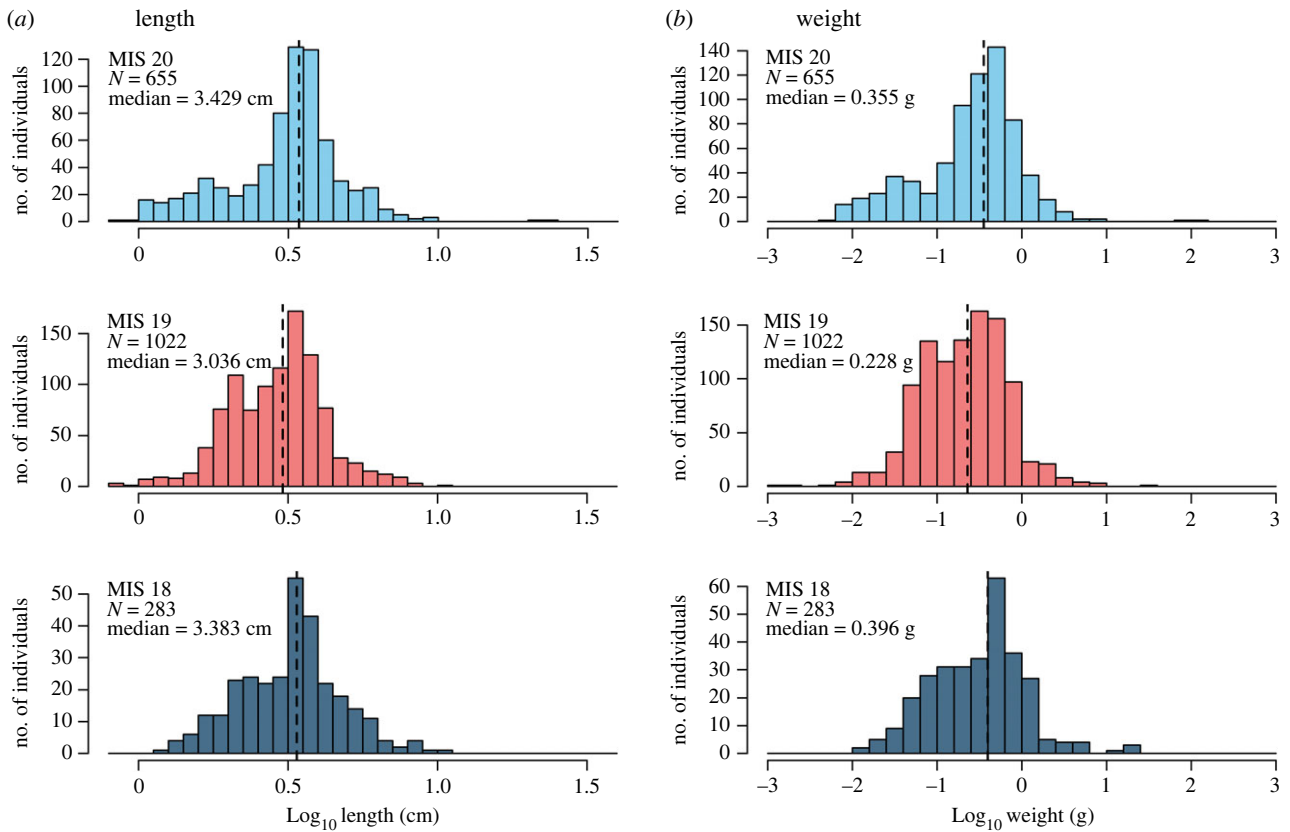


Figure 2. Fish length (a) and weight (b) frequency distributions (log-transformed) during MIS 20 (glacial), MIS 19 (interglacial) and MIS 18 (glacial). The median fish size at the assemblage level is smaller during the MIS 19 interglacial. Kruskal–Wallis test $\chi^2 = 65.104$, d.f. = 2, $p < 0.001$; pairwise Wilcoxon test: $p < 0.001$ for both MIS 20–MIS 19 and MIS 19–MIS 18. (Online version in colour.)

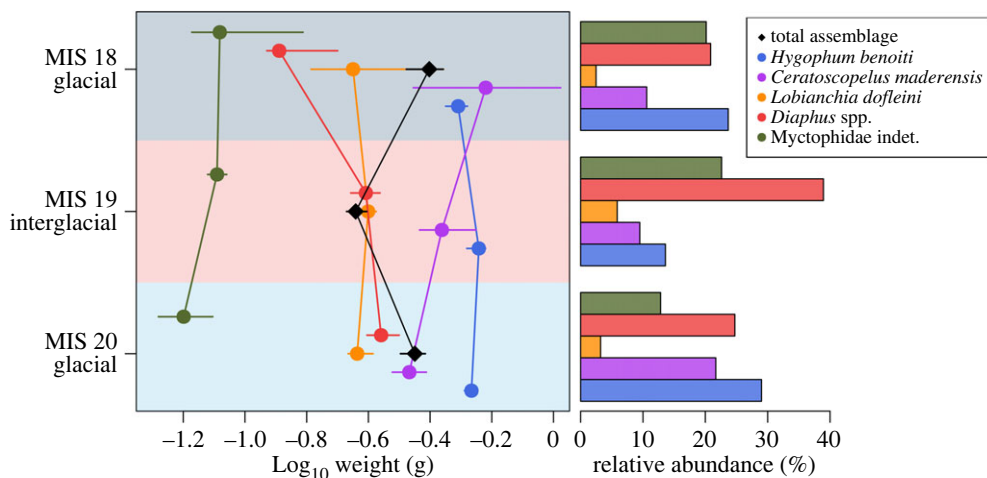


Figure 3. Median fish weight (with 95% bootstrapped confidence intervals) of the entire assemblage and the two most abundant cold- and warm-water species in the three studied intervals (all lanternfishes) and the corresponding abundances. Overall fish size decreases during the MIS 19 interglacial, but the individual species show different patterns. (Online version in colour.)

of *L. dofleini* increases relative to *H. benoiti* in the interglacial (electronic supplementary material, figure S2; electronic supplementary material, table S4; [60]). On the other hand, the temperate *Ceratoscopelus maderensis* shows a general increase in size from MIS 20 to MIS 18, whereas the sizes of the warm-water *Diaphus* spp. decrease.

The assemblages are clearly dominated by lanternfishes (Myctophidae constitute 89%, 96%, and 78% of the assemblages in MIS 20, MIS 19 and MIS 18, respectively; electronic supplementary material, table S4; [60]), whose median weight decreases by approximately 35% from 0.34 g

in MIS 20 glacial to 0.22 g in MIS 19 interglacial and increase again to 0.35 g in MIS 18 glacial (Kruskal–Wallis test $\chi^2 = 51.905$, d.f. = 2, $p < 0.001$; pairwise Wilcoxon test: $p < 0.001$ for both MIS 20–19 and MIS 19–18; electronic supplementary material, figure S4; [60]). By contrast, cods (Gadidae) may show the opposite trend, with their median weight having higher median value (2.24 g) in the interglacial, but lower in the glacials (Kruskal–Wallis test $\chi^2 = 6.626$, d.f. = 2, $p < 0.04$; pairwise Wilcoxon test: $p < 0.33$ for MIS 20–19, $p < 0.33$ for MIS 20–18 and $p < 0.04$ for MIS 19–18). However, we cannot reach a robust conclusion about this family given

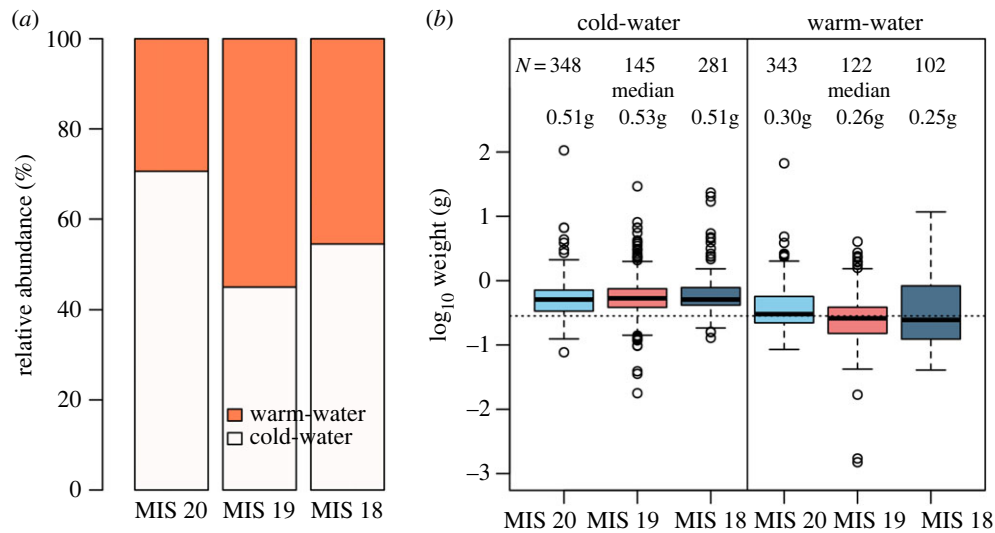


Figure 4. Changes in relative abundance and size of fish species belonging to the three climatic-affinity groups in MIS 20, MIS 19 and MIS 18. (a) Relative abundance of cold- and warm-water species. Cold-water species contribution decreases during the MIS 19 interglacial. (b) Log-transformed weight of cold- and warm-water species in each interval. The dashed line indicates the median weight in the entire dataset. The median weight among cold-water species does not significantly differ between the three stages (Kruskal–Wallis test $\chi^2 = 4.065$, d.f. = 2, $p = 0.13$; electronic supplementary material, figure S54; [60]). The weight of warm-water species decreases from MIS 20 to MIS 19 (Kruskal–Wallis test $\chi^2 = 16.843$, d.f. = 2, $p < 0.001$; pairwise Wilcoxon test $p < 0.001$ for MIS 20–19, $p = 0.05$ for MIS 20–18 and $p = 0.42$ for MIS 19–18). (Online version in colour.)

the small sample sizes (9, 17 and 8 otoliths in MIS 20, 19 and 18, respectively). Other families identified in the dataset have too few specimens to identify any significant trends (electronic supplementary material, figure S4; [60]).

The median weight among cold-water species does not significantly differ between the three stages (Kruskal–Wallis test $\chi^2 = 4.065$, d.f. = 2, $p = 0.13$; figure 4), while the weight of warm-water species decreases from MIS 20 to MIS 19 (Kruskal–Wallis test $\chi^2 = 16.843$, d.f. = 2, $p < 0.001$; pairwise Wilcoxon test $p < 0.001$ for MIS 20–19, $p = 0.05$ for MIS 20–18 and $p = 0.42$ for MIS 19–18). The relative abundance of cold-water (temperate and a few subpolar species) clearly drops during the MIS 19 interglacial, whereas warm-water species have a higher contribution to the MIS 19 assemblage (figure 4).

Change in assemblage composition through the studied glacial–interglacial–glacial transitions is mostly driven by cold-water mesopelagic fishes (figure 3 and electronic supplementary material, figure S5; [60]). *Ceratoscopelus maderensis* and *Hygophum benoiti* abundances clearly drop during the MIS 20–19 deglaciation, the latter increasing again significantly in MIS 18 along with *Vinciguerria poweriae*, despite the shallowing of the study area.

The observed shifts in size and assemblage composition cannot be explained by a variation in the otolith preservation, because the average taphonomic score of the otoliths from the three studied intervals is not significantly different (electronic supplementary material, figures S6 and S7; electronic supplementary material, table S5; [60]).

4. Discussion

The effect of past climate changes on mesopelagic fishes manifests through shifts in assemblage composition [11,12] and fish size [69]. Our results show an overall drop in mesopelagic fish median length and weight from the MIS 20 glacial to the MIS 19 interglacial in the eastern Mediterranean (figure 2), which is driven by lanternfishes that dominate the assemblages (figures 3 and 4 and electronic supplementary

material, figure S2; [60]). This decrease follows the expected effects of increasing temperature on body size of aquatic ectotherms [28,29,70], which have been observed for euphotic zone fishes today [5]. The MIS 20–19 deglaciation took place within approximately 3000 yr [40,41], much longer than the scale of decades of the modern climate change. Present-day anthropogenic climate change is unprecedented, and therefore its effects are not directly comparable to those of past climate change. Nevertheless, the past can guide our understanding of the natural variability of marine ecosystems and the response of organisms to extreme environmental change. A negative relationship between climate warming and mesopelagic fish size has been observed in other areas today [71], although some studies have also shown increase in size or no relationship at all [8], and small individuals have generally been overlooked in studies of climate change impact on fish growth [72]. Our results suggest that at long-term timescales, natural climate warming may lead to an overall decrease in median fish size at the community level, at least in mid-latitude regions.

Despite this overall shift, the individual myctophid genera and species in the Middle Pleistocene assemblages of the eastern Mediterranean do not follow the within-species size reduction observed in epipelagic fishes [5,31], but exhibit different and often opposing trends (figure 3), which indicates that patterns at the assemblage level are not primarily driven by common trends in average body size of individual species. The known shifts in the fish community composition (changes in the relative abundances of species) [11] between glacials and interglacials are observed again in our study. Cold-water (temperate and subpolar) mesopelagic species show a higher relative abundance in the glacial than in the interglacial assemblages. In the Early–Middle Pleistocene Transition, North Atlantic subsurface waters experienced warming phases during glacials after MIS 24 due to pulses of increased outflow of Mediterranean waters [73], which would enhance water mixing and facilitate the functional connectivity between the mesopelagic fish populations of the two regions. This pattern may explain the establishment

of subpolar species in the Mediterranean during Middle and Late Pleistocene glacials [11,12,58,59] and the higher relative abundance of cold-water species in MIS 20 and MIS 18 observed in this study.

Moreover, the mesopelagic species may have shifted their ranges to greater, cooler depths, following their preferred temperatures, as a response to climate warming, while maintaining their body size. A case in point is *Ceratoscopelus maderensis*, whose high resilience may be explained by its large depth range, particularly in the modern Mediterranean Sea (up to 2500 m in the Ionian Sea [74]). By contrast to euphotic zone fishes, mesopelagic fishes commonly change their depth distribution. They move hundreds of metres within the water column to adapt to changing water conditions [13] and show different bathymetric distributions in different seas [18,19,75]. This would explain size changes in individual species that may contradict expectations based on the climatic conditions (figure 3). However, the part of the Lindos Bay Formation sedimentary sequence that was sampled here is regressive, meaning that the palaeodepth decreased upwards in the section, from MIS 20 to MIS 18 [11,57]. Therefore, we cannot expect shifts to greater (and colder) depths from MIS 20 to MIS 19 as an adaptation to warming climate, which would explain why the size of *Ceratoscopelus maderensis* indeed decreases in the interglacial.

In addition, temperature effects on metabolism are size-specific [76,77]. Accordingly, it is possible for fish to maintain (or even increase) their size during warming, when the increased growth (over)compensates for higher mortality in the warmer ecosystem [78–80]. Size-specific impacts of temperature have been recorded in short- and long-term records, at least at the decadal scale [81]. This size-specific body size responses to warming climate could be another mechanism to explain the observed unchanged median body sizes of *L. dofleini* and *H. benoiti*, and the increased size of *C. maderensis* during the Pleistocene interglacial in the eastern Mediterranean, although further studies would be required to support this.

Finally, both direct and indirect effects of elevated temperature on fishes should be taken into account to explain the divergent patterns shown by the different mesopelagic fishes. The higher temperature expedites fish growth by increasing metabolism, but at the same time may limit food availability through bottom-up effects, resulting in a decrease in growth [82]. Although palaeoproductivity data for the eastern Mediterranean during MIS 20–18 are not available, data from the Western Mediterranean [83] indicate increase, rather than decrease, of primary productivity during the interglacial MIS 19, thus rejecting a negative feedback of warming on fish growth at that time.

5. Conclusion

Although the eastern Mediterranean mesopelagic fish assemblages seem to follow the predicted size reduction with

increasing temperature during the Middle Pleistocene MIS 19 interglacial, our results demonstrate that this was due to changes in species relative abundances coupled with size-dependent temperature effects rather than on individual species body size. Within-species, synchronous reductions in size across multiple mesopelagic species were not observed in the studied assemblages, suggesting that an increase in relative abundance of small mesopelagic fishes took place in the eastern Mediterranean during MIS 19 interglacial. Even though our study refers to a climate warming taking place over a few thousand years in the Pleistocene, rather than within decades as is predicted for the modern climate change, our results are consistent with the few available observations on mesopelagic fishes today. Therefore, accurate predictions of mesopelagic fish responses under future climate change scenarios may require an ecosystem-based and multispecies rather than a single-species approach. Considering the important function of mesopelagic fishes in energy and carbon transfer through marine ecosystems, the observed community-level decrease in size of mesopelagic fishes may suggest downgrading of the marine food-web structure and a reduction in carbon sequestration during the interglacial.

Data accessibility. The raw dataset produced in this study is available at <https://doi.org/10.5061/dryad.gxd2547pn> [84]; the R script at <https://doi.org/10.5281/zenodo.6643635> [85]; and electronic supplementary material can be accessed at <https://doi.org/10.5281/zenodo.6643637> [60].

Authors' contributions. K.A.: conceptualization, formal analysis, funding acquisition, investigation, methodology, writing—original draft, writing—review and editing; F.Q.: investigation, writing—review and editing; R.N.: formal analysis, investigation, methodology, writing—review and editing; T.S.: formal analysis, investigation, methodology, writing—original draft; M.C.: writing—review and editing; E.K.: investigation, writing—review and editing; J.F.: formal analysis; M.Z.: funding acquisition, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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