

***Interactive comment on “Refugia of marine fish in the Northeast Atlantic during the Last Glacial Maximum: concordant assessment from archaeozoology and palaeotemperature reconstructions” by A. J. Kettle et al.***

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This is an interesting and innovative paper combining ecological modeling with paleoclimatic data in order to estimate the biogeographic ranges of marine fish species under last glacial conditions. The motivation is given by archeozoological finds of these species at sites outside their present day range and the need to understand whether these finds represent long transport or range shifts of the fishes. The approach and the parametrization of the model are clearly explained and the results are most encouraging, but the authors resorted to a number of simplifications that I believe need to be

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properly thought through.

Specifically, I would like to comment on the following points:

The use of the paleoclimatic data is problematic. The authors opted to use the model-interpolated GLAMAP data by Paul and Schäfer-Neth (2003), which are convenient to use, but do not represent the current state of the art. The differences are in particular obvious for sea-ice extent, which could not have been reconstructed explicitly by GLAMAP but is almost entirely the result of the model-based interpolation, and for the Mediterranean, where GLAMAP has not generated any new data. I believe these two simplifications have too much an effect on the results and the authors are asked to use the appropriate new compilations in MARGO (Hayes et al., 2005 for the Mediterranean and de Vernal et al., 2005, 2006 for sea ice).

The above point is especially critical for the Mediterranean, where the compilation by Hayes et al. (2005) deviates very significantly from the interpolation by Paul and Schäfer-Neth (2003), which makes statements like “conditions in the eastern Mediterranean were not much different from the present” (page 17 line 8) simply incorrect (see for example Robinson et al., 2006, QSR; Castaneda et al., 2010, Paleooceanography).

On Page 17 line 18, the authors seem to be disturbed by the implied disjunct distribution of some species implied by the model between the Adriatic and the Western Mediterranean. The authors forget that their model is static – it does not simulate any ecologically meaningful range extension of a species. Therefore, there is no evidence that the potential habitat indicated by their model to occur in the Adriatic has actually ever been colonized. The statement on page 18 line 5 is therefore incorrect: the present model makes no predictions of where a given species “should have extended” to, only where it “could have existed”. The authors should also be aware of the fact that modeling potential distributions of species for the LGM Black Sea (Figure 6) is very problematic because this basin was at that time an isolated freshwater lake.

The present ecological niche model is hugely oversimplified, being nothing else than

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a Boolean AND between two static variables. It only considers temperature and depth as the controlling parameters for species distribution, lacks an analysis of occurrence of the species in the combined field of SST and bathymetry and ignores the vertical aspect of SST in the water column. Is it justifiable to assume that the species occur at all depths within the stated depth range throughout the SST envelope? Why should it be the temperature at the surface and not throughout the depth range of the species which controls their distribution?

The authors provide little clues as to how exactly the parameter envelope has been determined? Was any quantitative calibration carried out? What measure of model fit has been used? What is the shape of the error function for different parameter values? Is the chosen threshold value a sharp optimum fit or does it correspond to a broad peak? This seems to have been tested, but the sensitivity test mentioned on line 15 page 9 is not documented and it is not clear how it was carried out.

Related to the above point, the authors mention that species ranges at present do not represent their true potential habitat (page 16), but do not seem to explicitly include this in the parametrisation. This is very significant, considering that there is evidence for both depth and temperature shifts away from the pre-anthropogenic habitat that we observe today. This could have even been responsible for the observed apparent temperature and depth limits: is it possible that under natural conditions the niche of the fishes is not primarily constrained by these two parameters at all?

The calibration of the present-day fish occurrence climatic envelopes is based on the latest climatological data and literature data of various age. This creates an interesting offset between the SST values, which thus consistently reflect the extreme warming of the last decade, and the occurrence data, which are based on observations prior to this warming. Have the authors considered the effect of changing species ranges in the last decades and the current warming trend on the estimated climatic envelope? The authors present a detailed discussion on the temperature envelope (although they do not seem to consider the vertical temperature gradient in the water column), but

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the bathymetry envelope is not defined and explained at all. What exactly does it represent? How was the choice of values guided? I am puzzled by the fact that the envelopes as applied for the individual species (bathymetry=200 m for pollock) imply disjunct distributions (fragmented habitat). Is there any evidence for limited gene flow between such enclaves? How is the choice of niche parameters justified in this case?

The main assumption of the model that the authors discuss is that the ecology of the species has not changed through time. This is correct, but incomplete. There are at least two further assumptions that ought to be discussed: 1) that the full range of behaviours of the analysed species is represented in the calibration data, 2) that the covariance of the model parameters in the past was the same as in the calibration dataset. If any of these is not satisfied, the LGM results could be completely flawed.

The authors repeatedly state that the LGM represents a "situation of maximum perturbation of temperatures" (p3, line 5). This is of course not true. The LGM is defined by maximum extent of continental ice sheets, which has nothing to do with temperature. The authors should state explicitly what they understand under the LGM and refer to the relevant literature (e.g., Mix et al., 2001). They are using LGM paleoclimate data and these reflect the above definition of LGM. On page 4, the authors refer to a paper which documents a disappearance of species during the "coldest conditions of the LGM". I wonder whether this is really synchronous with the ice-volume defined LGM? Are the fish remains radiocarbon dated? Do these dates fall within the LGM chronozone? The authors should be aware of the fact that the LGM in this region does not represent the coldest interval of the last glacial (MIS2).

Minor points: The title as it stands is too long, the part after the colon should be dropped and it should begin with: "Ecological modeling of . . .", because this is what the paper really is about. The Abstract needs more structure. I suggest deleting sentences on lines 11-17. The abstract should focus on the results of the study. Page 3: in first line replace the positive and negative excursions by "climatic fluctuations"; delete the reference to mid-Holocene, as it is irrelevant here; delete sentence beginning "Archaeozo-

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ology reveals” as it is irrelevant here. Page 4: line 4 – the correct formulation would be that the remains of these species disappeared from archaeological sites in this region. The reasons for this can be many – shift of habitat of the species offshore or completely away from the region, changes in fishing practices etc. Page 8: line 2 – could the authors please explain what they mean by “best-guess”? This wording is surprising, considering that the authors stated before that they used actual reconstructions of these parameters, not guesses? Page 12: Section 4 should be called “Discussion”, because this is what it is. Page 14: line 7: I am not sure I understand this statement: what exactly do the refugia imply about the position of the ice sheets? The ice extent can be (and has been) reconstructed directly, so how can the position of these implied refugia affect these reconstructions? Fig. 1: the Aquamap key has to be explained. What do the values represent?

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