

Response to the Referees

We appreciate the efforts that both referees have made to compose detailed and thoughtful reports on our manuscript. In some cases, the comments brought up new issues that we were not previously aware of. We responded pointwise to each of the comments below. In almost all cases, we introduced corrections and modifications to the text and figures, while at the same time keeping the final manuscript as concise as possible.

Referee 1

1352/24-1353/1: Explain in more detail, why is it important, to understand how spatial distributions changed at cool climates during LGM, when you wish to predict change in geographic distribution of marine species with future climate warming.

Fish populations have been documented to change distributions since the mid-XXth century. Most of the studies remain unsure on whether climate is to be held solely responsible for the change or if another equally important force (i.e., fishing pressure), may be driving the process (see, e.g., Beare et al., 2004). To confirm that climate alone is responsible, one would need to gather data from fish populations under stressful climatic conditions where fishing pressure could be safely ruled out of the equation. Though the LGM would have been stressful for marine fishes due to its low, rather than high, temperatures, we believe it could represent (in the “negative”?) the scenario we are looking for to confirm “climate” as the main driving force behind disjunctions of fish populations, both under cold or warm climate regimes.

We have added a sentence to the introductory paragraph that captures and clarifies this idea based on published ideas: *‘Although the spatial distribution of marine species may be largely determined by water temperatures (e.g., Kucera et al., 2005; Lenoir et al., 2010), the complicated interactions of marine species groups within ecosystems – with evidence of step-like regime shifts (Beaugrand and Reid, 2003) – make predictions of future range modification difficult (Belyea, 2007), and the best way to predict future marine ecosystem response may be to understand the extreme climate conditions of the past.’*

1356/10: I do not understand the meaning of “a lake in the North Sea”.

We have rechecked the Pampoulie et al. (2008) reference. There is no mistake in the argument used by these authors. They mention the possible glacial refugium in a lake in the southern North Sea twice. They reference a geological survey map as the source of information. We have kept lake idea in the manuscript, but have modified the wording a bit to make it more like Pampoulie et al. (2008).

1365/26-28: The authors state that fish behaviour might have changed because of human exploitation. I wish to draw their attention to two recent papers demonstrating that strong fishing pressure indeed changes vital demographic parameters of fish populations and behavioural traits (Planque et al., J. mar. Syst. 79: 403-417; Perry et al. J.mar. Syst. 79: 427-435). For example, strong fishing pressure removes particularly the older, larger individuals and truncated age structures of fish populations result from this. Potential consequences are, inter alia, reduction in reproductive output, shorter life cycles, reduction of spawning period and recruitment decrease.

We have added the following passages to the paragraph dealing with the change in fish behavior in response to fishing pressure: *‘This is not mere speculation since strong fishing pressure has been*

repeatedly documented to provoke changes in the behaviour of fish populations (Perry et al., 2010; Planque et al., 2010).’ ...

‘Indeed, the aforementioned studies (Perry et al., 2010; Planque et al., 2010) reveal that vital demographic parameters of fish populations, such as a shorter life cycle, can be a response to a systematic fishing of the largest specimens, making certain stocks more vulnerable to extinction. This could have been most easily achieved on the most accessible biotopes (eg., estuaries, shallow waters, etc.) where, even without a particularly high fishing pressure, removal of such fishes could bring about the cascade of changes leading to the extinction of a not-too-large population.’

1369/1-3: The authors cite one paper according to which demersal North Sea fish species have shifted north by 170 km between 1962-2001. However, there are examples from small pelagic fish species which have extended and contracted their area of distribution by several thousand kilometers within a few years associated with climate variability, for example sardines off California (McFarlane et al. 2000. Prog. Oceanogr.47: 147-169), Chile and Japan. Also, anchovies and sardines, which had their northern distribution range up to the Channel area, are found all over the North Sea up to Norway since the mid-1990s (Beare et al. 2004. Mar. Ecol. Prog. Ser. 284: 269-278). A very brief introduction to these and similar papers would strengthen the manuscript.

In the second last paragraph highlighted by the referee, the following passage has been added: ‘Other time series studies evidence that range shifts are in the order of several thousand kilometers in a few years for such pelagic species as sardines and anchovies, due to their non-territorial behaviour and higher dispersal capabilities (McFarlane et al., 2000; Beare et al., 2004).’

Some indication of economic importance of the fish species under consideration should be given. For example: Annual average landings of last 20 years as % of total European catches.

We have consulted FAO Fishstat database product for the numbers that referee recommends. Because of the large changes in the fisheries over 20 years, it makes more sense to quote the latest figures as representative values over the past 5 years. We have added the following sentence to the last paragraph of the introduction: ‘They are also economically important. Of the total European capture production of $\sim 10.0 \times 10^6$ tons in 2008, pollock, haddock, and salmon accounted for $\sim 4.4 \times 10^5$, $\sim 3.0 \times 10^5$, and 1.2×10^3 tons, respectively, with a combined value of approximately 26% of the total US\$6.2 billion for European fisheries export products (FAO Fishstat Plus v. 2.32; <http://www.fao.org/fishery/statistics/software/fishstat/en>).’

Referee 2 (Prof. M. Kucera)

A. 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 parameterization 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 properly thought through.

We appreciate the good critique that Prof. Kucera has given our work.

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

The use of paleoclimatic data is problematic. The authors opted to use the model-interpolated GLAMAP data by Paul and Schafer-Neth (2003), which are convenient to use, but do not represent the current state

of the art. The differences are obvious for sea-ice extent, which could not have been reconstructed explicitly by GLAMAP but is almost entirely the result of a model-based interpolation, and for the Mediterranean, where GLAMAP had not generated any new data. I believe these simplifications have too much of 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).

Prof. Kucera makes a valid point that the most recent palaeoclimatic assessments should be used, and we have added the MARGO palaeo-SST reconstructions on his recommendation, in addition to the Paul and Schafer-Neth (2003) fields. The best practice is to use an ensemble of palaeo-SST reconstructions to assess the uncertainty of the species distributions during the LGM. This is what we have done in the amended version of the manuscript. Following his recommendation, we have also included the point data for the de Vernal ice cover overplotted on top of the Paul and Schafer-Neth (2003) fields.

In the manuscript, we describe the gridding procedure to address the problem that the MARGO fields are actually quite sparse and need to be interpolated to generate the continuous fields for the ENM.

C. 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 Schafer-Neth (2003), which makes statements like ‘conditions in the eastern Mediterranean were not much different from the present’ simply incorrect (see for example Robinson et al., 2006, QSR; Castenada et al., 2010, Paleoceanography).

In the comparison of the GLAMAP and MARGO fields, we point out summertime LGM temperatures for the eastern Mediterranean have been revised downward, following the work of Hayes et al. (2005).

D. 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 ecological range extension of the 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 prediction 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 is very problematic because this basin was at that time an isolated freshwater lake.

Prof. Kucera is correct, in the Discussion section, we have added the passage: ‘*Likewise, the predicted LGM range of the species of our study indicate that there may have been a geographic disjunction between the western Mediterranean and the Adriatic Sea, highlighting that our ENM can only predict the fundamental ecological niche and that the realized niche in the Adriatic Sea and eastern Mediterranean remains less certain*’.

We have added the following passage to clarify model predictions of species presence in the Black Sea and Red Sea: ‘*The predicted fundamental ecological niche in the Black Sea and Red Sea was probably not realized for the species of this investigation because of geographic disjunction*’.

E. The present ecological niche model is hugely oversimplified, being nothing else than 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 with the stated depth range of 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 intersection of bioclimatic envelopes is a powerful technique that is used by Fishbase to show modern marine species distributions (Kaschner et al., 2006; Ready et al., 2010) and is also similar to the approach of Lenoir et al. (2010). The main advantage is its transparency, and it has been shown to perform well in comparison with other ENMs (Ready et al., 2010). We have added a sentence of at the beginning of the introduction to underline why we have used this approach: '*Although there are other ENMs available, important advantages of the method of bioclimatic envelopes are: 1. its transparency in the interpretation of a small dataset (Phillips, 2006; Ready et al., 2010), and 2. proven track record in predicting modern-day ranges of fish species from imperfect survey data (Ready et al., 2010)*'.

It is true that there are vertical depth gradients in the upper ocean so the sea surface temperature is not the same as the temperature at the bottom of the water column on the continental shelf where the fish are living. On the other hand, in the Methods section we cite the judgement of experts that southern range of cod is defined by 10C annual average sea surface temperature isotherm. It is an empirical observation that works to explain the distribution of this species. Also, the ENM for cod that was constructed by Bigg et al. (2008) is based on SST. Likewise, the surface temperature criterion has been used by Kaschner et al. (2006) and Ready et al. (2010) for the Aquamap project to predict modern species ranges on the basis of survey data (even though the habitat of some species is deep). Lenoir et al. (2010) has also justified this approach stating that temperatures at the surface and 100 m depth have a very high degree of correlation. Our use of SST as a defining criterion for the distribution of these fish is in line with most previous work dealing with resource assessments and palaeoclimatic reconstructions. We have added the sentence to the Methods section: '*As well, Lenoir et al. (2010) point out that there is a high correlation between surface temperatures and temperatures at 100 m, and this supports widespread practice in resource studies and palaeoclimatic reconstructions of using SST for the upper ocean conditions.*'.

F. 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 was the shape of the error function for the 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.

For our review paper to explain unusual features of fish distribution in a handful of archaeological sites, we used a subjective procedure to assess environmental thresholds that define the niche envelope of the species. This is appropriate where the archaeozoological dataset that we want to explain is so sparse, and it is in line with palaeoclimatic reconstructions especially before the Pleistocene where there is an emphasis on the meaning of particular guide fossils. We have rewritten the first paragraph of the Methods section to capture these ideas, and in particular, we have added the sentence: '*Although resource assessments (Kaschner et al., 2006; Lenoir et al., 2010; Ready et al., 2010) and palaeoclimatic reconstructions (Kucera et al., 2005) have followed a statistical approach where large databases have been available, sparse archaeozoological or palaeontological datasets have value if they contain a striking species ('indicator species' or 'guide fossil', Peacock, 1989) that must indicate a certain threshold temperature, and this is highlighted in palaeoenvironment reconstructions further back in time (e.g., Huber et al., 2000).*'

G. 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 parameterization. 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?

We believe that the species ranges depend primarily on water temperature and that range on the continental shelf is determined primarily by depth limitations of the species. The temperature criterion for the distribution of marine species is in line with Prof. Kucera's own beliefs as described in Hayes et al. (2005). It is also in line with other ENM's that are used to describe fish distributions: Fishbase Aquamap (Kaschner et al., 2006; Ready et al. 2010) and Bigg et al. (2008). On the basis of these previous studies, it is reasonable to suggest that the niche of the fishes is effectively constrained by these two parameters.

In the Discussion, we point out there may have been circumstances in the past where the fish may have changed the rules governing their niche. It is based on two archaeozoological reports that describe an unusual distribution of fish remains. We point out, however, that the implication is that overfishing has removed these species from nearshore areas, but not necessarily affected the outer (deeper) limits of the depth distribution or the temperature dependence. Thus, the two archaeozoological reports do not refute the findings of our ENM.

H. (1) 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? (2) 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 the bathymetry envelope is not defined or explained at all. What exactly does it represent? How was the choice of values guided? (3) I am puzzled by the fact that the envelopes as applied for the individual species 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?

(1) For the present day distribution of the sea surface temperature, we have used the World Ocean Atlas (WOA, 2005), similar to what Prof. Kucera used in his publication, Hayes et al. (2005). Prof. Kucera's impression of a time mismatch between temperature and fish datasets is not correct. The WOA is based on a massive database of temperature observations that stretch back over a century. The averaging and gridding procedure means that recent temperature warming trends are given little weight. This feature of averaging out long-term instrumental records of SST over the last century has made WOA especially useful for Prof. Kucera's palaeoclimatic community to calibrate core-top data for modern conditions (Mix et al., 2001).

For the fish locations, there is a similar long-term weighting that is implicit in the Fishbase data and also the expert assessments of Whitehead et al. (1986). With such an extended time frame in the climatologies for SST and fish location survey, these two datasets are not mismatched in time and reflect average conditions mostly from the second half of the 20th century.

(2) Depth is important for determining how far the fish range offshore (Kaschner et al., 2006; Ready et al., 2010). We have added a sentence in the Methods section to clarify this: *In addition to thermal preferences, the species also have a preferred depth habitat (given by Fishbase and Whitehead (1986)), which defines the seaward extent of the range.*

(3) Except for salmon, there are not many molecular marker studies for the other three species to elucidate their current population structure. The published studies reveal that the species have a weak population structure that was erased during the LGM and has not had a chance to be effectively re-established in the short intervening time interval. We have located the most important molecular marker publications for haddock, pollock and shad and included the following sentence in the amended manuscript: *'This is particularly true for haddock, pollock, and allis shad where the few molecular marker studies have indicated weak population structure among stocks, which was effectively erased during the LGM (see Jamieson and Birley (1989) and Reiss et al. (2009) for haddock; Charrier et al. (2006) for pollock; and Alexandino and Boisneau (2000) for shad).'*

I. 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.

(1) This argument is related to G above where Prof. Kucera expressed concern about whether the temperature and maximum depth criteria effectively captured the niche of the fish in the study. The structure of our ENM follows that used by modern fisheries resource experts involved in the Fishbase project (Kaschner et al., 2006; Ready et al., 2010), and also Lenoir et al. (2010).

(2) The issue of covariance is interesting: the link between the temperature and depth criteria. It has not been addressed in the studies on which we patterned our own work (Kaschner et al., 2006; Ready et al., 2008; Bigg et al., 2008; Lenoir et al., 2010). It is a concept that can only really be addressed by micropalaeontologists like Prof. Kucera, who have access to the largest databases of palaeoclimatic data. It is difficult to address this issue with just a few archaeozoological reports. We have added the following sentence to the Methods section: *'Following the convention used to assess modern fish resource distributions with large databases (Kaschner et al., 2006); Ready et al., 2010), we have assumed that the salient niche features for the species in our study are captured with each environmental parameter acting independently'*.

J. 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).

We appreciate Prof. Kucera guiding us to the relevant literature clarifying the chronology, definition and temperature conditions of the LGM. In the introductory paragraph, we have used ~21000 calendar years before present as the palaeoclimatic consensus for the LGM, and referenced Mix et al. (2001) and Sarntheim et al. (2003) for further information about the issue. We have removed descriptions for the LGM being the time of coldest temperatures.

The archaeozoological data that we discuss is presented in Table 1. Some of it is radiocarbon dated but most is assessed on the basis of archaeological levels. It is interesting that some remains seem to fall outside the LGM chronozone, suggesting a persistence of the North Atlantic ecosystems in the

western Mediterranean until the beginning of the Holocene. We have emphasized this in the introduction.

K. 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 is really about.

Referee 1 felt that the title effectively represented the content of the publication. Our manuscript is really a review of existing information, which includes some ecological modeling but also a synthesis of archaeozoological data, molecular markers, and glacial refugia. The manuscript does not focus on ecological modelling. Following the suggestion of Referee 1, we have kept the original title.

L. The Abstract needs more structure. I suggest deleting sentences on lines 11-17. The abstract should really focus on the results of the study.

The abstract is normal length for scientific papers – about 250 words. It conforms to the guidelines of the journal website: *The abstract should be intelligible to the general reader without reference to the text. After a brief introduction of the topic, the summary presents the key points of the article and provides future directions where research could focus on in the near future.* The lines identified by Prof. Kucera summarize our motivation for undertaking this project and highlight the future research directions for other scientists.

M. Page 3: in the first line replace the positive and negative excursions by “climatic fluctuations”; delete the reference to the mid-Holocene, as it is irrelevant here; delete sentence beginning “Archaeozoology reveals” as it is irrelevant here.

The passage ‘positive and negative excursions’ in the first sentence has been changed according to Prof. Kucera’s suggestion. We have kept the reference to the mid-Holocene in the following sentence because it helps to understand the last clause. We have kept the sentence beginning ‘Archaeology reveals’. We disagree that this sentence is irrelevant, but believe instead that it encapsulates an important theme in the manuscript.

O. Page 4, line 4 – the correct formulation would be that the remains of these species disappeared from the 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 practice, etc.

The sentence has been modified to specify that the species disappeared from the archaeological sites of the region.

P. 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?

Prof. Kucera is correct that it is a bad choice of wording to describe the paleo-environmental fields that we used. We have replaced ‘best guess fields’ with ‘published reconstructions’.

Q. Page 12: Section 4 should be called ‘Discussion’, because this is what it is.

The change has been made.

R. 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?

The issue of the location, thickness and evolution of the ice sheets is not clear as Prof. Kucera believes, and this point is highlighted by Mix et al. (2001). If one talks to the geophysicists working on isostatic rebound, they need a priori assessments for the glacier location, glacier thickness, and glacier timing. The nature of their models means that there is not an obvious correct answer for these parameters, but a combination of different a priori conditions will lead to similar post-glacial isostatic rebound. Ice extent is therefore known only approximately, and this point comes across in Figure 8 where the ice sheet locations of Prof. Peltier have the square, blocky shape that give the spatial resolution of his best guess assessments. Along with Prof. Lambeck, Prof. Peltier is one of the most skilled and respected scientists of this scientific branch. If there is independent information that an ice sheet could not have been in a certain place at a certain time (as indicated by molecular markers, for example), the geophysicists consider the updated evidence seriously.

We have modified the relevant sentence in the Discussion section: *‘The identification of some of these glacial refugia pose important questions about the locations of the European ice sheets (Sejrup et al., 2005), which has been been identified as an important open question in a recent palaeoclimatological review (Mix et al., 2001)’*.

S. Fig. 1: the Aquamap key has to be explained. What do these values represent?

We have added the following sentence to the figure caption to explain the Fishbase Aquamaps: *‘The Fishbase Aquamap is a metric of relative environmental suitability from that is based on the application of environmental envelopes to explain fish survey data in terms of gridded fields of bathymetry, temperature, salinity, ice cover, and primary production (Kaschner et al., 2006; Reedy et al., 2010)’*. The two references given are detailed, and the interested reader can find extra information about the technique. Other references to the Fishbase Aquamap approach have been added to the manuscript.