

1 **Refugia of Marine Fish in the Northeast Atlantic During the**  
2 **Last Glacial Maximum: Concordant Assessment from**  
3 **Archaeozoology and Palaeotemperature Reconstructions**

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## 1 **Abstract**

2 Archaeozoological finds of the remains of marine and amphihaline fish from the Last Glacial  
3 Maximum (LGM) *ca.* 21 ka ago show evidence of very different species ranges compared to  
4 the present. We show how an ecological niche model (ENM) based on palaeoclimatic  
5 reconstructions of sea surface temperature and bathymetry can be used to effectively predict  
6 the spatial range of marine fish during the LGM. The results indicate that the ranges of  
7 marine fish species that are now in northwestern Europe were displaced significantly  
8 southward from the modern distribution. There is strong evidence that there was an invasion  
9 of economically important fish into the western Mediterranean through the Straits of  
10 Gibraltar, where they were exploited by Palaeolithic human populations. There has been  
11 much recent interest in the marine glacial refugia to understand how the ranges of the  
12 economically important fish species will be displaced with the future climate warming.  
13 Recent ENM studies have suggested that species ranges may not have been displaced far  
14 southward during the coldest conditions of the LGM. However, archaeozoological evidence  
15 and recent LGM ocean temperature reconstructions indicate that there were large range  
16 changes, and certain marine species were able invade the western Mediterranean. These  
17 findings are important for ongoing studies of molecular ecology that aim to assess marine  
18 glacial refugia from the genetic structure of living populations, and they pose questions about  
19 the genetic identity of vanished marine populations during the LGM. The research presents a  
20 challenge for future archaeozoological work to verify palaeoclimatic reconstructions and  
21 delimit the glacial refugia.

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## 23 **1 Introduction**

24 To predict how the geographic ranges of marine species in northwest Europe will change with  
25 future climate warming, it is important to understand their environmental response  
26 characteristics and how their spatial distributions changed during the climate fluctuations of  
27 the Pleistocene glaciations. Although the spatial distribution of marine species may be largely  
28 determined by water temperatures (e.g., Kucera et al., 2005; Lenoir et al., 2010), the  
29 complicated interactions of different marine species within ecosystems – with evidence of  
30 step-like regime shifts (Beaugrand and Reid, 2003) – make predictions of future range  
31 modification difficult (Belyea, 2007). The best way to predict the future response of marine  
32 ecosystems may be to understand documented changes under the extreme climate conditions

1 of the past. Much palaeoclimatic information exists for the cold conditions of the Last Glacial  
2 Maximum (LGM) *ca.* 21 000 calender years before present (Mix et al., 2001; Sarnthein et al.,  
3 2003) as well at the mid-Holocene warm period 6000 years ago (Bradley, 1999), but the  
4 response of marine species across the full range of the temperature changes is not well-  
5 known. The LGM is particularly important to address this issue because it represents a  
6 situation of large perturbation of temperatures from the present condition and therefore  
7 affords the clearest picture of how marine species respond to environmental temperature  
8 change. Archaeozoology reveals important information about past climate change and  
9 corroborates palaeoclimatic information from other sources. Palaeoclimatic evidence  
10 suggests that Scandinavia was covered by glacial ice sheets, and in northern Europe  
11 permafrost conditions extended to the Massif Centrale in France with tundra conditions  
12 extending into Spain (e.g., Butzer, 1964; Bradley, 1999). In these climatic conditions,  
13 northern terrestrial animal species ranged over western and southwestern Europe where they  
14 were utilized by human cultures, and their remains are found in the palaeolithic  
15 archaeological sites of the region (e.g., Butzer, 1964). Animal and plant species survived in  
16 glacial refugia in the Iberian peninsula, Italy, and the Balkans, and it is from these centers that  
17 Europe was recolonized during the Holocene. Genetic evidence has complemented  
18 archaeozoological evidence in elaborating on the paths of colonization for terrestrial animals,  
19 freshwater fish, and plants (e.g., Hewitt, 2000; Stewart and Lister, 2001; Provan and Bennett,  
20 2008). For the marine fish species, there is much less information, mostly because the  
21 archaeozoological record has mostly been lost as sea levels rose by approximately 120 m  
22 since the LGM (e.g., Provan and Bennett, 2008). However, genetic studies (e.g., Maggs et al.,  
23 2008) and the sparse archaeozoological evidence indicate startling shifts in the geographic  
24 ranges of some species in response to climate change. Here, we present an overview of how  
25 the ranges of four marine and amphihaline species changed during the LGM and apply a  
26 simple ecological niche model (ENM) to explain how these altered ranges are consistent with  
27 sea surface temperature (SST) changes during the glacial period.

28 Identifications of fish remains from archaeological sites have revealed large changes in the  
29 ranges of some marine and amphihaline species during the LGM. The migratory allis and  
30 twaite shad (*Alosa alosa* and *A. fallax*, respectively) and European eel (*Anguilla anguilla*)  
31 disappeared from archaeological sites on the Atlantic drainage basins of France and  
32 Cantabria, Spain during the LGM, and probably survived in refugia further to the south (Le  
33 Gall, 2008). For the eel, this refugium was probably on the Atlantic coasts of Portugal and

1 Morocco (e.g., Kettle et al., 2008). The glacial refuge of the shad is unclear, but remains have  
2 been discovered on the upper Tagus River system at Aridos-1 from the Mindel-Riss  
3 interglacial approximately 300 ka BP (Morales, 1980; Le Gall, 2000), and it is likely to have  
4 survived the LGM on the Iberian Peninsula and northwest Africa. From southern Spain, the  
5 boreal gadid species, haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius*  
6 *pollachius*) have been reported by Rodrigo (1994) for the Cueva de Nerja near Malaga dating  
7 to the LGM. These results were significant because these species are currently found in  
8 northwest Europe, and the southernmost range for haddock and pollock is currently the Bay  
9 of Biscay and northern Portugal, respectively (Whitehead et al., 1986). The most recent  
10 analyses of the LGM deposits from the Cueva de Nerja have revealed that the northern gadids  
11 (including saithe *Pollachius virens*, cod *Gadus morhua*, and ling *Molva molva*) make up more  
12 than 30% of the identified fish remains and thus represented a significant economic presence  
13 among the exploited fish (Cortés-Sánchez et al., 2008; Morales-Muñiz and Roselló-Izquierdo,  
14 2008). The exploitation of gadids continued for an extended period of time after the LGM  
15 until the early Holocene as sea levels were returning to present levels and sea surface  
16 temperatures approached present values.

17 Among the most spectacular shifts in species ranges have been reports of the remains of  
18 Atlantic salmon (*Salmo salar*) in archaeological sites from the Mediterranean drainage basins  
19 of France, Spain, and Italy dating from the LGM up to the early Holocene. Additional small  
20 art objects unambiguously depicting salmon have been located at the Grand grotte de Bize on  
21 a Mediterranean drainage basin (Le Gall, 1994a). These reports from late Palaeolithic–early  
22 Mesolithic sites in France, Spain, and Italy (Juan-Muns i Plans, 1985; Juan-Muns i Plans et  
23 al., 1991) suggest the presence of resident salmon populations in the western Mediterranean  
24 Sea. The current southernmost range of Atlantic salmon in northwest Europe is northern  
25 Portugal, which indicates that immigrant populations would have had to pass through the  
26 Straits of Gibraltar when temperatures in southern Spain during the LGM were similar to  
27 northern Europe at present. However, the archaeozoological evidence is contested. Many of  
28 the sites in southern France are near Atlantic drainage basins, and it is possible that the  
29 Atlantic salmon remains in the Mediterranean watersheds may have been transported as part  
30 of a seasonal migration of fishermen (Le Gall, 1983, 1984, 1992, 1994a, 1994b). This has  
31 even been invoked to explain Atlantic salmon finds in the more distant Menton caves on the  
32 French-Italian border (Rivière, 1886; Clark, 1948). As well, many of the early identifications  
33 of Atlantic salmon at the Caune de Belvis and the Grotte Jean-Pierre I by Desse and Granier

1 (1976) and at Grimaldi (Barme Grande II) have been subsequently questioned and revised to  
2 trout (*Salmo trutta*) by Le Gall (1994a), Desse-Berset (1994), and Desse and Desse-Berset  
3 (2002), respectively. It is difficult to distinguish Atlantic salmon and trout from their skeletal  
4 elements, and many of the early salmon identifications were made mainly on the basis of the  
5 unusual size of vertebral elements. The revision of the initial identifications may have been  
6 made on reflection of the zoogeographic implications of there being endemic Mediterranean  
7 Atlantic salmon populations during the LGM. Up until now, the prevailing paradigm has  
8 been that the SST in the western Mediterranean during the LGM was too high to meet the  
9 oxygen requirements of the species (Le Gall, 1983, 1984, 1994b). On the other hand, recent  
10 unambiguous determinations of Atlantic salmon in Solutrean levels in the Cueva de Nerja  
11 indicate that ocean temperatures were cool enough during the LGM to permit the passage of  
12 the species through the Straits of Gibraltar (Morales-Muñiz and Roselló-Izquierdo, 2008).

13 Part of the reason why these archaeozoological finds are important is that there are few  
14 studies that have investigated how the geographic distribution of marine species changed  
15 during the LGM, and most of this is based on molecular markers. Hence, there are few a  
16 priori hypotheses of what fish species should be found in archaeozoological collections. This  
17 situation contrasts strikingly with the state of knowledge for terrestrial plants and animals and  
18 freshwater fish, where there is much zooarchaeological and genetic evidence for LGM refugia  
19 in southern Europe and recolonization pathways to northern Europe during the Holocene  
20 (e.g., Hewitt, 2000; Stewart and Lister, 2001; Provan and Bennett, 2008). Most of the  
21 important economic marine fish species have a high gene flow and weak genetic structure that  
22 make it difficult to link local population structure with the existence of glacial refugia.  
23 Reviewing the genetic structure and LGM history of cod, Pampoulie et al. (2008) speculated  
24 that glacial refuge populations survived on the Rockall Plateau, southwest Ireland, Irminger  
25 Sea, and possibly also a glacial lake in the southern North Sea. However, these predictions  
26 are confusing because the LGM palaeoclimatic reconstruction of Paul and Schäfer-Neth  
27 (2003) suggests that the ocean temperatures and sea ice conditions of these areas may have  
28 been too severe to serve as refugia. The issue of assessing the Mediterranean presence of  
29 North Atlantic marine species is important not only for determining the glacial refugia of  
30 economically important fish, but also for establishing an accurate paradigm for  
31 palaeoenvironmental reconstructions using sediment core records. There is currently some  
32 uncertainty about the provenance of some North Atlantic planktonic species found in

1 sediment cores of the western Mediterranean, and this represents a puzzle for  
2 palaeoenvironmental reconstructions (Rohling et al., 1998).

3 ENMs attempt to predict the spatial distribution of a species based on databases of climatic  
4 (e.g., temperature, rainfall) and other information, and the most robust examples might predict  
5 the spatial distribution based on threshold envelopes of temperature, for example, above and  
6 below which no viable populations are observed to occur. ENMs have been successfully  
7 applied to explain the present-day distributions of some terrestrial species and then carefully  
8 calibrated to predict the past distributions during the LGM using palaeoclimatic model data  
9 (Waltari et al., 2007). However, for marine species these models have only recently been  
10 applied, and for some species, there are sometimes errors in the predictions. The extension of  
11 ENMs to explain marine fish distributions during the LGM has recently been performed by  
12 Bigg et al. (2008) who used two algorithms to predict the glacial distribution of cod.  
13 Although one algorithm, based on a maximum entropy method, predicted suitable LGM  
14 habitat along the Atlantic coast of northwest Europe and also large areas of the Mediterranean  
15 and the Black Sea, the actual occupation of these areas in southern Europe was judged  
16 unlikely because of geographic disjunction. A second algorithm, based on ecophysiological  
17 constraints, predicted only limited southward displacement during glacial times, and this  
18 clearly shows important disagreements with recent fossil evidence from the Cueva de Nerja in  
19 southern Spain (e.g., Cortés-Sánchez et al., 2008; Morales-Muñiz and Roselló-Izquierdo,  
20 2008). Hence, there is still a crucial gap in the understanding of the influence of oceanic  
21 conditions that governed the spatial distribution of the marine species during the LGM. The  
22 issue is important because future climate warming scenarios predict that the spatial ranges of  
23 important species are expected to shift northward (e.g., Perry et al., 2005) and important  
24 amphihaline species, like salmon, are predicted to become extinct in the southern parts of  
25 their range (Lassalle and Rochard, 2009).

26 In this contribution, we consider the changes in spatial distribution of four species during the  
27 LGM: haddock, pollock, the eastern Atlantic shad species, and Atlantic salmon. Although  
28 most marine species must have experienced range changes during the LGM, these four  
29 species have been selected mainly because of the long-standing conundrum suggested by the  
30 unusual locations of their subfossil evidence. They are also economically important. Of the  
31 total European capture production of  $\sim 10.0 \times 10^6$  tons in 2008, pollock, haddock, and salmon  
32 accounted for  $\sim 4.4 \times 10^5$ ,  $\sim 3.0 \times 10^5$ , and  $1.2 \times 10^3$  tons, respectively, with a combined value of

1 approximately 26% of the total US\$6.2 billion for European fisheries export products (FAO  
2 Fishstat Plus v. 2.32; <http://www.fao.org/fishery/statistics/software/fishstat/en>). In the  
3 Section 2 (Methods), we present the current understanding of the environmental requirements  
4 of the fish species, together with the ENM algorithms used to determine their present  
5 distribution. In Section 3 (Results), we present an alternative ENM approach to estimate  
6 LGM distributions and use palaeoclimatic SST reconstruction from the LGM to estimate how  
7 the species ranges changes. In Section 4 (Discussion), we synthesize the information,  
8 indicating consistencies between our results and emerging genetic information from other  
9 marine species, and we point out potentially promising lines of research for the future.

10

## 11 **2 Methods: An Ecological Niche Model (ENM) based on temperature and** 12 **bathymetry**

13 Our predictions of the LGM distribution of marine species are based on a simple ENM that is  
14 constructed from the intersection of two environmental conditions (SST and bathymetry).  
15 Based on the approximate correspondence between the environmental fields and expert  
16 assessments of the species' ranges, we define the approximate present day envelope of  
17 threshold environmental conditions that circumscribes the species niche. Then, we infer the  
18 LGM distributions based on published reconstructions of the SST and bathymetry during  
19 glacial times. Important advantages of this method of bioclimatic envelopes are: 1. its  
20 transparency in the interpretation of a small dataset (Phillips, 2006; Ready et al., 2010), and 2.  
21 proven track record in predicting modern-day ranges of fish species from imperfect survey  
22 data (Ready et al., 2010). Although resource assessments (Kaschner et al., 2006; Lenoir et  
23 al., 2010; Ready et al., 2010) and palaeoclimatic reconstructions (Kucera et al., 2005) have  
24 followed a statistical approach where large databases of have been available, sparse  
25 archaeozoological or palaeontological datasets have value if they contain a striking species  
26 ('indicator species' or 'guide fossils', Peacock, 1989) that must indicate certain threshold  
27 conditions. This has been exploited in palaeoenvironmental reconstructions further back in  
28 time where the data record may not be as rich as for the LGM (e.g., Huber et al., 2000).  
29 Following the convention used to assess modern fish resource distributions with large  
30 databases (Kaschner et al., 2006; Lenoir et al., 2010; Ready et al., 2010), we have assumed  
31 that the salient niche features for the species in our study are captured with each  
32 environmental parameter acting independently.

1 The present day distribution of the four marine and amphihaline species is shown in Fig. 1.  
2 Information is available from several sources, but we present expert assessments from two  
3 recognized authorities: Fishbase (<http://www.fishbase.us/search.php>) and Whitehead et al.  
4 (1986). Other references are broadly consistent with the chosen expert summaries in terms of  
5 the geographic distribution, but may add extra regional information, for example, about where  
6 a species may be particularly common (ICES-Fishmap: Haddock (2009)). Presenting only an  
7 envelope of presence-absence information with minimal information about abundance for  
8 some species, the information in Whitehead et al. (1986) is the simplest and most robust. The  
9 Fishbase Aquamaps present a graded zonation of distribution that is based on sea surface  
10 temperature, sea surface salinity (SSS), productivity, bathymetry, and an annual ice cover (see  
11 Kaschner et al. (2006) and Ready et al. (2008)). Although the extra information implied by  
12 the abundance appears useful, the algorithm is calibrated based on survey information, and it  
13 may not reproduce expert assessments. For example, for Atlantic salmon in Fig. 1d, there is a  
14 predicted distribution in the Mediterranean and Black Seas based on habitat conditions, but  
15 the present distributions of wild populations are limited to the Atlantic coasts of northwest  
16 Europe as indicated by Whitehead et al. (1986).

17 The minimum and maximum summertime (July–August–September, JAS) SST envelopes  
18 that define the southern and northern extent of each species are shown in Fig. 1. The SSTs  
19 are taken from a present-day climatological atlas at 1° resolution that is shown in Fig. 2 (from  
20 the World Ocean Atlas of Levitus, 2006; abbreviated WOA05). Temperature is recognized as  
21 an important determinant of the spatial distribution of fish (Lenoir et al., 2010), and this is  
22 grounded on theoretical considerations of oxygen limitation and the temperature-dependence  
23 of the metabolic processes (Pörtner, 2001; Pörtner and Knust, 2007). Although species show  
24 temperature-dependence at every stage in their life cycle, Bigg et al. (2008) consider  
25 temperatures in late spring and early summer as the primary factor affecting the spawning  
26 range of cod, and Lenoir et al. (2010) confirm the importance of temperature as a defining  
27 criterion for the youngest fish stages. For their ENMs, Bigg et al. (2008) use SST as the  
28 metric of the spatial distribution to generate distribution maps. This does not at first seem like  
29 an obvious metric for bottom temperature conditions, which are important for a demersal  
30 species like cod. On the other hand, the 10°C annual average SST isotherm provides an  
31 important functional definition of the southern limit of the spatial distribution of cod on both  
32 sides of the Atlantic Ocean (Brander, 1996). As well, Lenoir et al. (2010) point out that there  
33 is a high correlation between surface temperatures and temperatures at 100 m, and this

1 supports the widespread practice in resource studies and palaeoclimatic reconstructions of  
2 using SST for the upper ocean conditions to determine species distributions. For our  
3 study, we selected the summertime SST (JAS) as the primary criteria defining the spatial  
4 distribution of the species, instead of the wintertime (December–January–February, DJF) or  
5 annual average SST. In addition to thermal preferences, the species also have a preferred  
6 depth habitat (Lenoir et al., 2010), which defines the seaward extent of the range and this has  
7 been taken from Fishbase and Whitehead et al. (1986). Along with bathymetry limits  
8 (ETOPO-5, <http://www.ngdc.noaa.gov/mgg/global/etopo5.HTML>), the isotherm envelopes  
9 form the basis of the present day distribution ranges shown in Fig. 3. These maps were  
10 generated by matching the summertime SST with the species distributions shown in Fig. 1,  
11 and a 1°C uncertainty in the definition of the thermal envelopes does not change the  
12 conclusions of this analysis.

13 The chosen temperature envelopes are broadly consistent with the temperature thresholds of  
14 the four species observed during the field and laboratory studies. For haddock, ICES-  
15 Fishmap: Haddock (2009) gives a minimum temperature threshold of 6.5°C, and Brodziak  
16 (2005) reports the juvenile and adult fish have been caught during fisheries surveys between  
17 temperatures of 2–16°C. Peck et al. (2003) gives the temperature of maximum growth at  
18 12°C, which is approximately at the center of the summer climatological envelope of 6–18°C  
19 that has been used to define its range in Fig. 1. For pollock, also a demersal species, the  
20 empirically-defined summer climatological SST envelope of 10–18°C for the northern and  
21 southern range of the species (Fig. 1) is close to the physiological range of temperatures of 9–  
22 18°C, outside of which severe growth decreases are observed (Person-Le Ruyet et al., 2006).  
23 These temperatures thresholds for haddock and pollock are broadly consistent with Lenoir et  
24 al. (2010) using a statistical analysis of a larger database. For the allis shad, which spawns in  
25 freshwater in springtime, the observed migration from the ocean takes place when river  
26 temperatures are between 13.3–23°C as measured by Acolas *et al.* (2006), and this defines the  
27 proper freshwater environment for spawning and early rearing of young. This observed  
28 temperature range is very close to the empirical climatological average summer SSTs that  
29 have been used to define the spatial distribution (13–22°C; shown in Fig. 1c). For the twaite  
30 shad the lower temperature envelope may be slightly reduced compared to allis shad to  
31 explain its more northerly spatial distribution of occasional occurrence in Norway and Iceland  
32 (but not spawning at these northern locations).

1 For Atlantic salmon, the northern and southern boundaries of the range are empirically  
2 determined as the 6°C and 19°C summer SST isotherms (Fig. 1d). There are different  
3 possible reasons for this temperature envelope. The fish is highly susceptible at the post-  
4 smolt stage just after it migrates from the rivers to the ocean in spring–early summer.  
5 Although the mechanism is unclear, stock size is negatively correlated with June SST, and  
6 post-smolts are negatively affected by the early arrival of warm ocean temperatures  
7 (Friedland et al., 2003). The empirical summer SST envelope is similar to the observed  
8 temperature of the downstream migration in Norway in June: 2.5–15.5°C (Hvidsten et al.,  
9 1998). Another hypothesized mechanism to explain the spatial range of adult salmon relates  
10 to its high dissolved oxygen requirements ( $>7 \text{ mg O}_2 \text{ L}^{-1}$ ), whose saturation value depends  
11 mainly on the temperature but also the salinity of seawater (Le Gall, 1983, 1984). Le Gall  
12 (1994b) stated that the southern distribution of the species – and particularly its absence in the  
13 Mediterranean – is governed by this oxygen requirement, and the theoretical basis of the  
14 temperature dependence of aerobic activity has been more recently clarified by Pörtner and  
15 Knust (2007).

16 Figure 3 also shows the locations of the unusual archaeological features for the time interval  
17 from the LGM to the early Holocene (Table 1). For haddock, pollock, and Atlantic salmon,  
18 the LGM distribution is far outside of the present ranges, suggesting that there were extreme  
19 changes in the past distributions during the glacial periods.

20 The probable spatial distribution of the fish species during the LGM were independently  
21 assessed from LGM SST and bathymetry criteria. Although CLIMAP Project Members  
22 (1976) produced the first global view of LGM climate conditions, recent efforts have led to  
23 an updated community consensus of LGM conditions. These have been downloaded from the  
24 Glacial Ocean Atlas (<http://www.glacialoceanatlas.org/>): the gridded surface data fields of  
25 Paul and Schäfer-Neth (2003) and the synthesis dataset of MARGO Project Members (2009).  
26 The background of these datasets highlights the unresolved challenges of this field, with the  
27 fields of Paul and Schäfer-Neth (2003) representing a compilation of objective measurements  
28 and subjective expert opinion to achieve the best guess gridded field that is necessary for a  
29 modelling study. By contrast, the dataset of MARGO Project Members (2009) employs a  
30 more conservative approach to devise statistics for  $5^\circ \times 5^\circ$  latitude-longitude boxes where data  
31 occur, and this means that there are data gaps and resolution problems using the sparse record  
32 of deep sea cores. The interpolation issue of the point determinations of palaeo-SSTs is still

1 an unresolved issue (Schäfer-Neth et al., 2005), but it is important for ENM studies such as  
2 ours, which seek to trace a pathway of favorable environmental conditions between ocean  
3 basins. We have therefore used a simple scheme to interpolate the dataset of MARGO Project  
4 Members (2009) onto the  $1^{\circ}\times 1^{\circ}$  grid used by Paul and Schäfer-Neth (2003), using a  
5 weighting factor based on inverse square distance that follows broadly on the WOA05  
6 approach. We consider data within a threshold distance of 1800 km to ensure that  
7 information is propagated from at least one point of the original dataset, and this interpolated  
8 product is hereafter referred to as ‘MARGO-interpolation’. Although this simple  
9 interpolation scheme does not take account of the preferred zonal projection of information in  
10 the North Atlantic Ocean (i.e., as is implicitly assumed by Paul and Schäfer-Neth (2003)  
11 using expert determinations of isolines), the MARGO palaeotemperature information is dense  
12 enough that realistic SST fields are produced. Taken together, the fields of Paul and Schäfer-  
13 Neth (2003) and MARGO-interpolation represent a range of palaeo-SST conditions to test the  
14 predictions of our ENM, and this follows the recommended practice of Nogués-Bravo (2009)  
15 to assess the uncertainty of reconstructed palaeoclimate, where this is available.

16

### 17 **3 Results: Fish distributions during the Last Glacial Maximum (LGM)**

18 The two palaeo-SST datasets for the northeast Atlantic from Paul and Schäfer-Neth (2003)  
19 and MARGO-interpolation are shown in Figure 4 for winter (January-February-March) and  
20 summer (July-August-September). The difference between the LGM reconstructions and the  
21 present day climatology (Fig. 5) illustrates the temperature changes in the northeast Atlantic  
22 during the LGM. Most of the mid-latitude areas exhibit some cooling during the LGM, with  
23 the most significant decreases around the UK in summer (exceeding  $12^{\circ}\text{C}$  for the Paul and  
24 Schäfer-Neth (2003) dataset). In the Mediterranean Sea, temperature decreases are less  
25 severe, with  $\sim 8\text{--}10^{\circ}\text{C}$  summertime decreases in the west and  $\sim 4\text{--}6^{\circ}\text{C}$  summertime decreases  
26 in the east. Summer temperature conditions at the Strait of Gibraltar during the LGM would  
27 have been similar to the south coast of the UK at present. Although the spatial features of the  
28 the two palaeo-SST reconstructions are broadly similar, the newer information of MARGO  
29 Project Members (2009) suggests temperatures of the Nordic Seas were not as cold as Paul  
30 and Schäfer-Neth (2003), while temperatures in the eastern Mediterranean were several  
31 degrees cooler than previously believed especially in summer (Hayes et al., 2005).

1 The LGM distributions of fish species (Fig. 6) have been assessed using ENMs based on these  
2 two palaeo-SST fields and the palaeotopography fields of Peltier (1994). All species show a  
3 significant southward displacement away from their present ranges, but the cooler palaeo-SST  
4 predictions of Paul and Schäfer-Neth (2003) have especially important implications for the  
5 location of the LGM northern boundaries. Both ENM results are consistent with the available  
6 archaeozoological results. The Cueva de Nerja in the Strait of Gibraltar was well within the  
7 estimated LGM range of haddock and pollock, and the ENMs predict that these species may  
8 have populated the western Mediterranean Sea as far east as the Adriatic Sea, or even the  
9 Aegean Sea according to the MARGO-interpolation fields. The predicted fundamental  
10 ecological niche in the Black Sea and Red Sea was probably not realized for the species of  
11 this investigation because of geographic disjunction.

12 Atlantic salmon could likewise swim through the Strait of Gibraltar to form populations in the  
13 western Mediterranean Sea, consistent with its archaeozoological presence in the  
14 Mediterranean watersheds of Spain, France, and Italy during the LGM. This species is cold-  
15 adapted and is found at present in northern Europe as far south as northern Portugal (although  
16 there are historical reports of the species as far south as the Guadalquivir River up to 20<sup>th</sup>  
17 century (B. Elvira, verbal communication)). Both ENMs for the LGM predict that it  
18 maintained a continuous presence on the Gironde–Dordogne river system through the LGM  
19 where its uninterrupted archaeological presence across the LGM has been documented.

20 The allis shad requires warmer SST conditions, and both ENMs indicates that it was displaced  
21 from the Atlantic watersheds of France during the LGM, and this is consistent with its  
22 apparent absence from archaeological sites in the Dordogne region (Le Gall, 2008). The  
23 recent identification of the remains of (allis) shad in Magdalenian levels of the Lapa dos  
24 Coelhos archaeological site on the Tagus watershed of central Portugal gives support to the  
25 existence of a glacial refuge in the southern Iberian Peninsula during the LGM (Roselló and  
26 Morales, 2010). The model prediction of a theoretical niche extension into the eastern  
27 Mediterranean is not much further than its current documented eastern limit at Sicily, but it is  
28 also unclear how much of this fundamental niche would have been occupied with potential  
29 competition with other shad species already in the Mediterranean (Nogués-Bravo, 2009).

30 A second important message in Fig. 6 and Fig. 7 is the extent to which the species ranges  
31 were reduced during the southern displacement and confined to the continental slope regions.  
32 For the Paul and Schäfer-Neth (2003) SST fields in Fig. 6, the LGM ranges were decreased to

1 approximately 19, 19, 33, and 14% of the present range for haddock, pollock, allis shad, and  
2 salmon, respectively. For the MARGO-interpolation fields in Fig. 7, the corresponding LGM  
3 range was about 53, 31, 47, and 39% of the modern day range. The results for the gadids,  
4 haddock and pollock, are broadly consistent with the reduction of the range of cod in the  
5 North Atlantic reported by Bigg et al. (2008): ~20% of present day extent. Although the  
6 largest contiguous area of species is presently the North Sea, the largest contiguous area for  
7 all four species during the LGM may have been the shallow shelf area between Tunisia and  
8 Sicily. Significantly, the MARGO-interpolation fields suggest that the cold-adapted species,  
9 haddock and salmon, may have maintained a presence in the Nordic seas, although accuracy  
10 of the palaeo-SST reconstructions in this region are still uncertain (MARGO Project  
11 Members, 2009).

12

#### 13 **4 Discussion**

14 The ENM results presented here give a very different prediction of LGM glacial refuge areas  
15 for some of the economically important fish species of northwest Europe compared with the  
16 few previous published studies. The main finding is that the glacial refuge of four highly  
17 vagile fish species are significantly shifted away from their present biogeographical range  
18 mostly in northwest Europe. There is strong evidence from two palaeo-SST reconstructions  
19 and archaeozoological identifications that cold-adapted gadids and Atlantic salmon invaded  
20 the western Mediterranean through the Strait of Gibraltar. The results are startling because  
21 the predicted LGM spatial ranges are different from previous assumptions and modelling  
22 studies. For example, Pampoulie et al. (2008) speculate that cod survived the LGM on the  
23 Rockall Plateau and the Irminger Sea in a reduced subarea of the present range (Fig. 8). Also,  
24 the ecophysiological model Bigg et al. (2008) predicted that cod survived the LGM in  
25 continental shelf areas of northwest Europe and that populations were displaced only slightly  
26 further south compared to the present locations. The predictions of our ENM are supported  
27 by subfossil archaeological evidence of the fish species in archaeological sites far to the south  
28 of their presently-recognized southern boundaries.

29 It is difficult to independently verify the predictions of our ENM with genetic information.  
30 Molecular markers are not well-suited to elucidating the glacial refugia of highly vagile fish  
31 species (Gysels et al., 2004b) like the examples of our study. Highly mobile fish can follow  
32 optimal sea temperatures during changing climate conditions, so that the location of their

1 glacial refugia is unclear. This is particularly true for haddock, pollock, and allis shad where  
2 the few molecular marker studies have indicated weak population structure among stocks,  
3 which was effectively erased during the LGM (see Jamieson and Birley (1989) and Reiss et  
4 al. (2009) for haddock; Charrier et al. (2006) for pollock; and Alexandino and Boisneau  
5 (2000) for shad). For some species, the population age estimated from molecular markers  
6 may be inexplicably older than the known length of habitat occupation since the LGM  
7 (Francisco et al., 2009). Fish of low dispersal ability are valuable tracers of glacial refugia,  
8 and the sand goby (*Pomatoschistus minutus*) is one such model marine species whose present  
9 population structure is a legacy of range constrictions during the glacial period (Gysels et al.,  
10 2004a; Larmuseau et al., 2009). The population has a contiguous distribution in northern  
11 Europe, but is fragmented in the Mediterranean, consistent with a species that expanded south  
12 during glaciations and retreated northwards during the interglacials as climate conditions  
13 became warmer during the Holocene.

14 For some species, molecular marker studies reveal patterns of recolonization from glacial  
15 refugia. Many of the hypothesized refugia in Fig. 8 are located in different parts of  
16 southwestern Europe and northwestern Africa, south of the ice sheets and sea ice cover (Fig.  
17 9). The Bay of Biscay, Iberian Peninsula, and Macaronesia (Madeiras, Azores, and Canaries)  
18 have all been invoked as glacial refugia of various marine species with a present distribution  
19 in northwest Europe. This is consistent with the predictions of our SST-based ENMs.  
20 However, smaller periglacial refugia – the Hurd Deep near the mouth of the glacial Channel  
21 River and southwest Ireland – have also been inferred from genetic evidence for other species.  
22 These regions may have been subject to ice cover for part of the year (Fig. 9), but this does  
23 not preclude them as glacial refugia for marine species (Gómez et al., 2007). Other refugia  
24 have been hypothesized further north in northwest Scotland, northern North Sea, Faeroe  
25 Islands, Iceland, and Norway for species adapted to colder conditions and longer sea ice  
26 periods (Fig. 9). The identification of some of these glacial refugia pose important questions  
27 about the locations of the European ice sheets (Sejrup et al., 2005), which has been identified  
28 as an important open question in a recent palaeoclimatological review (Mix et al., 2001).

29 Atlantic salmon is an important exception whose genetic structure reveals a complex and  
30 interesting recolonization history, which introduces another dimension to our results. Our  
31 study suggests that Brittany/Hurd Deep was the northernmost range for this species, and that  
32 the species was simply displaced southward during the LGM. The unusual genetic structure

1 in the Baltic Sea may have resulted from population isolation during the complex marine  
2 transgression history resulting from the interplay of sea level changes and the isostatic  
3 rebound in the early Quaternary (Lepiksaar, 2001, p. 40). However, it has also been used to  
4 infer recolonization from possible glacial refugia in the southern North Sea or beyond the  
5 eastern edge of the Fennoscandian ice sheet (e.g., Consuegra et al., 2002; Langefors, 2005;  
6 King et al., 2007; but see also Makhrov et al., 2005). A westward recolonization pathway  
7 into the Baltic Sea from the White Sea after the LGM was previously perceived as unlikely.  
8 On the other hand, the genetic signatures of the other marine species indicate a possible link  
9 between extant populations in the Baltic Sea (and eastern Atlantic) with those further east in  
10 the Arctic and Pacific Oceans (Luttikhuisen et al., 2003; Addison and Hart, 2005; Nikula et  
11 al., 2007).

12 The ENM predictions of Bigg *et al.* (2008) for cod are valuable because they are among the  
13 first that have been developed for the marine domain. The model is being used for other  
14 North Atlantic species to infer LGM spatial distributions (Provan et al., 2009). Bigg et al.  
15 (2008) used two different ENMs for cod that were calibrated to present conditions, and it is  
16 important to investigate the possible reasons for the partial discrepancy of their models with  
17 our results. The maximum entropy ENM used by Bigg et al. (2008) was based on  
18 bathymetry, SST, and SSS. This produced an LGM distribution for cod that stretched from  
19 northwest Europe into large areas of the Mediterranean, consistent with the report of  
20 archaeozoological remains from the Cueva de Nerja. The ecophysiological ENM used by  
21 Bigg et al. (2008) incorporated a spawning temperature threshold of 0–9°C between February  
22 and June. This is different from the temperature range that we have used for haddock (i.e., an  
23 analogous demersal gadid species with a similar range) in Fig. 1a, whose spatial range we  
24 have defined to lie between the summertime isotherms of 6–18°C (or the 3–12°C wintertime  
25 isotherms, not shown). The ENM temperature envelope used by Bigg et al. (2008) was  
26 slightly lower than our choice. It may have resulted in northern offsets of both the northern  
27 and southern present-day species boundaries when evaluated against field surveys, as noted in  
28 the original publication. When projected back to the LGM, these thermal envelopes have  
29 implications for the predicted glacial refugia. The direct comparison of the different  
30 temperature criteria is difficult between the ecophysiological model of Bigg et al. (2008) and  
31 the temperature envelopes of our study, partly because strong seasonal variation of the North  
32 Atlantic near surface ocean temperature. An important message in Bigg et al. (2008) is that  
33 the LGM distributions of the marine species can be predicted with just a few parameters

1 (bathymetry and SST), and this is an important feature of robust simplicity that is maintained  
2 in our study.

3 The assumption of ‘niche stability through time’ forms the foundation of all ENM approaches  
4 (Nogués-Bravo, 2009), but it has not been addressed by Bigg et al. (2008) or in our study, and  
5 it is difficult to prove without a large database of independent information to delimit past  
6 distributions. For our work, it translates into the assumption that the fish responded to ocean  
7 temperature and depth during the LGM in the same way as at present. On the other hand,  
8 some evidence indicates that the fish may have changed their behavior in the past for  
9 unknown reasons, possibly associated with human exploitation or climate change. For  
10 example, Beerenhout (1994) pointed out the remains of full-grown haddock in early Neolithic  
11 sites in the Netherlands where they were caught in brackish water estuarine environments.  
12 The report is startling because the species is currently subject to commercial exploitation at  
13 the northern edge of the North Sea at approximately 200 m depth (ICES-Fishmap: Haddock  
14 (2009)). The Neolithic human populations of the Netherlands did not have the technological  
15 means to secure haddock from its 20<sup>th</sup> century habitat, and there is an important implication  
16 that the fish range may have changed to a very different stable state in response to human  
17 exploitation. From the late-Palaeolithic period, a similar message is presented by the haddock  
18 finds from the Epipalaeolithic levels of the Cueva de Nerja, and these fish were also probably  
19 obtained as part of an inshore, shallow-water fishery. Changes in the trophic structure of  
20 marine ecosystems have been inferred from changes in species assemblages and sizes based  
21 on evidence from Stone Age archaeological sites, and there is an implication that it may have  
22 been due to human exploitation (Desse and Desse-Berset, 1993; Morales and Roselló, 2004).  
23 This may be linked with alterations in preferred habitats of fish populations. In assessing the  
24 possibility of a Mesolithic deep-sea fishery of northern Europe, Pickard and Bonsall (2004)  
25 have had to address the provenance of certain species in archaeological sites that presently  
26 occur offshore in deep water, and specifically identify bluefin tuna (*Thunnus thynnus*; i.e., an  
27 offshore species with observed spawning migrations inshore), golden redfish (*Sebastes*  
28 *marinus*), hake (*Merluccius merluccius*), halibut (*Hippoglossus hippoglossus*), tusk (*Brosme*  
29 *brosme*), and wolffish (*Anarhichas lupus*). Although the authors assume that ‘the habitat  
30 preferences of prehistoric fish populations were broadly similar to those of modern species’,  
31 the presence of significant numbers of remains of so many deep water species in Mesolithic  
32 archaeological sites, forces consideration that the fish may have changed their habitat  
33 preferences. This is not mere speculation since strong fishing pressure has been repeatedly

1 documented to provoke changes in the behaviour of fish populations (Perry et al., 2010;  
2 Planque et al., 2010). Alternatively, such shifts may have been provoked by the systematic  
3 fishing of inshore populations that may have led to local extinctions of those living in the  
4 shallowest and most accessible waters. Indeed, the aforementioned studies (Perry et al., 2010;  
5 Planque et al., 2010) reveal that vital demographic parameters of fish populations, such as a  
6 shorter life cycle, can be a response to a systematic fishing of the largest specimens, making  
7 certain stocks more vulnerable to extinction. This could have been most easily achieved on  
8 the most accessible biotopes (e.g., estuaries, shallow waters, etc.) where, even without a  
9 particularly high fishing pressure, removal of such fishes could bring about the cascade of  
10 changes leading to the extinction of a not-too-large population.

11 The results of our study represent an evolving picture of the marine species distributions that  
12 will be revised with future work on palaeoclimatic environmental reconstructions and  
13 modelling activities. Palaeoclimatic reconstructions of SST have evolved since the initial  
14 CLIMAP Project Members (1976) assessments, and there are ocean areas where the LGM  
15 assessments of SST and SSS are unclear and where different proxy methods may disagree  
16 (MARGO Project Members, 2009). On the other hand, from the archaeozoological  
17 perspective, there appears to be a convergence of evidence for the climatic conditions in the  
18 Mediterranean basin during the LGM. The LGM SST reconstruction in Figure 4 and 5  
19 indicates that whereas western Mediterranean SST conditions decreased drastically and were  
20 low enough to support populations of northern gadids and Atlantic salmon, annual average  
21 SSTs in the eastern Mediterranean were only about 1.5–3°C cooler than present (Hayes et al.,  
22 2005). Marine ecosystems in the eastern Mediterranean were not subjected to the same  
23 intense cooling conditions as in the western basin and may have been similar to modern  
24 conditions. The new LGM temperature reconstructions force a departure from an earlier  
25 paradigm that SST's were too warm to permit the migration of these species through the Strait  
26 of Gibraltar (e.g., Le Gall, 1994b). Rather than a barrier at the Strait of Gibraltar, our ENM  
27 indicates that there may have been an important thermal boundary in the middle of the  
28 Mediterranean at Sicily, and this is consistent with the genetic studies of other marine species  
29 that show an important division at Tunisia-Sicily saddle (Domingues et al., 2005). Likewise,  
30 the predicted LGM range of the species of our study indicate that there may have been a  
31 geographic disjunction between the western Mediterranean and the Adriatic Sea, highlighting  
32 that our ENM can only predict the fundamental ecological niche and that the realized niche in  
33 the Adriatic Sea and eastern Mediterranean remains less certain. On the other hand, the

1 significance of the barrier represented by the Italian Peninsula on the free migration between  
2 populations in the western Mediterranean and the Adriatic Sea may help to explain the  
3 distinct genetic signatures of certain marine species in these two basins (Gysels et al., 2004a;  
4 Debes et al., 2008; Maggio et al., 2009).

5 Future experimental work may aim to verify the predictions of the ENM that have been  
6 presented here. For example, genetic studies might aim to determine the structure of the  
7 vanished populations in the Mediterranean (Nielsen and Hansen, 2008). For the  
8 archaeological LGM Atlantic salmon population in northern Spain, Consuegra et al. (2002)  
9 found a dominant haplotype that has almost vanished from modern populations in the region.  
10 However, the question of the genetic structure of the hypothesized LGM salmon populations  
11 in the Mediterranean is open. The amount of exchange through the Straits of Gibraltar during  
12 the LGM is unknown, and it is not clear if the Mediterranean population, at the extreme of the  
13 species' range, had the opportunity to develop its own genetic signature.

14 Our ENM makes predictions about the extent of the expansion of haddock, pollock, allis shad,  
15 and Atlantic salmon into the central Mediterranean that can only be unequivocally resolved  
16 with further archaeozoological studies. The ENM effectively explains observations of LGM  
17 fish species distributions at the Strait of Gibraltar and in southern France, but it also makes  
18 predictions of a potential ecological niche presence as far east as Sicily and the Adriatic Sea.  
19 The southernmost distribution of Atlantic salmon is predicted to be at approximately the  
20 latitude of northern Morocco, but there are few Palaeolithic archaeological sites in this area to  
21 test the ENM predictions. One alternative approach that has not been exploited by  
22 archaeozoologists is the quantification of fish otoliths from shallow sediment cores on the  
23 continental shelf. The concept has been explored by Elder et al. (1996) who used the otoliths  
24 of a small fish species *Ceratoscopelus maderensis* off the eastern seaboard of the United  
25 States to demonstrate significant changes in range between glacial and postglacial times.  
26 Otoliths of cod were also recovered in their bottom samples. Although the importance of  
27 these finds was immediately recognized to assess the LGM distribution of an important  
28 economic species, the sample density was too low to generate meaningful statistics. There is  
29 also potential evidence from the mollusc remains in shallow marine deposits and  
30 archaeological sites. Malatesta and Zarlenga (1986) cite many examples of indicator  
31 molluscs ('Northern Guests') as evidence of repeated species invasions (and retreats) of the  
32 Mediterranean Sea from northwest Europe during the coldest intervals of the Pleistocene

1 glaciations. For example, the range of the Atlantic quahog (*Arctica islandica*) extended into  
2 the western Mediterranean Sea during the LGM, but the species became extinct in its southern  
3 European domain approximately 9800 years BP and currently does not survive south of  
4 Brittany (Froget et al., 1972; Dahlgren et al., 2000). Along with the invasion of Atlantic fish  
5 through the Strait of Gibraltar during the LGM, the presence of these molluscs may force a re-  
6 interpretation of LGM planktonic ecosystem assemblages from sediment cores in the western  
7 Mediterranean (Rohling et al., 1998). Although ENMs and genetic evidence provide  
8 indications of past species' ranges and refugia, physical evidence provided by fossil or  
9 subfossil material provides the most unambiguous identification of actual glacial refugia.

10 Ultimately, the importance of understanding the past distributions of economic species during  
11 the LGM is to assess their thermal niche and predict how their ranges might change with  
12 future climate warming. Analyzing fish survey time series from the North Sea, Perry et al.  
13 (2005) calculated that the ranges of demersal species have shifted north approximately 170  
14 km between 1962–2001. Other studies present evidence of rapid range shifts on the order of  
15 several thousand kilometers over a few years for such pelagic species as sardines and  
16 anchovies, due to their nonterritorial behaviour and higher dispersal capabilities. Predictions  
17 of future temperature increases have been used to predict the extinction of migratory species  
18 from the southern parts of their ranges (e.g., Lassalle and Rochard, 2009), but the calibration  
19 of these models depends on how species responded to climatic temperature perturbations in  
20 the past. The LGM results presented here capture the southern displacement of certain marine  
21 species under the coldest temperature conditions. The warm conditions during the mid-  
22 Holocene warm period offer a potential proxy for future climate warming. At this time, warm  
23 water species like the European sea bass (*Dicentrarchus labrax*) were displaced from their  
24 historically-recognized range south of the British Isles to become economically important for  
25 the Mesolithic cultures of Denmark (e.g. Enghoff et al., 2007) and the German Baltic Sea  
26 coast (Heinrich, 2001; Schmölcke et al., 2006). Likewise, the Atlantic quahog, whose  
27 present northern distribution stops at the White Sea, ranged to Spitsbergen, western Greenland  
28 and far across the northern coast of Russia during the warmer climate conditions of the mid-  
29 Holocene (Dahlgren et al., 2000). The archaeozoological evidence thus provides critical data  
30 to predict how the spatial ranges of marine species may change in the coming decades and  
31 centuries.

32

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5

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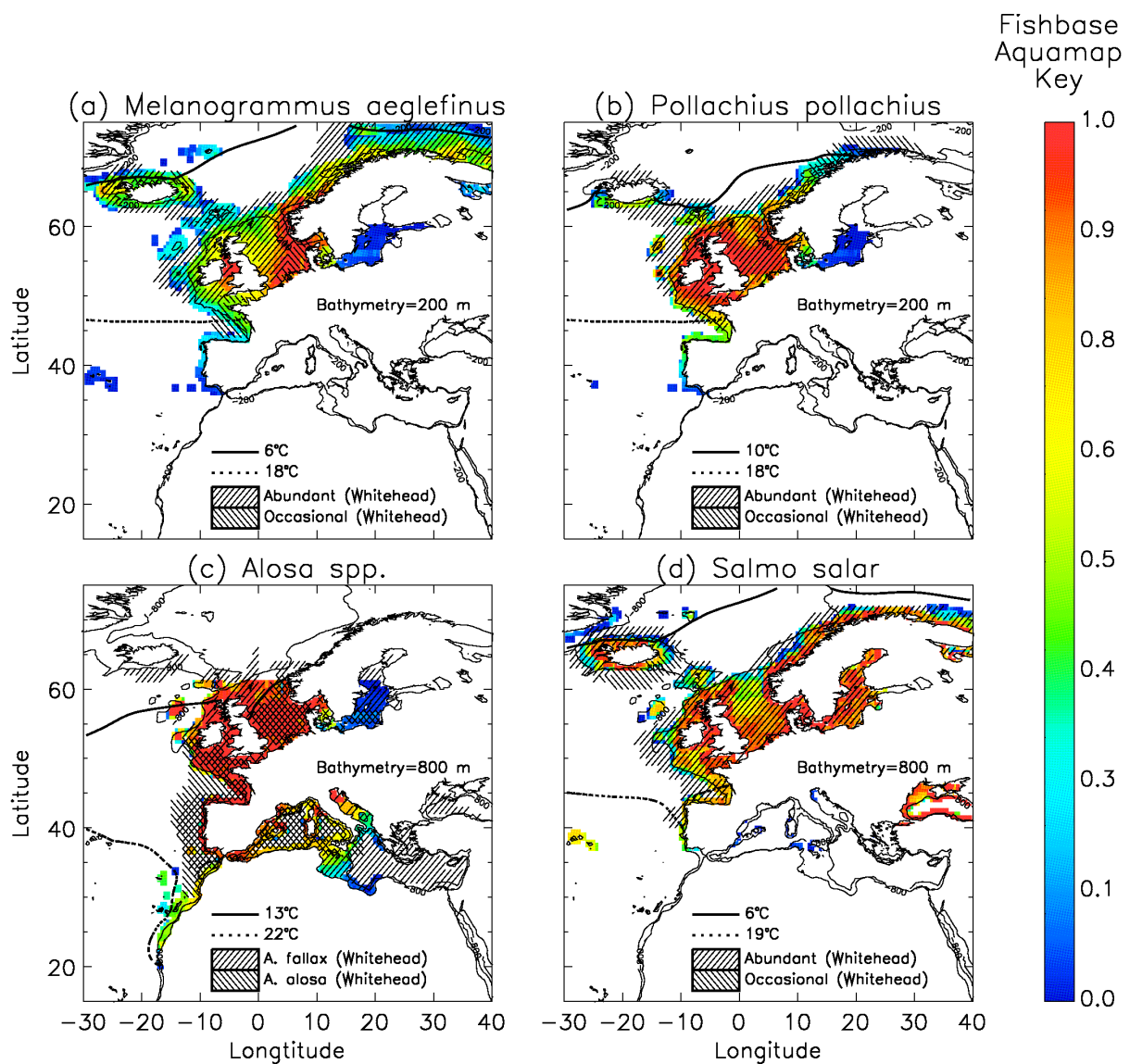
1 Table 1. Location of presence/absence of the remains (or artwork) of haddock, pollock, shad,  
 2 and Atlantic salmon in pre-Holocene archaeological sites outside their present geographic  
 3 range. The indices in the table identify the location of the archaeological sites in Fig. 3 and 6.  
 4 Allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*) are placed together in the table  
 5 because their archaeozoological remains are often difficult to distinguish. (C. Bonsall reports  
 6 an error in Table 1 of Pickard and Bonsall (2004), which shows the Mesolithic remains of  
 7 allis shad at Advik, Varanger fjord, Norway but is not found in the primary source of Renouf  
 8 (1989)).

Species	Archaeological site	Time period	Reference
Haddock ( <i>Melanogrammus aeglefinus</i> )	1 Cueva de Nerja, Spain	LGM/Gravettian & Solutrean (c. 24– 17.5 ky BP)	Rodrigo (1994), Aura Tortosa et al. (2002), Cortéz-Sánchez et al. (2008), Morales-Muñiz and Roselló-Izquierdo (2008)
Pollock ( <i>Pollachius pollachius</i> )	1 Cueva de Nerja, Spain	LGM/Gravettian & Solutrean (c. 24– 17.5 ky BP)	Rodrigo (1994), Aura Tortosa et al. (2002), Cortéz-Sánchez et al. (2008), Morales-Muñiz and Roselló-Izquierdo (2008)
Shad ( <i>Alosa alosa</i> and <i>A. fallax</i> )	1 Pégourié, Lot, France ( <i>A. alosa</i> in Atlantic drainage)	Absence during LGM; small percentage at level 7 (12250 ±350 uncal BP); majority of fish remains at 11000 BP in levels 4–6	Le Gall (1993, 1994b, 1995, 2000), Martin and Le Gall (2000)
	2 Sous-Balme, l’Ain, France ( <i>A. alosa</i> or <i>A. alosa</i> )	Sauveterriens anciens, 9000 BP	Le Gall (1994b, 2000)

*rhodensias* in  
Mediterranean  
drainage)

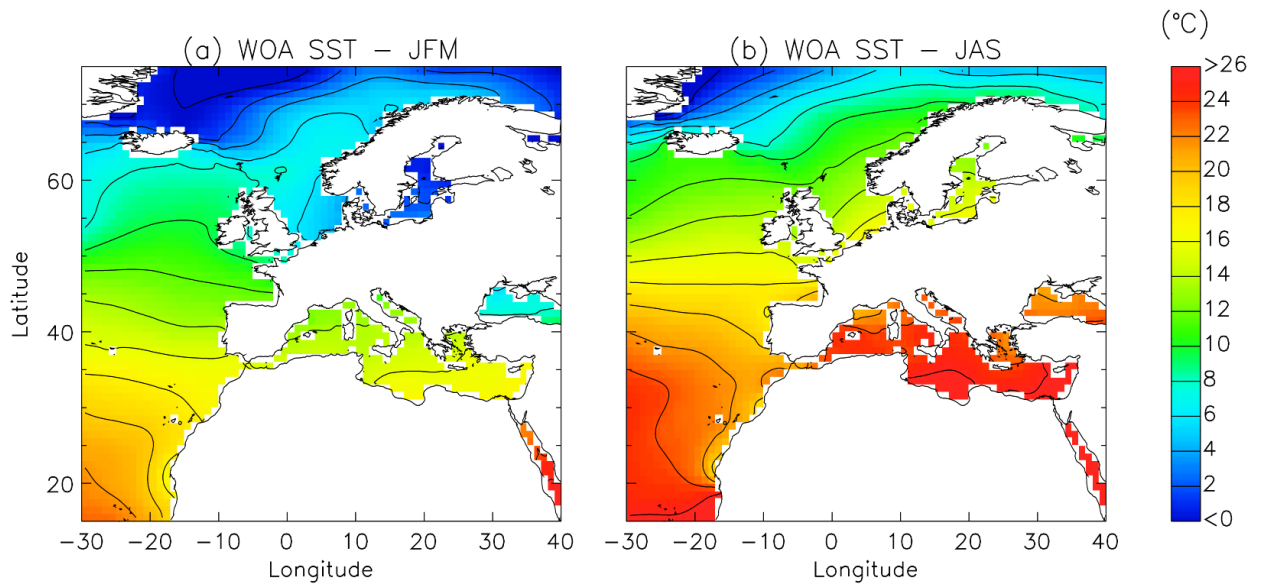
	3	Aridos-1, Tagus River, Spain (Atlantic drainage)	Mindel-Riss Interglacial (~300 ka BP)	Morales (1980), Le Gall (2000)
	4	Lapa dos Coelhos, Almonda tributary of Tagus River, Portugal	Magdalenian	Roselló and Morales (in press)
Atlantic salmon ( <i>Salmo salar</i> )	1	Grotte Jean-Pierre I, Saint-Thibaud-de-Couz, Savoie, France	Magdalénien supérieur Mésolithique ancien	Desse and Granier à (1976); evidence disputed by Desse-Berset (1994)
	2	L'Abeurador, France	Younger Dryas and Preboreal	Le Gall (1983, 1984, 1994a)
	3	Caune de Belvis, Aude, France	Levels 2, 3, 4 (~12270±280 uncal BP)	Desse and Granier (1976), Juan-Muns i Plans et al. (1991); evidence disputed by Le Gall (1994a)
	4	La Grande Grotte de Bize, Aude, France (artwork)	Upper Magdalenien (12550±210 uncal BP)	Le Gall (1994a, Le Gall, 2001)
	5	Canecaude 1, Aude, France	Middle Magdalenian (14230±160 uncal BP)	Le Gall (1994a)
	6	La Grotte Gazel, Aude, France	Middle Magdalenian–Azilien	Costamagno and Laroulandie (2004; citing Desse-Berset,

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- |    |  |  |  |
|----|--|--|--|
| 7  | La Grotte de l'Oeil, Aude, France        | Upper Magdalenian (13800–12300 BP)             | Le Gall (1994a), Costamagno and Laroulandie (2004)   |
| 8  | L'Arbreda, Serinyà, Girona, Spain        | Gravettian, Solutrean                          | Juan-Muns i Plans (1985), Juan-Muns (1987), Juan-Muns i Plans et al. (1991)                          |
| 9  | Davant Pau, Serinyà, Girona, Spain       | Solutrean                                      | Juan-Muns i Plans (1985), Juan-Muns i Plans et al. (1991)  |
| 10 | Reclau Viver, Serinyà, Girona, Spain     | Solutrean                                      | Juan-Muns i Plans (1985), Juan-Muns i Plans et al. (1991)  |
| 11 | Baoussé-Roussé, Grottes de Menton, Italy | Palaeolithic                                   | Rivières (1886)  |
| 12 | Barme Grande, Grimaldi cave, Italy       | ?  | Juan-Muns i Plans et al. (1991; citing Clark, 1948)  |
| 13 | Cueva de Nerja, Spain                    | Solutrean (18420±530, 17940±200, 15990±260 BP) | Morales-Muñiz and Roselló-Izquierdo (2008) (large <i>Salmo</i> sp identified as <i>Salmo salar</i> ) |
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 2 Figure 1. Spatial distribution of (a) haddock (*Melanogrammus aeglefinus*), (b) pollock  
 3 (*Pollachius pollachius*), (c) allis and twaite shad (*Alosa alosa* and *Alosa fallax*), and (d)  
 4 Atlantic salmon (*Salmo salar*). Information is from the Fishbase Aquamap (colour-scale) and  
 5 atlas of Whitehead et al. (1986; denoted by ‘Whitehead’ and shown by hatching). The  
 6 Fishbase Aquamap is a metric of relative environmental suitability that is based on the  
 7 application of environmental envelopes to explain fish survey data in terms of gridded fields  
 8 of bathymetry, temperature, salinity, ice cover, and primary production (Kaschner et al., 2006;  
 9 Ready et al., 2010). The bathymetry is from ETOPO-5, with sea level and the single  
 10 indicated contour (200 m or 800 m) plotted on the map. The two shad species are plotted  
 11 together because their archaeozoological remains are often difficult to distinguish.

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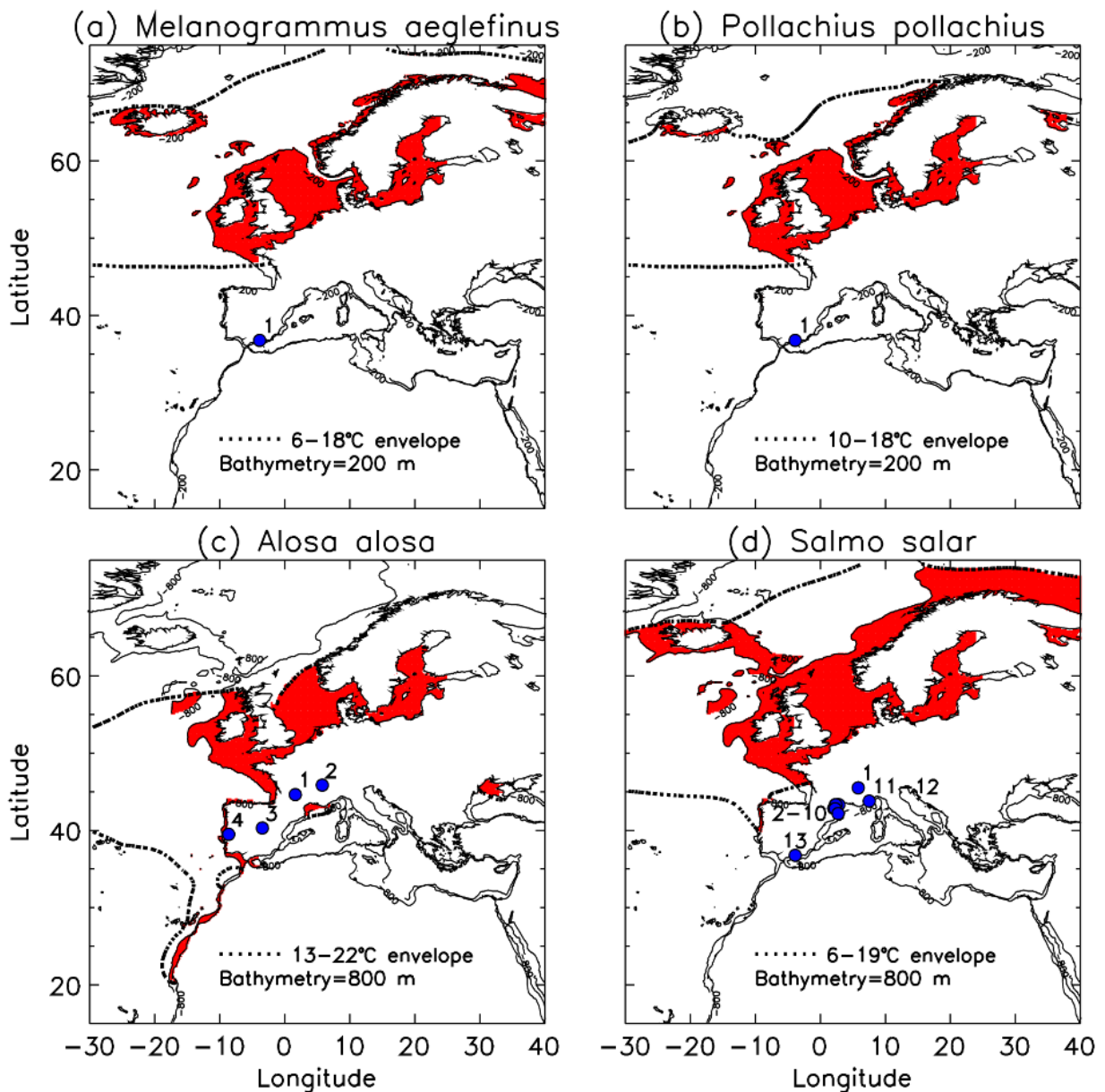


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2 Figure 2. Climatological sea surface temperature of the northeast Atlantic in (a) winter  
 3 (January, February, March) and (b) summer (July, August, September) from WOA05  
 4 (Levitus, 2006).

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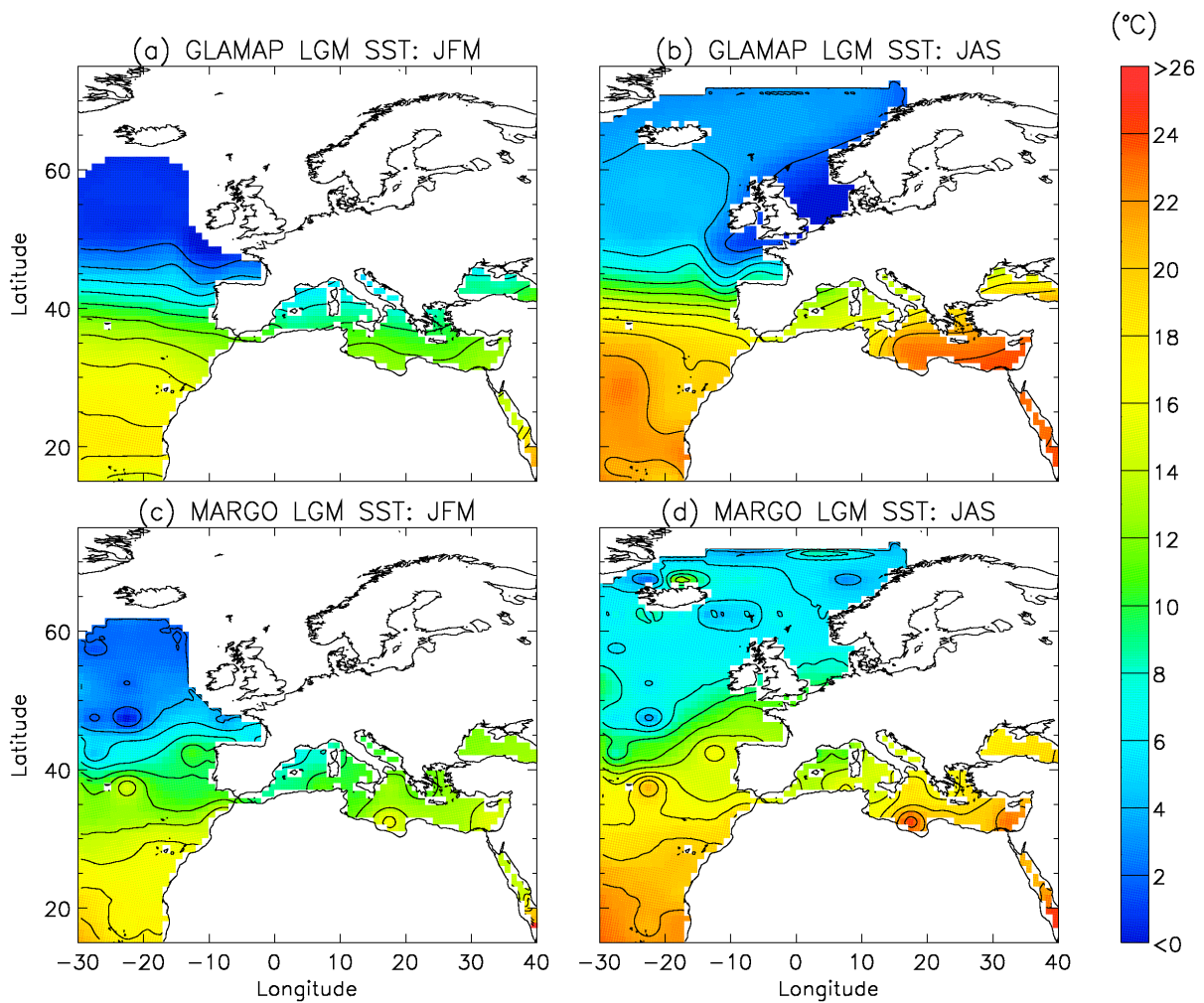
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 2 Figure 3. Simplified species ranges using simplified criteria based on the summer SST and  
 3 bathymetry envelopes shown in each diagram. The archaeozoological finds are given by blue  
 4 dots with the number key given in Table 1. For (a) and (b), the archaeological site is 1. Cueva  
 5 de Nerja, Spain. For (c), the archaeological sites are 1. Pégourié, Atlantic France, 2. Sous  
 6 Balme, Mediterranean France, 3. Aridos-1, Spain, and 4. Lapa dos Coelhos, Portugal. For  
 7 (d), the archaeological sites are 1. Grotte Jean-Pierre I, Mediterranean France, 11. Baoussé-  
 8 Roussé, Grottes de Menton, Italy, 12. Barne Grande, Grimaldi caves, Italy, 13. Cueva de  
 9 Nerja, Spain, and a cluster of different sites along the Mediterranean coast of France and  
 10 Catalonia with labels 2–10. The bathymetry is from ETOPO-5 with sea level and the single  
 11 additional bathymetric contour indicated on the maps.

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4 Figure 4. Climatological SST from the LGM as determined by Paul and Schäfer-Neth (2003)  
5 for (a) winter and (b) summer and by MARGO Project Members (2009) for (c) winter and  
6 summer. The MARGO-interpolated fields were calculated using a simple interpolation  
7 method based on an inverse distance-squared weighting factor using the  $5^{\circ} \times 5^{\circ}$  summary data  
8 of MARGO Project Members (2009).

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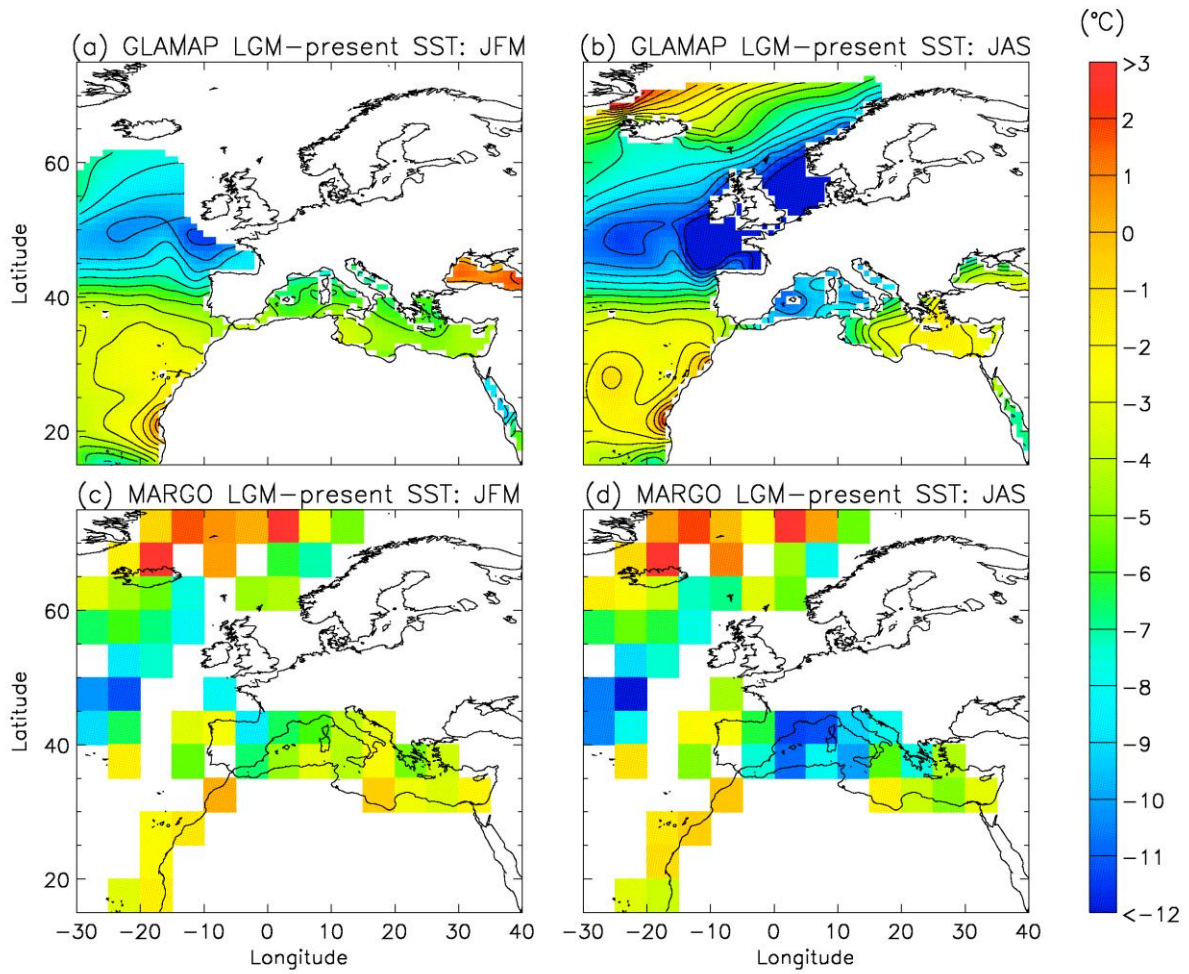
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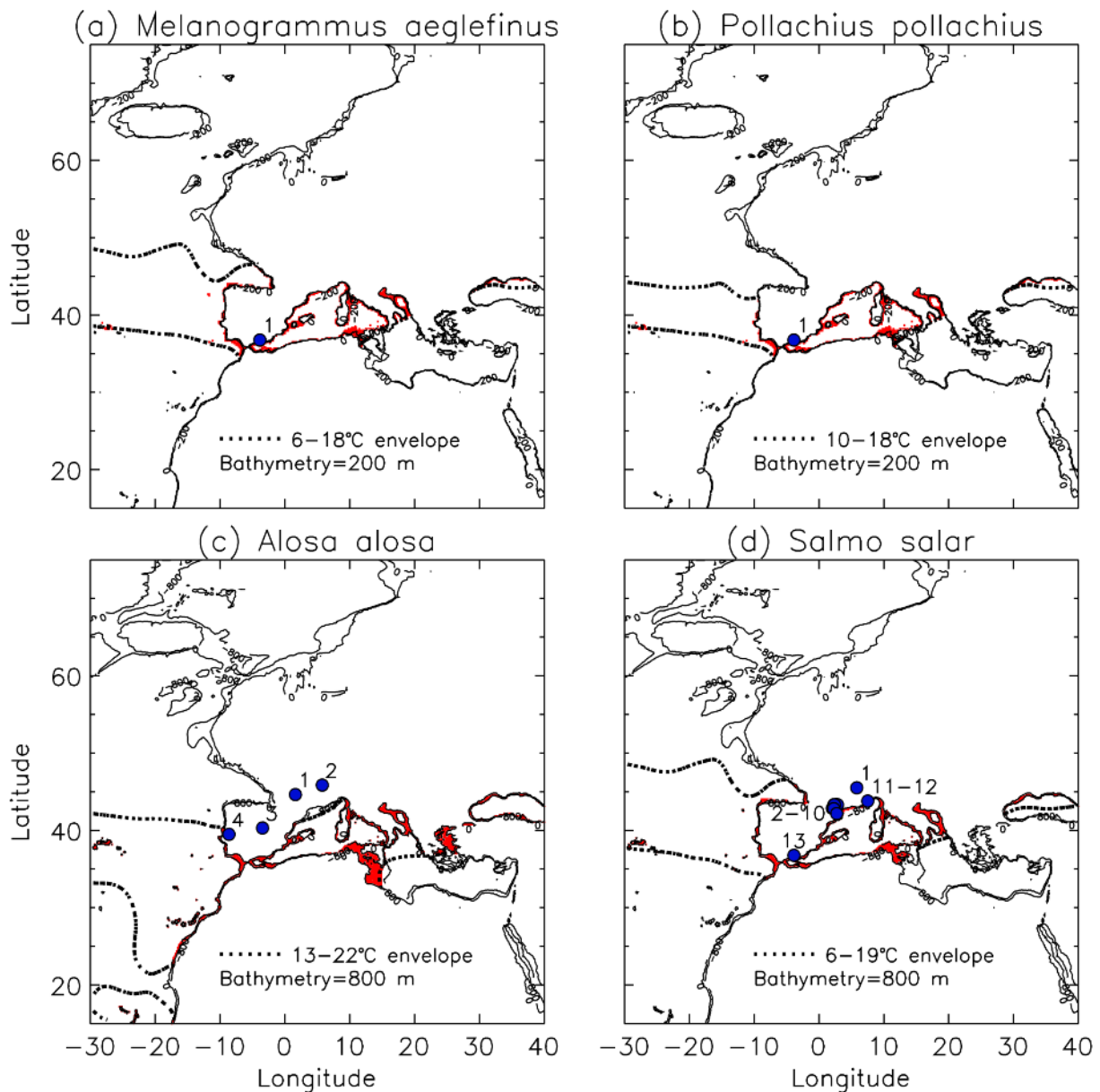
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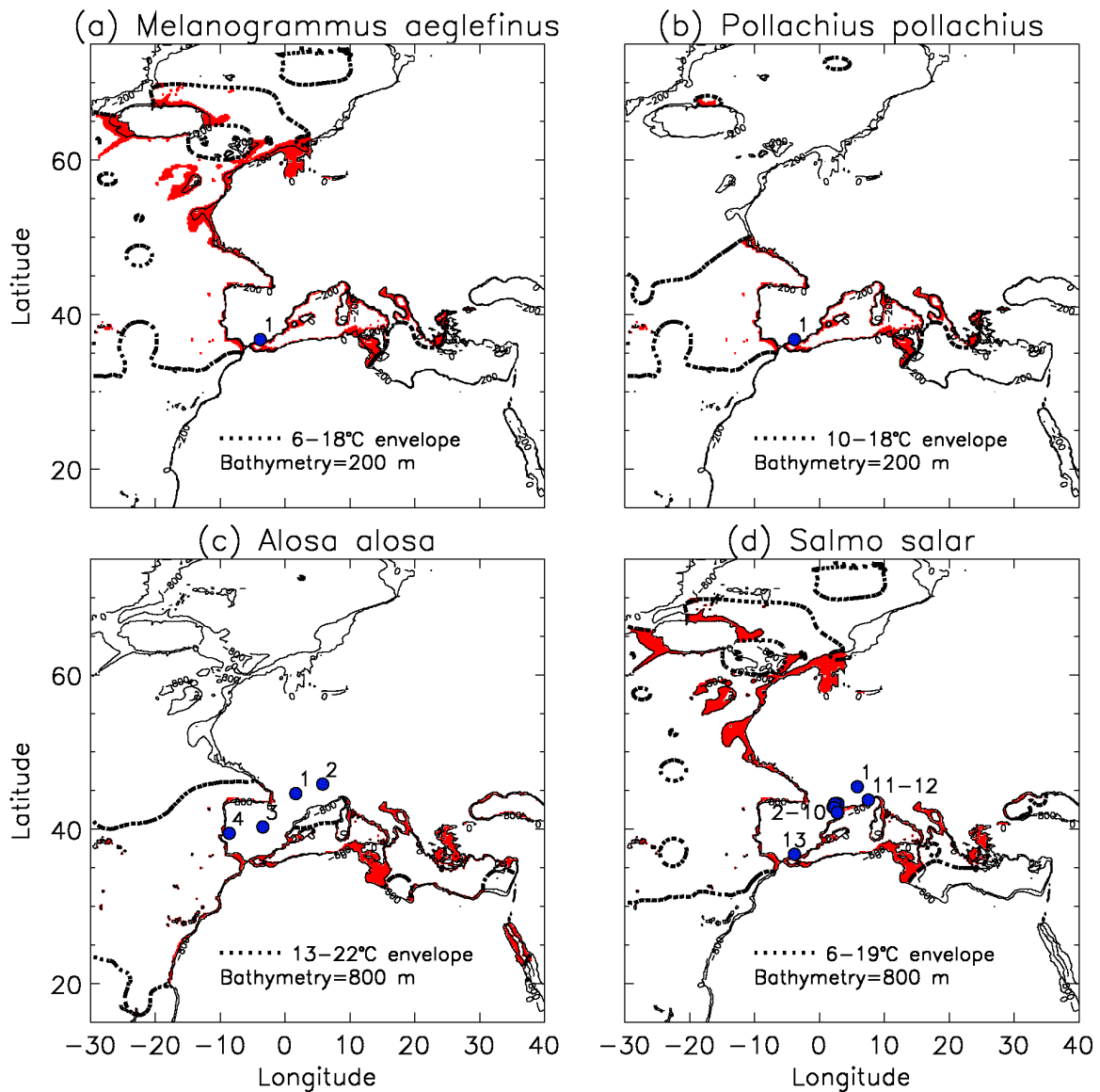
3 Figure 5. Difference in climatological SST LGM-present for Paul and Schäfer-Neth (2003)  
4 (a) winter and (b) summer and for MARGO Project Members (c) winter and (d) summer. For  
5 each palaeo-environmental reconstruction, the present day SST climatology is from the World  
6 Ocean Atlas of Levitus (2006).

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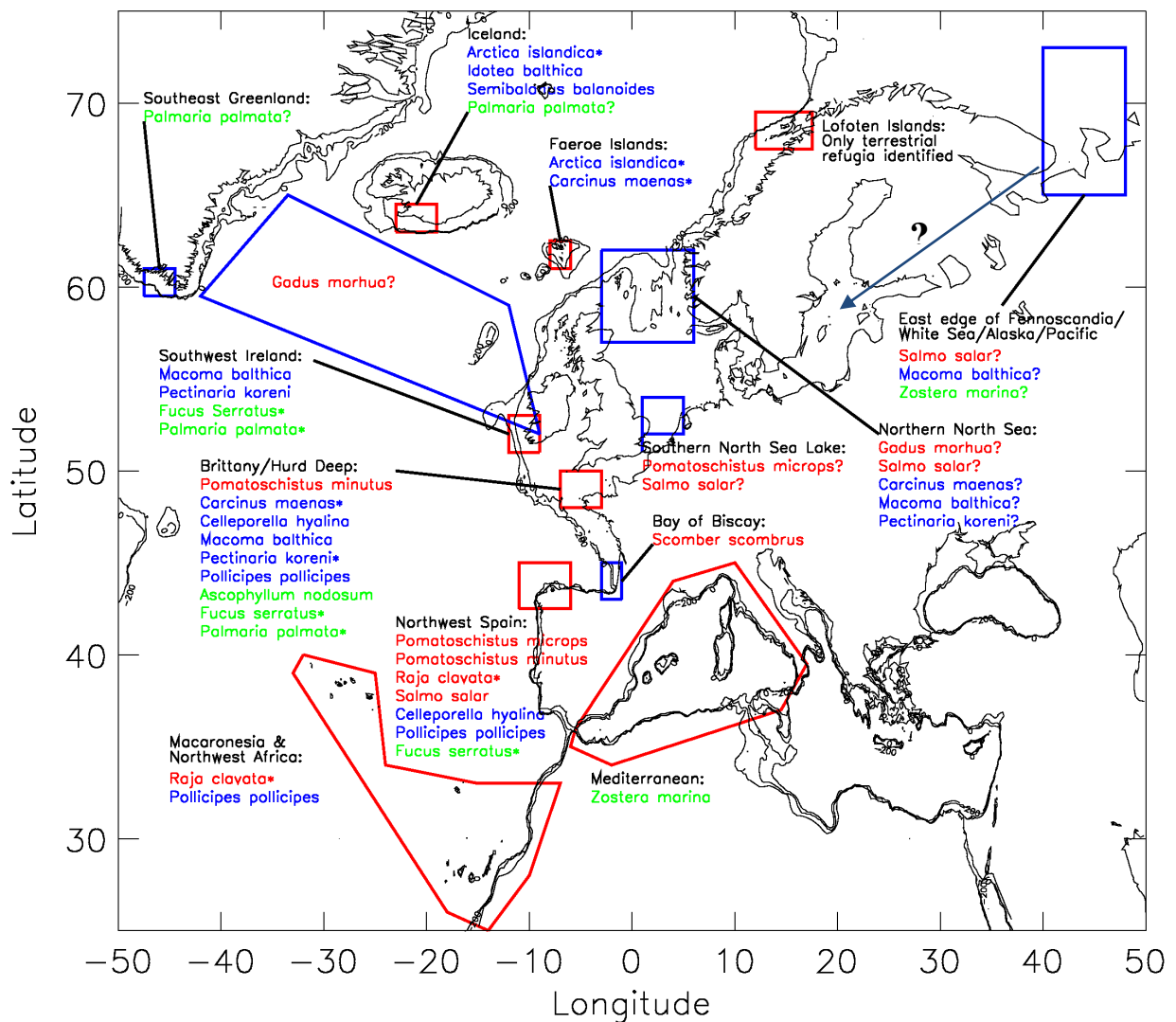
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 2 Figure 6. Predicted species ranges from the LGM reconstruction of Paul and Schäfer-Neth  
 3 (2003) for (a) haddock, (b) pollock, (c) allis shad, and (d) Atlantic salmon. The ranges are  
 4 based on the same criteria as for the present distribution in Fig. 3. The archaeological site key  
 5 is the same as Fig. 3. The LGM ranges within the frame of these maps are 14–33% of the  
 6 present day ranges, and the LGM distributions are almost completely shifted away from  
 7 present-day ranges shown in Fig. 3. The LGM bathymetry is derived from the 1° sea level  
 8 data of Peltier (1994) at 21 ka before present, interpolated to the 5' fields of ETOPO-5. LGM  
 9 sea level and the single additional bathymetric contour are indicated on the map.

10



1  
 2 Figure 7. Predicted species ranges from the LGM reconstruction using the interpolated  $5^{\circ} \times 5^{\circ}$   
 3 fields of MARGO Project Members (2009) for (a) haddock, (b) pollock, (c) allis shad, and (d)  
 4 Atlantic salmon. The ranges are based on the same criteria as for the present distribution in  
 5 Fig. 3. The archaeological site key is the same as Fig. 3. The LGM ranges within the frame  
 6 of these maps are 31–53% of the present day ranges, and the LGM distributions are displaced  
 7 southward from present-day ranges shown in Fig. 3. The LGM bathymetry is derived from  
 8 the  $1^{\circ}$  sea level data of Peltier (1994) at 21 ka before present, interpolated to the  $5'$  fields of  
 9 ETOPO-5. LGM sea level and the single additional bathymetric contour are indicated on the  
 10 map.

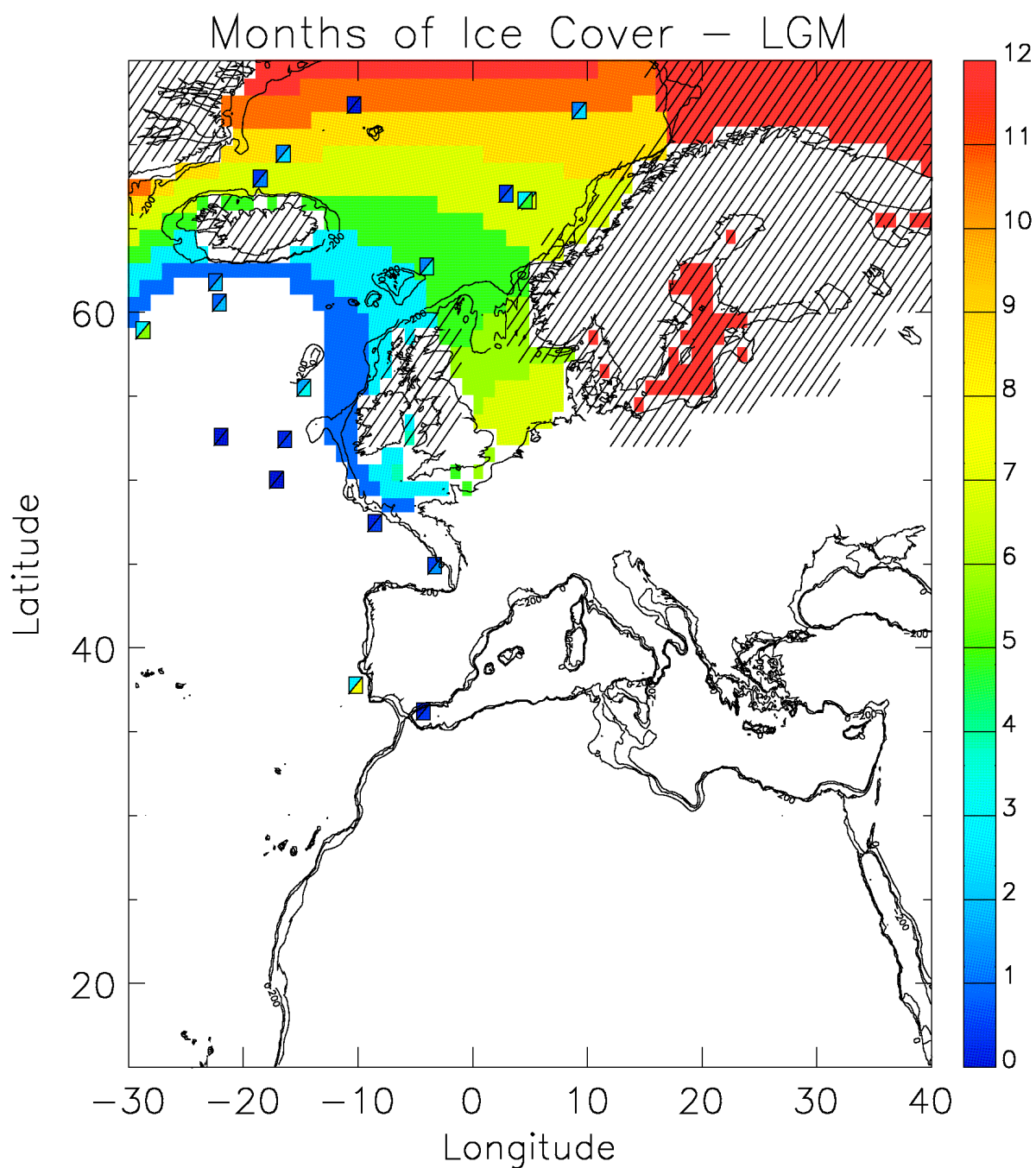
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2 Figure 8. Marine glacial refugia of plants (green font), invertebrates (blue font), and teleosts  
3 (red font), modified from reviews in Gómez et al. (2007), Hoarau et al. (2007), Maggs et al.  
4 (2008), Larmuseau et al. (2009) and Olsen et al. (2010), together with their cited primary  
5 reports. Thin black lines show the present and LGM coastline, and the 200 m LGM isobaths.  
6 The red boxes present the possible marine refugia reviewed by Maggs et al. (2008). These are  
7 supported by a reanalysis of genetics results, except for the Lofoten Islands (i.e., a recognized  
8 terrestrial, but not marine, glacial refugium) and the Mediterranean (i.e., a controversial  
9 marine refuge area for northeast Atlantic species (Larmuseau et al., 2009) without supporting  
10 species in the review of Maggs et al. (2008)). The blue boxes and species marked with  
11 question marks ? present other speculated marine refugia without firm support from  
12 archaeozoological or genetic evidence (e.g., the glacial refugia for *Gadus morhua* as given in  
13 Pampoulie et al. (2008)). Marine glacial refugia have identified for plants (*Ascophyllum*  
14 *nodosum* (Olsen et al., 2010); *Fucus serratus* (Coyer et al., 2003; Hoarau et al., 2007);

1 *Palmaria palmata* (Provan et al., 2005); *Zostera marina* (Olsen et al., 2004)), invertebrates  
2 (*Carcinus maenas* (Roman and Palumbi, 2004); *Celleporella hyalina* (Gómez et al., 2007);  
3 *Idotea balthica* (Wares, 2001); *Pectinaria koreni* (Jolly et al., 2005, 2006); *Macoma balthica*  
4 (Luttikhuizen et al., 2003; Nikula et al., 2007); *Pollicipes pollicipes* (Campo et al., 2010);  
5 *Semibalanus balanoides* (Wares and Cunningham, 2001)), and teleosts (*Pomatoschistus*  
6 *microps* (Gysels et al., 2004b); *Pomatoschistus minutus* (Larmuseau et al., 2009); *Raja*  
7 *clavata* (Chevolot et al., 2006); *Salmo salar* (Consuegra et al., 2002; Langefors, 2005);  
8 *Scomber scombrus* (Nesbø et al., 2000)). Species marked with an asterisk \* have been  
9 critically reviewed by Maggs et al. (2008). Some of the unusual (and sometimes diverse)  
10 genetic signatures in the North Sea and Baltic are speculated to arise from recolonization from  
11 east of the Fennoscandian ice sheet and possibly as far as the Pacific Ocean which was ice-  
12 free at high latitudes during the LGM (Olsen et al., 2004).

13



1  
 2 Figure 9. Months of ice cover from LGM (Paul and Schäfer-Neth, 2003) with glacier template  
 3 at 21 ka before present indicated by hatching (Peltier, 1994). The LGM bathymetry (sea level  
 4 and 200 m depth) is derived from the 1° sea level data of Peltier (1994) at 21 ka before  
 5 present, interpolated to the 5' fields of ETOPO-5. The present-day coastline is indicated on  
 6 the map. The small boxes give a more recent assessment (De Vernal et al., 2005) of the  
 7 average number of months of sea ice (top left triangle gives the average number of months;

- 1 the lower right triangle gives the average-plus-one-standard-deviation). During the LGM, the
- 2 Nordic seas may have been mostly ice-free during the summer months.