**Climate
of the Past
Discussions**

Refugia of marine fish in the Northeast Atlantic during the Last Glacial Maximum: concordant assessment from archaeozoology and palaeotemperature reconstructions

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Abstract

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

1 Introduction

To predict how the geographic ranges of marine species in Northwest Europe will change with future climate warming, it is important to understand their environmental response characteristics and how their spatial distributions changed across the full

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range of positive and negative temperature excursions of the Pleistocene glaciations. Although much palaeoclimatic information exists for the cold conditions of the Last Glacial Maximum (LGM) ca. 21 ka before present as well as at the mid-Holocene warm period 6000 years ago (Bradley, 1999), the response of marine species across the full

5 range of the temperature changes is not well-known. The LGM is particularly important to address this issue because it represents a situation of maximum perturbation of temperatures from the present condition and therefore affords the clearest picture of how marine species respond to environmental temperature change. Archaeozoology reveals important information about past climate change and corroborates palaeocli-

10 matic information from other sources. Palaeoclimatic evidence suggests that Scandinavia was covered by glacial ice sheets, and in Northern Europe permafrost conditions extended to the Massif Centrale in France with tundra conditions extending into Spain (e.g., Butzer, 1964; Bradley, 1999). In these climatic conditions, northern terrestrial animal species ranged over Western and Southwestern Europe where they were utilized

15 by human cultures, and their remains are found in the palaeolithic archaeological sites of the region (e.g., Butzer, 1964). Animal and plant species survived in glacial refugia in the Iberian peninsula, Italy, and the Balkans, and it is from these centers that Europe was recolonized during the Holocene. Genetic evidence has complemented archaeozoological evidence in elaborating on the paths of colonization for terrestrial animals,

20 freshwater fish, and plants (e.g., Hewitt, 2000; Stewart and Lister, 2001; Provan and Bennett, 2008). However, for the marine fish species, there is much less information, mostly because the archaeozoological record has mostly been lost as sea levels rose by approximately 120 m since the LGM (e.g., Provan and Bennett, 2008). However, genetic studies (e.g., Maggs et al., 2008) and the sparse archaeozoological evidence

25 indicate startling shifts in the geographic ranges of some species in response to climate change. Here, we present an overview of how the ranges of four marine and amphihaline species changed during the LGM and apply a simple ecological niche model (ENM) to explain how these altered ranges are consistent with sea surface temperature (SST) changes during the glacial period.

Identifications of fish remains from archaeological sites have revealed large changes in the ranges of some marine and amphihaline species during the LGM. The migratory allis and twaite shad (*Alosa alosa* and *A. fallax*, respectively) and eel (*Anguilla anguilla*) species disappeared from the Atlantic coasts of France and Cantabria, Spain, during

5   the coldest conditions of the LGM, and survived in refugia further to the south (Le Gall, 2008). For the eel, this refugium was probably on the Atlantic coasts of Portugal and Morocco (e.g., Kettle et al., 2008). The glacial refuge of the shad is unclear, but remains have been discovered on the upper Tagus River system at Aridos-1 from the Mindel-Riss interglacial approximately 300 ka BP (Morales, 1980; Le Gall, 2000), and

10   it is likely to have survived the LGM on the Iberian Peninsula and Northwest Africa. From Southern Spain, the boreal gadid species, haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius pollachius*) have been reported by Rodrigo (1994) for the Cueva de Nerja near Malaga dating to the LGM. These results were significant because these species are currently found in Northwest Europe, and the southernmost

15   range for haddock and pollock is currently the Bay of Biscay and Northern Portugal, respectively (Whitehead et al., 1986). The most recent analyses of the LGM deposits from the Cueva de Nerja have revealed that the northern gadids (including saithe *Pollachius virens*, cod *Gadus morhua*, and ling *Molva molva*) make up more than 30% of the identified fish remains and thus represented a significant economic presence

20   among the exploited fish (Cortés-Sánchez et al., 2008; Morales-Muñiz and Roselló-Izquierdo, 2008). The exploitation of gadids continued for an extended period of time until the early Holocene as sea levels were returning to present levels and sea surface temperatures approached present values.

Among the most spectacular shifts in species ranges have been reports of the re-

25   mains of Atlantic salmon (*Salmo salar*) in archaeological sites from the Mediterranean drainage basins of France, Spain, and Italy dating from the LGM up to the early Holocene. Additional small art objects unambiguously depicting salmon have been located at the Grand grotte de Bize on a Mediterranean drainage basin (Le Gall, 1994a). These reports from late Palaeolithic–early Mesolithic sites in France, Spain, and Italy

(Juan-Muns i Plans, 1985; Juan-Muns i Plans et al., 1991) suggest the presence of resident salmon populations in the Western Mediterranean Sea. The current southernmost range of Atlantic salmon in Northwest Europe is Northern Portugal, which indicates that immigrant populations would have had to pass through the Straits of
5 Gibraltar when temperatures in Southern Spain during the LGM were similar to Northern Europe at present. However, the archaeozoological evidence is contested. Many of the sites in Southern France are near Atlantic drainage basins, and it is possible that the Atlantic salmon remains in the Mediterranean watersheds may have been transported as part of a seasonal migration of fishermen (Le Gall, 1983, 1984, 1992,
10 1994a,b). This has even been invoked to explain Atlantic salmon finds in the more distant Menton caves on the French-Italian border (Rivière, 1886; Clark, 1948). As well, many of the early identifications of Atlantic salmon at the Caune de Belvis and the Grotte Jean-Pierre I by Desse and Granier (1976) and at Grimaldi (Barme Grande II) have been subsequently questioned and revised to trout (*Salmo trutta*) by Le Gall
15 (1994a), Desse-Berset (1994), and Desse and Desse-Berset (2002), respectively. It is difficult to distinguish Atlantic salmon and trout from their skeletal elements, and many of the early salmon identifications were made mainly on the basis of the unusual size of vertebral elements. The revision of the initial identifications may have been made on reflection of the zoogeographic implications of there being endemic Mediterranean
20 Atlantic salmon populations during the LGM. Up until now, the prevailing paradigm has been that the SST in the Western Mediterranean during the LGM was too high to meet the oxygen requirements of the species (Le Gall, 1983, 1984, 1994b). On the other hand, recent unambiguous determinations of Atlantic salmon in Solutrean levels in the Cueva de Nerja indicate that ocean temperatures were cool enough during the LGM to
25 permit the passage of the species through the Straits of Gibraltar (Morales-Muñiz and Roselló-Izquierdo, 2008).

Part of the reason why these archaeozoological finds are important is that there are few studies that have investigated how the geographic distribution of marine species changed during the LGM, and most of this based on molecular markers. Hence, there

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are few a priori hypotheses of what fish species should be found in archaeozoological collections. This situation contrasts strikingly with the state of knowledge for terrestrial plants and animals and freshwater fish, where there is much zooarchaeological and genetic evidence for LGM refugia in Southern Europe and recolonization pathways to
5   Northern Europe during the Holocene (e.g., Hewitt, 2000; Stewart and Lister, 2001; Provan and Bennett, 2008). Most of the important economic marine fish species have a high gene flow that make it difficult to link local population structure with the existence of glacial refugia. Reviewing the genetic structure and LGM history of cod, Pampoulie et al. (2008) speculated that glacial refuge populations survived on the Rockall Plateau,
10 Southwest Ireland, and the Irminger Sea, and possibly also a lake in the North Sea. However, these predictions are confusing because the LGM palaeoclimatic reconstruction of Paul and Schäfer-Neth (2003) suggests that the ocean temperatures and sea ice conditions of these areas may have been too severe to serve as refugia. As a demersal species, cod would have additionally remained on continental shelf habitats.
15   ENMs attempt to predict the spatial distribution of a species based on databases of climatic (e.g., temperature, rainfall) and other information, and the most robust examples might predict the spatial distribution based on threshold envelopes of temperature, for example, above and below which no viable populations are observed to occur. ENMs have been successfully applied to explain the present-day distributions of some
20 terrestrial species and then carefully calibrated to predict the past distributions during the LGM using palaeoclimatic model data (Waltari et al., 2007). However, for marine species these models have only recently been applied, and for some species, there are sometimes errors in the predictions. The extension of ENMs to explain marine fish distributions during the LGM has recently been performed by Bigg et al. (2008) who used
25 two algorithms to predict the glacial distribution of cod. Although one algorithm, based on a maximum entropy method, predicted suitable LGM habitat along the Atlantic coast of Northwest Europe and also large areas of the Mediterranean and the Black Sea, the actual occupation of these areas in Southern Europe was judged unlikely because of geographic disjunction. A second algorithm, based on ecophysiological constraints,

predicted only limited southward displacement during glacial times, and this clearly shows important disagreements with recent fossil evidence from the Cueva de Nerja in Southern Spain (e.g., Cortés-Sánchez et al., 2008; Morales-Muñiz and Roselló-Izquierdo, 2008). Hence, there is still a crucial gap in the understanding of the influence

5 of oceanic conditions that governed the spatial distribution of the marine species during the LGM. The issue is important because future climate warming scenarios predict that the spatial ranges of important species are expected to shift northward (e.g., Perry et al., 2005) and important amphihaline species, like salmon, are predicted to become extinct in the southern parts of their range (Lassalle and Rochard, 2009).

10 In this contribution, we consider the changes in spatial distribution of four species during the LGM: haddock, pollock, allis shad, and Atlantic salmon. Although many species have revealed changes in distribution during the LGM, these four species have been selected as representative examples mainly because of the long-standing conundrum suggested by the unusual locations of their subfossil evidence. In the Sect. 2

15 (Methods), we present the current understanding of the environmental requirements of the fish species, together with the ENM algorithms used to determine their present distribution. In Sect. 3 (Results), we present an alternative ENM approach to estimate LGM distributions and use palaeoclimatic SST reconstruction from the LGM to estimate how the species ranges changes. In Sect. 4 (Discussion), we synthesize the informa-

20 tion, indicating consistencies between our results and emerging genetic information from other marine species, and we point out potentially promising lines of research for the future.

2 Methods: an Ecological Niche Model (ENM) based on temperature and bathymetry

25 Our predictions of the LGM distribution of marine species are based on a simple ENM that is constructed from the intersection of two environmental conditions (SST and bathymetry). Using an empirical approach, we define the present day environmental

conditions where the species occurs. Then, we infer the LGM distributions based on the best-guess reconstructions of the SST and bathymetry during the LGM.

The present day distribution of the four marine and amphihaline species is shown in Fig. 1. Each panel in the figure shows a single species except for Fig. 1c, which shows the ranges of the two related shad species *Alosa alosa* and *A. fallax* together (these species are sometimes difficult to distinguish from their skeletal elements). Information is available from several sources, but we present expert assessments from two recognized sources: Fishbase (http://www.fishbase.us/search.php) and Whitehead et al. (1986). Other references are broadly consistent with the chosen expert summaries in terms of the geographic distribution, but may add extra regional information, for example, about where a species may be particularly common (ICES-Fishmap: Haddock, 2009). Presenting only an envelope of presence-absence information with minimal information about abundance for some species, the information in Whitehead et al. (1986) is the simplest and most robust. The Fishbase Aquamaps present a graded zonation of distribution that is based on sea surface temperature, sea surface salinity (SSS), productivity, bathymetry, and an annual ice cover (modified from Kaschner et al., 2006). Although the extra information implied by the abundance appears useful, the algorithm is calibrated based on survey information, and it may not reproduce expert assessments. For example, for Atlantic salmon in Fig. 1d, there is a predicted distribution in the Mediterranean and Black Seas based on habitat conditions, but the present distributions of wild populations are limited to the Atlantic coasts of Northwest Europe as indicated by Whitehead et al. (1986).

The minimum and maximum summertime (July-August-September, JAS) SST envelopes that define the southern and northern extent of each species are shown in Fig. 1. The SSTs are taken from a present-day climatological atlas at 1° resolution that is shown in Fig. 2 (from the World Ocean Atlas of Levitus, 2006; abbreviated WOA05). Temperature is recognized to be the most important determinant of the spatial distribution of fish, and this is grounded on theoretical considerations of oxygen limitation and the temperature-dependence of the metabolic processes (Pörtner,

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2001; Pörtner and Knust, 2007). Although species show temperature-dependence at every stage in their life cycle, Bigg et al. (2008) consider temperatures in late spring and early summer as the primary factor affecting the spawning range of cod. They use SST as the metric of the spatial distribution to generate maps. This does not at first seem like an obvious metric for bottom temperature conditions, which are important for a demersal species like cod. On the other hand, the 10 °C annual average SST isotherm provides an important functional definition of the southern limit of the spatial distribution of cod on both sides of the Atlantic Ocean (Brander, 1996). For our study, we selected the summertime SST (JAS) as the primary criteria defining the spatial distribution of the species, instead of the wintertime (December-January-February, DJF) or annual average SST. Along with bathymetry limits (ETOPO-5, http://www.ngdc.noaa.gov/mgg/global/etopo5.HTML), the isotherm envelopes form the basis of the present day distribution ranges shown in Fig. 3. These maps were generated by matching the summertime SST with the species distributions shown in Fig. 1, and a 1 °C uncertainty in the definition of the thermal envelopes does not change the conclusions of this analysis.

The chosen temperature envelopes are broadly consistent with the temperature thresholds of the four species observed during the field and laboratory studies. For haddock, (ICES-Fishmap: Haddock, 2009) gives a minimum temperature threshold of 6.5 °C, and Brodziak (2005) reports the juvenile and adult fish have been caught during fisheries surveys between temperatures of 2–16 °C. Peck et al. (2003) gives the temperature of maximum growth at 12 °C, which is approximately at the center of the summer climatological envelope of 6–18 °C that has been used to define its range in Fig. 1. For pollock, also a demersal species, the empirically-defined summer climatological SST envelope of 10–18 °C for the northern and southern range of the species (Fig. 1) is close to the physiological range of temperatures of 9–18 °C, outside of which severe growth decreases are observed (Person-Le Ruyet et al., 2006). For the allis shad, which spawns in freshwater in springtime, the observed migration from the ocean takes place when river temperatures are between 13.3–23 °C as measured by

Acolas et al. (2006), and this defines the proper freshwater environment for spawning and early rearing of young. This observed temperature range is very close to the empirical climatological average summer SSTs that have been used to define the spatial distribution (13–22 °C; shown in Fig. 1c). For the twaite shad the lower temperature envelope may be slightly reduced compared to allis shad to explain its more northerly spatial distribution in Norway and Iceland.

For Atlantic salmon, the northern and southern boundaries of the range are empirically determined as the 6 °C and 19 °C summer SST isotherms (Fig. 1d). There are different possible reasons for this temperature envelope. The fish is highly susceptible at the post-smolt stage just after it migrates from the rivers to the ocean in spring–early summer. Although the mechanism is unclear, stock size is negatively correlated with June SST, and post-smolts are negatively affected by the early arrival of warm ocean temperatures (Friedland et al., 2003). The empirical summer SST envelope is similar to the observed temperature of the downstream migration in Norway in June: 2.5–15.5 °C (Hvidsten et al., 1998). Another hypothesized mechanism to explain the spatial range of adult salmon relates to its high dissolved oxygen requirements ($>7 \, \text{mg} \, O_2 \, L^{-1}$), whose saturation value depends mainly on the temperature but also the salinity of seawater (Le Gall, 1983, 1984). Le Gall (1994b) stated that the southern distribution of the species – and particularly its absence in the Mediterranean – is governed by this oxygen requirement, and the theoretical basis of the temperature dependence of aerobic activity has been more recently clarified by Pörtner and Knust (2007).

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

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3 Results: fish distributions during the Last Glacial Maximum (LGM)

The SST and topography criteria can also be used to estimate the probable spatial distribution of the fish species during the LGM. Figure 4 shows the Northeast Atlantic LGM SST reconstruction from Paul and Schäfer-Neth (2003) for winter (January-February-March) and summer (July-August-September). The difference between the LGM reconstructions and the present day climatology (Fig. 5) illustrates the temperature changes in the Northeast Atlantic during the LGM. Most of the mid-latitude areas exhibit some cooling during the LGM, with the most significant cooling (exceeding 12 °C) around the UK in summer. In the Mediterranean Sea, temperature decreases are less severe, with ∼8–10 °C summertime decreases in the west and ∼4–6 °C summertime decreases in the east. Summer temperature conditions at the Strait of Gibraltar during the LGM would have been similar to the south coast of the UK at present.

The LGM distributions of fish species (Fig. 6) have been assessed using the ENM based on these palaeo-SST fields and the palaeotopography fields of Peltier (1994). All species show a significant southward shift and an almost complete displacement away from their present ranges. The ENM results are consistent with the available archaeozoological results. The Cueva de Nerja in the Strait of Gibraltar was well within the estimated LGM range of haddock and pollock, and the ENM predicts that these species may have populated the Western Mediterranean Sea as far east as the Adriatic Sea. Atlantic salmon could likewise swim through the Strait of Gibraltar to form populations in the Western Mediterranean Sea, consistent with its archaeozoological presence in the Mediterranean watersheds of Spain, France, and Italy during the LGM. This species is cold-adapted and is found at present in Northern Europe as far south as Northern Portugal (although there are historical reports of the species as far south as the Guadalquivir River up to 20th century (B. Elvira, personal communication)). The ENM model for the LGM predicts that it was never displaced south of Atlantic France and that it maintained a continuous presence on the Gironde–Dordogne river system. This is consistent with the uninterrupted presence of its remains in the Palaeolithic

Magdalenian archaeological sites in this river basin. The allis shad requires warmer SST conditions, and the ENM indicates that it was displaced from the Atlantic watersheds of France and Northern Spain during the LGM, and this is consistent with its apparent absence from archaeological sites in the Dordogne region (Le Gall, 2008). The recent identification of the remains of (allis) shad in Magdalenian levels of the Lapa dos Coelhos archaeological site on the Tagus watershed of Central Portugal gives support to the existence of a glacial refuge in the Southern Iberian Peninsula during the LGM (Roselló and Morales, 2010).

A second important message in Fig. 6 is the extent to which the species ranges were reduced during the southern displacement and confined to the continental slope regions. Within the spatial domain delimited by Fig. 6, the LGM ranges were decreased to approximately 19, 19, 33, and 14% of the present range for haddock, pollock, allis shad, and salmon, respectively. The results for the gadids, haddock and pollock, are approximately the same as the reduction of the range of cod in the North Atlantic reported by Bigg et al. (2008): ∼20% of present day extent. Although the largest contiguous area of species is presently the North Sea, our ENM predicts that during the LGM the largest contiguous area for all four species may have been the shallow shelf area between Tunisia and Sicily.

4 Conclusions

The ENM results presented here give a very different prediction of LGM glacial refuge areas for some of the economically important fish species of Northwest Europe compared with the few previous published studies. The main finding is that the glacial refuges of four highly vagile fish species are almost completely shifted away from their present biogeographical range mostly in Northwest Europe. There is strong evidence from palaeo-SST reconstructions and archaeozoological identifications that cold-adapted gadids and Atlantic salmon invaded the Western Mediterranean through the Strait of Gibraltar. The results are startling because the predicted LGM spatial

ranges are different from previous assumptions and modelling studies. For example, Pampoulie et al. (2008) speculate that cod survived the LGM on the Rockall Plateau and the Irminger Sea in a reduced subarea of the present range (Fig. 7). Also, the eco-physiological model Bigg et al. (2008) predicted that cod survived the LGM in continen-
5   tal shelf areas of Northwest Europe and that populations were displaced only slightly further south compared to the present locations. The predictions of our ENM are supported by subfossil archaeological evidence of the fish species in archaeological sites far to the south of their presently-recognized southern boundaries.

It is difficult to independently verify the predictions of our ENM with genetic informa-
10   tion. Molecular markers are not well-suited to elucidating the glacial refugia of highly vagile fish species (Gysels et al., 2004b) like the four examples of our study. Highly mobile fish can follow optimal sea temperatures during changing climate conditions, so that the location of their glacial refugia is unclear. For some species, the population age estimated from molecular markers may be inexplicably older than the known length of
15   habitat occupation since the LGM (Francisco et al., 2009). Fish of low dispersal ability are valuable tracers of glacial refugia, and the sand goby (*Pomatoschistus minutus*) is one such model marine species whose present population structure is a legacy of range constrictions during the glacial period (Gysels et al., 2004a; Larmuseau et al., 2009). The population has a contiguous distribution in Northern Europe, but is frag-
20   mented in the Mediterranean, consistent with a species that expanded south during glaciations and retreated northwards during the interglacials as climate conditions became warmer during the Holocene.

For some species, molecular marker studies reveal patterns of recolonization from glacial refugia. Many of the hypothesized refugia in Fig. 7 are located in different parts
25   of Southwestern Europe and Northwestern Africa, south of the ice sheets and sea ice cover (Fig. 8). The Bay of Biscay, Iberian Peninsula, and Macaronesia (Madeiras, Azores, and Canaries) have all been invoked as glacial refugia of various marine species with a present distribution in Northwest Europe. This is consistent with the predictions of our SST-based ENM. However, smaller periglacial refugia – the Hurd Deep

near the mouth of the glacial Channel River and Southwest Ireland – have also been inferred from genetic evidence for other species. These regions would have been subject to ice cover for part of the year (Fig. 8), but this does not preclude them as glacial refugia for marine species (Gómez et al., 2007). Other refugia have been hypothesized

5　further north in Northwest Scotland, Northern North Sea, Faeroe Islands, Iceland, and Norway for species adapted to colder conditions and longer sea ice periods (Fig. 7). The identification of some of these glacial refugia poses important questions about the locations of the European ice sheets (Sejrup et al., 2005), but they are mostly outside the climate envelope for the species of our study.

10　　Atlantic salmon is an important exception whose genetic structure reveals a complex and interesting recolonization history, which introduces another dimension to our results. Our study suggests that Brittany/Hurd Deep was the northernmost range for this species, and that the species was simply displaced southward during the LGM. The unusual genetic structure in the Baltic Sea may have resulted from population iso-

15　lation during the complex marine transgression history resulting from the interplay of sea level changes and the isostatic rebound in the early Quaternary (Lepiksaar, 2001, p. 40). However, it has also been used to infer recolonization from possible glacial refugia in the Southern North Sea or beyond the eastern edge of the Fennoscandian ice sheet (e.g., Consuegra et al., 2002; Langefors, 2005; King et al., 2007; but see also

20　Makhrov et al., 2005). A westward recolonization pathway into the Baltic Sea from the White Sea after the LGM was previously perceived as unlikely. On the other hand, the genetic signatures of the other marine species indicate a possible link between extant populations in the Baltic Sea (and Eastern Atlantic) with those further east in the Arctic and Pacific Oceans (Luttikhuizen et al., 2003; Addison and Hart, 2005; Nikula et al.,

25　2007).

　　The ENM predictions of Bigg et al. (2008) for cod are valuable because they are among the first that have been developed for the marine domain. The model is being used for other North Atlantic species to infer LGM spatial distributions (Provan et al., 2009). Bigg et al. (2008) used two different ENMs for cod that were calibrated to

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present conditions, and it is important to investigate the possible reasons for the partial discrepancy of their models with our results. The maximum entropy ENM used by Bigg et al. (2008) was based on bathymetry, SST, and SSS. This produced an LGM distribution for cod that stretched from Northwest Europe into large areas of the Mediterranean, consistent with the report of archaeozoological remains from the Cueva de Nerja. The ecophysiological ENM used by Bigg et al. (2008) incorporated a spawning temperature threshold of 0–9 ˚C between February and June. This is different from the temperature range that we have used for haddock (i.e., an analogous demersal gadid species with a similar range) in Fig. 1a, whose spatial range we have defined to lie between the summertime isotherms of 6–18 ˚C (or the 3–12 ˚C wintertime isotherms, not shown). The ENM temperature envelope used by Bigg et al. (2008) was slightly lower than our choice. It may have resulted in northern offsets of both the northern and southern present-day species boundaries when evaluated against field surveys, as noted in the original publication. When projected back to the LGM, these thermal envelopes have implications for the predicted glacial refugia. The direct comparison of the different temperature criteria is difficult between the ecophysiological model of Bigg et al. (2008) and the temperature envelopes of our study, partly because strong seasonal variation of the North Atlantic near surface ocean temperature. An important message in Bigg et al. (2008) is that the LGM distributions of the marine species can be predicted with just a few parameters (bathymetry and SST), and this is an important feature of robust simplicity that is maintained in our study.

The assumption of "niche stability through time" forms the foundation of all ENM approaches (Nogués-Bravo, 2009), but it has not been addressed by Bigg et al. (2008) or in our study, and it is difficult to prove. For our study, it translates into the assumption that the fish responded to ocean temperature and depth during the LGM in the same way as at present. On the other hand, some evidence indicates that the fish may have changed their behavior in the past for unknown reasons, possibly associated with human exploitation or climate change. For example, Beerenhout (1994) pointed out the remains of full-grown haddock in early Neolithic sites in the Netherlands where they

were caught in brackish water estuarine environments. The report is startling because the species is currently subject to commercial exploitation at the northern edge of the North Sea at approximately 200 m depth (ICES-Fishmap: Haddock, 2009). The Neolithic human populations of the Netherlands did not have the technological means to secure haddock from its 20th century habitat, and there is an important implication that the fish range may have changed to a very different stable state in response to human exploitation. From the late-Palaeolithic period, a similar message is presented by the haddock finds from the Epipalaeolithic levels of the Cueva de Nerja, and these fish were also probably obtained as part of an inshore, shallow-water fishery. Changes in the trophic structure of marine ecosystems have been inferred from changes in species assemblages and sizes based on evidence from Stone Age archaeological sites, and there is an implication that it may have been due to human exploitation (Desse and Desse-Berset, 1993; Morales and Roselló, 2004). This may be linked with alterations in preferred habitats of fish populations. In assessing the possibility of a Mesolithic deep-sea fishery, Pickard and Bonsall (2004) have had to address the provenance of certain species in archaeological sites that presently occur offshore in deep water, and specifically identify bluefin tuna (*Thunnus thynnus*; i.e., an offshore species with observed spawning migrations inshore), golden redfish (*Sebastes marinus*), hake (*Merluccius merluccius*), halibut (*Hippoglossus hippoglossus*), tusk (*Brosme brosme*), and wolffish (*Anarhichas lupus*). Although the authors assume that "the habitat preferences of prehistoric fish populations were broadly similar to those of modern species", the presence of significant numbers of remains of so many deep water species in Mesolithic archaeological sites, forces consideration that the fish may have changed their habitat preferences. Alternatively, such shifts may have been provoked by the systematic fishing of inshore populations that may have led to local extinctions of those living in the shallowest and most accessible waters.

The results of our study represent an evolving picture of the marine species distributions that will be revised with future work on palaeoclimatic environmental reconstructions and modelling activities. Palaeoclimatic reconstructions of SST have evolved

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since the initial CLIMAP Project Members (1976) assessments, and there are ocean areas where the LGM assessments of SST and SSS are unclear and where different proxy methods may disagree (MARGO Project Members, 2009). On the other hand, from the archaeozoological perspective, there appears to be a convergence of evi-
5 dence for the climatic conditions in the Mediterranean basin during the LGM. The LGM SST reconstruction in Figs. 4 and 5 indicates that whereas Western Mediterranean SST conditions were low enough to support populations of northern gadids and Atlantic salmon, conditions in the Eastern Mediterranean were not much different from the present. The new LGM temperature reconstructions force a departure from an
10 earlier paradigm that SST's were too warm to permit the migration of these species through the Strait of Gibraltar (e.g., Le Gall, 1994b). Rather than a barrier at the Strait of Gibraltar, our ENM indicates that there may have been an important thermal boundary in the middle of the Mediterranean at Sicily, and this is consistent with the genetic studies of other marine species that show an important division at Tunisia-Sicily sad-
15 dle (Domingues et al., 2005). 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, and some present-day marine species in the Adriatic have a distinct genetic signature from other Mediterranean populations (Gysels et al., 2004a; Maggio et al., 2009).
20 Future experimental work may aim to verify the predictions of the ENM that have been presented here. For example, genetic studies might aim to determine the structure of the vanished populations in the Mediterranean (Nielsen and Hansen, 2008). For the archaeological LGM Atlantic salmon population in Northern Spain, Consuegra et al. (2002) found a dominant haplotype that has almost vanished from modern pop-
25 ulations in the region. However, the question of the genetic structure of the hypothesized LGM salmon populations in the Mediterranean is open. The amount of exchange through the Straits of Gibraltar during the LGM is unknown, and it is not clear if the Mediterranean population, at the extreme of the species' range, had the opportunity to develop its own genetic signature.

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Our ENM makes predictions about the extent of the expansion of haddock, pollock, allis shad, and Atlantic salmon into the Central Mediterranean that can only be unequivocally resolved with further archaeozoological studies. The ENM effectively explains observations of LGM fish species distributions at the Strait of Gibraltar and in Southern France, but it also makes predictions that the species should have extended as far east as Sicily and the Adriatic Sea. The southernmost distribution of Atlantic salmon is predicted to be at approximately the latitude of Northern Morocco, but there are few Palaeolithic archaeological sites in this area to test the ENM predictions. One alternative approach that has not been exploited by archaeozoologists is the quantification of fish otoliths from shallow sediment cores on the continental shelf. The concept has been explored by Elder et al. (1996) who used the otoliths of a small fish species *Ceratoscopelus maderensis* off the eastern seaboard of the United States to demonstrate significant changes in range between glacial and postglacial times. Otoliths of cod were also recovered in their bottom samples. Although the importance of these finds was immediately recognized to assess the LGM distribution of an important economic species, the sample density was too low to generate meaningful statistics. There is also potential evidence from the mollusc remains in shallow marine deposits and archaeological sites. Malatesta and Zarlenga (1986) cite many examples of indicator molluscs ("Northern Guests") as evidence of repeated species invasions (and retreats) of the Mediterranean Sea from Northwest Europe during the coldest intervals of the Pleistocene glaciations. For example, the range of the Atlantic quahog (*Arctica islandica*) extended into the Western Mediterranean Sea during the LGM, but the species became extinct in its Southern European domain approximately 9800 years BP and currently does not survive south of Brittany (Froget et al., 1972; Dahlgren et al., 2000). Although ENMs and genetic evidence provide indications of past species' ranges and refugia, physical evidence provided by fossil or subfossil material provides the most unambiguous identification of spatial ranges during the LGM.

Ultimately, the importance of understanding the past distributions of economic species during the LGM is to assess their thermal niche and predict how their ranges

might change with future climate warming. Analyzing fish survey time series from the North Sea, Perry et al. (2005) calculated that the ranges of demersal species have shifted north approximately 170 km between 1962–2001. Predictions of future temperature increases have been used to predict the extinction of migratory species from the southern parts of their ranges (e.g., Lassalle and Rochard, 2009), but the calibration of these models depends on how species responded to climatic temperature perturbations in the past. The LGM results presented here capture the southern displacement of certain marine species under the coldest temperature conditions. The warm conditions during the mid-Holocene warm period offer a potential proxy for future climate warming. At this time, warm water species like the European sea bass (*Dicentrarchus labrax*) were displaced from their historically-recognized range south of the British Isles to become economically important for the Mesolithic cultures of Denmark (e.g., Enghoff et al., 2007) and the German Baltic Sea coast (Heinrich, 2001; Schmölcke et al., 2006). Likewise, the Atlantic quahog, whose present northern distribution stops at the White Sea, ranged to Spitsbergen, Western Greenland and far across the northern coast of Russia during the warmer climate conditions of the mid-Holocene (Dahlgren et al., 2000). The archaeozoological evidence thus provides critical data to predict how the spatial ranges of marine species may change in the coming decades and centuries.

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

Species		Archaeological site	Time period	Reference
Haddock (*Melanogrammus aeglefinus*)	1	Cueva de Nerja, Spain	LGM/Gravettian and 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 (*Pollachius pollachius*)	1	Cueva de Nerja, Spain	LGM/Gravettian and 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 (*Alosa alosa* and *A. fallax*)	1	Pégourié, Lot, France (*A. alosa* in Atlantic drainage)	Absence during LGM; small percentage at level 7 (12 250 ± 350 uncal BP); majority of fish remains at 11 000 BP in levels 4–6	Le Gall (1993, 1994b, 1995, 2000), Martin and Le Gall (2000)
	2	Sous-Balme, l'Ain, France (*A. alosa* or *A. alosa rhodensias* in Mediterranean drainage)	Sauveterriens anciens, 9000 BP	Le Gall (1994b, 2000)
	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 (*Salmo salar*)	1	Grotte Jean-Pierre I, Saint-Thibaud-de-Couz, Savoie, France	Magdalénien supérieur à Mésolithique ancien	Desse and Granier (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 (~12 270 ± 280 uncal BP)	Desse and Granier (1976), Juan-Muns i Plans et al. (1991); evidence disputed by Le Gall (1994a)

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Table 1. Continued.

Species	Archaeological site	Time period	Reference
4	La Grande Grotte de Bize, Aude, France (artwork)	Upper Magdalenien (12 550 ± 210 uncal BP)	Le Gall (1994a, Le Gall, 2001)
5	Canecaude 1, Aude, France	Middle Magdalenian (14 230 ± 160 uncal BP)	Le Gall (1994a)
6	La Grotte Gazel, Aude, France	Middle Magdalenian–Azilien	Costamagno and Laroulandie (2004; citing Desse-Berset, unpublished)
7	La Grotte de l'Oeil, Aude, France	Upper Magdalenian (13 800–12 300 uncal 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 (18 420 ± 530, 17 940 ± 200, 15 990 ± 260 uncal BP)	Morales-Muñiz and Roselló-Izquierdo (2008) (large *Salmo* sp identified as *Salmo salar*)

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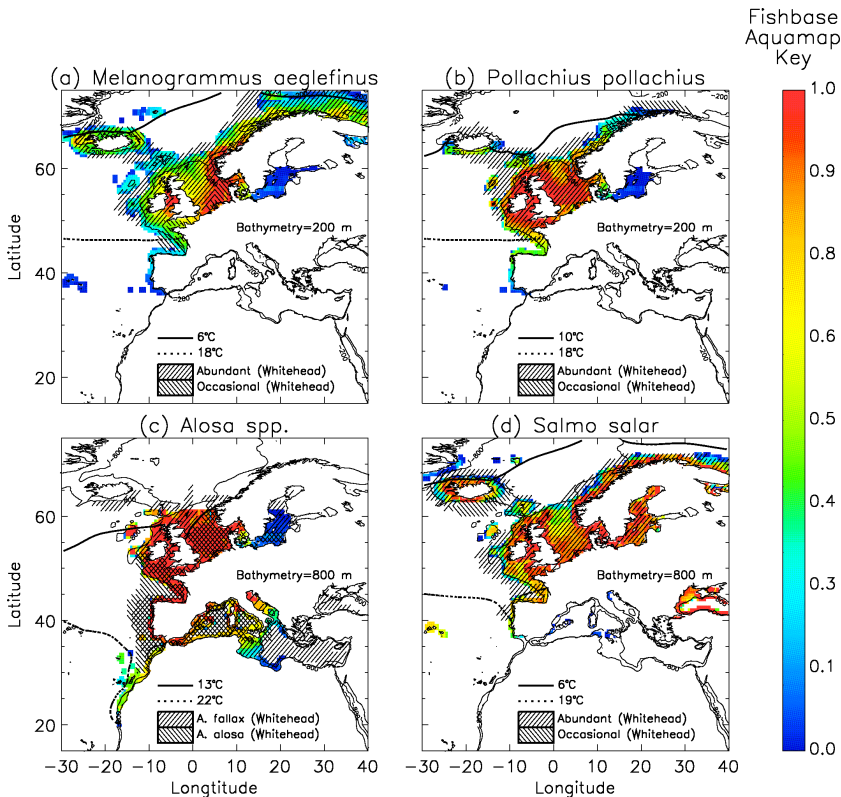
Fig. 1. Spatial distribution of **(a)** haddock (*Melanogrammus aeglefinnus*), **(b)** pollock (*Pollachius pollachius*), **(c)** allis shad (*Alosa alosa*) with twaite shad (*Alosa fallax*) included, and **(d)** Atlantic salmon (*Salmo salar*). Information is from Fishbase (colour-scale) and Whitehead et al. (1986; denoted by "Whitehead" and shown by hatching). The bathymetry is from ETOPO-5, with sea level and the single indicated contour (200 m or 800 m) plotted on the map. In (c) the ranges of the two shad species are plotted together because their archaeozoological remains are often difficult to distinguish, but the sea surface isotherms shown support the ENM analysis for allis shad.
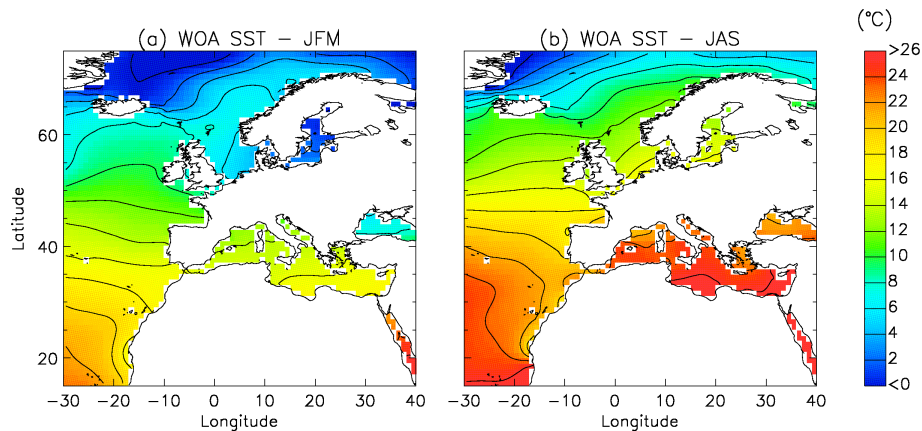
Fig. 2. Climatological sea surface temperature of the Northeast Atlantic in **(a)** winter (January, February, March) and **(b)** summer (July, August, September) from WOA05 (Levitus, 2006).
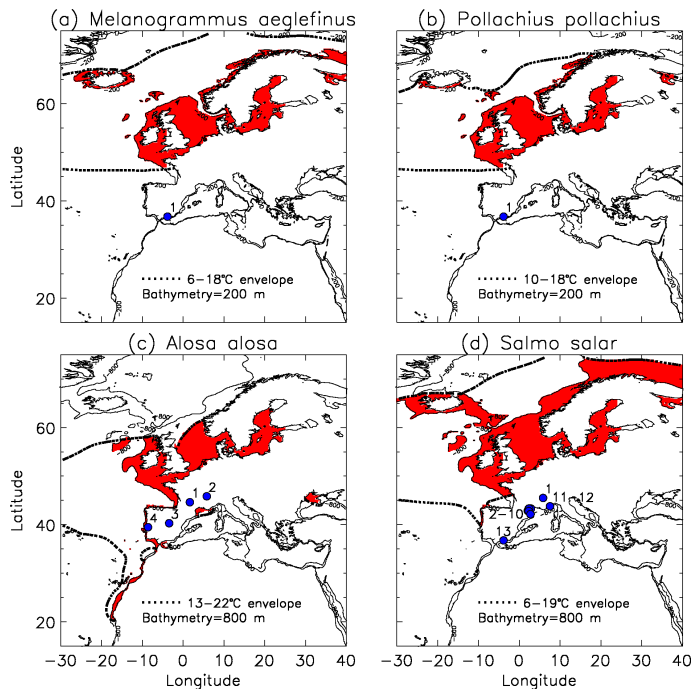
Fig. 3. Simplified species ranges using simplified criteria based on the summer SST and bathymetry envelopes shown in each diagram. The archaeozoological finds are given by blue dots with the number key given in Table 1. For **(a)** and **(b)**, the archaeological site is 1. Cueva de Nerja, Spain. For **(c)**, the archaeological sites are 1. Pégourié, Atlantic France, 2. Sous Balme, Mediterranean France, 3. Aridos-1, Spain, and 4. Lapa dos Coelhos, Portugal. For **(d)**, the archaeological sites are 1. Grotte Jean-Pierre I, Mediterranean France, 11. Baoussé-Roussé, Grottes de Menton, Italy, 12. Barme Grande, Grimaldi caves, Italy, 13. Cueva de Nerja, Spain, and a cluster of different sites along the Mediterranean coast of France and Catalonia with labels 2–10. The bathymetry is from ETOPO-5 with sea level and the single additional bathymetric contour indicated on the maps.
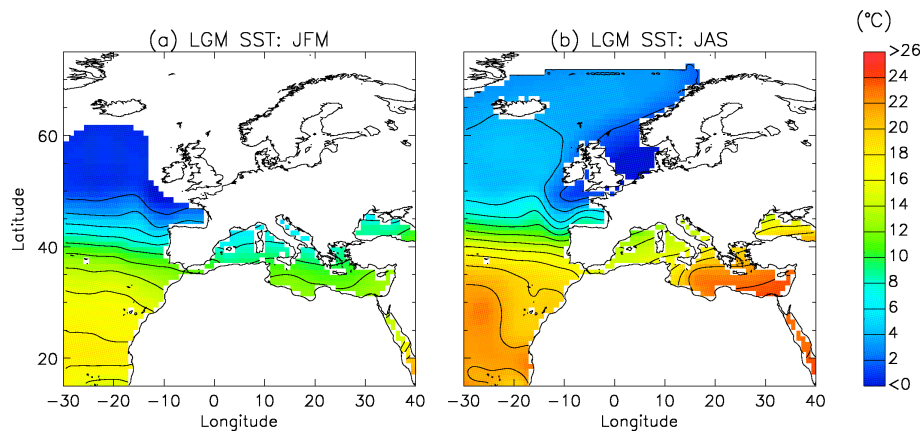
Fig. 4. Climatological SST from the LGM for **(a)** winter and **(b)** summer (from Paul and Schäfer-Neth, 2003).
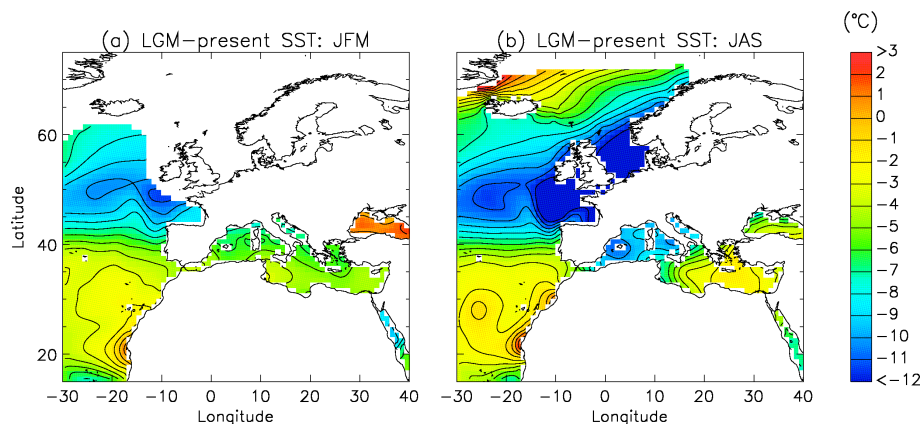
Fig. 5. Difference in climatological SST LGM-present for **(a)** winter and **(b)** summer. The LGM temperature reconstruction is from Paul and Schäfer-Neth (2003) and present data SST climatology from WOA05 (Levitus, 2006).
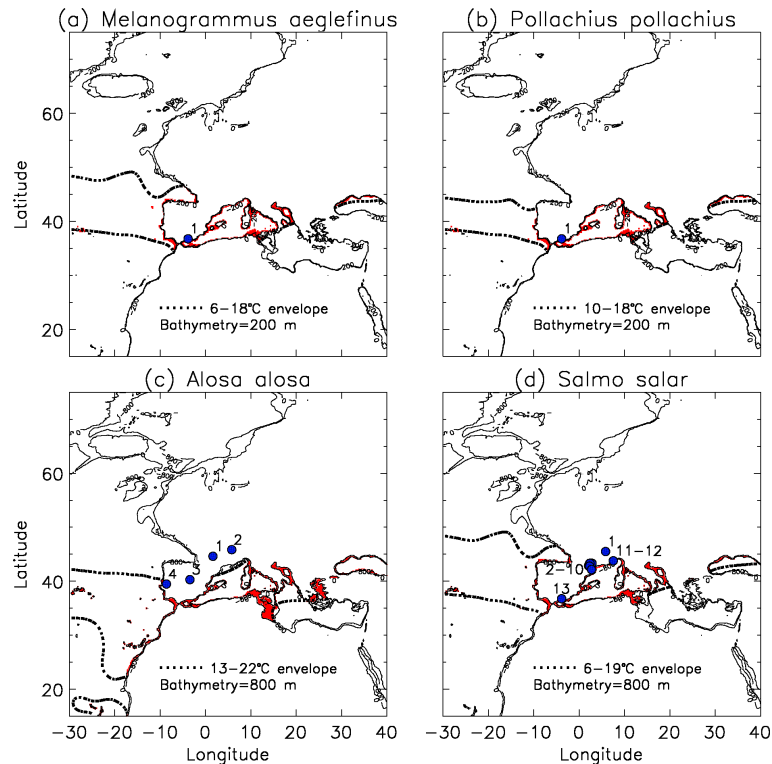
Fig. 6. Predicted species ranges from the LGM for **(a)** haddock, **(b)** pollock, **(c)** allis shad, and **(d)** Atlantic salmon. The ranges are based on the same criteria as for the present distribution in Fig. 3. The archaeological site key is the same as Fig. 3. The LGM ranges within the frame of these maps are 14–33% of the present day ranges, and the LGM distributions are almost completely shifted away from present-day ranges shown in Fig. 3. The LGM bathymetry is derived from the 1° sea level data of Peltier (1994) at 21 ka before present, interpolated to the 5' fields of ETOPO-5. LGM sea level and the single additional bathymetric contour are indicated on the map.

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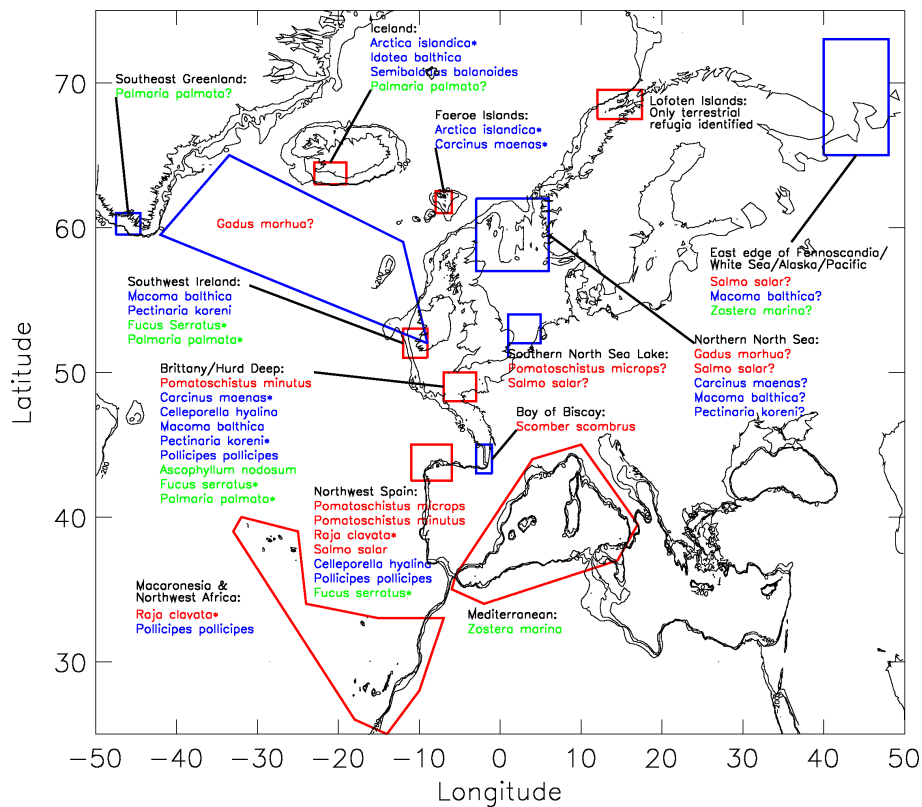
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Fig. 7. Marine glacial refugia of plants (green font), invertebrates (blue font), and teleosts (red font), modified from reviews in Gómez et al. (2007), Hoarau et al. (2007), Maggs et al. (2008), Larmuseau et al. (2009) and Olsen et al. (2010), together with their cited primary reports. Thin black lines show the present and LGM coastline, and the 200 m LGM isobaths. The red boxes present the possible marine refugia reviewed by Maggs et al. (2008). These are supported by a reanalysis of genetics results, except for the Lofoten Islands (i.e., a recognized terrestrial, but not marine, glacial refugium) and the Mediterranean (i.e., a controversial marine refuge area for Northeast Atlantic species (Larmuseau et al., 2009) without supporting species in the review of Maggs et al. (2008)). The blue boxes and species marked with question marks ? present other speculated marine refugia without firm support from archaeozoological or genetic evidence (e.g., the glacial refugia for *Gadus morhua* as given in Pampoulie et al., 2008). Marine glacial refugia have identified for plants (*Ascophyllum nodosum* (Olsen et al., 2010); *Fucus serratus* (Coyer et al., 2003; Hoarau et al., 2007); *Palmaria palmata* (Provan et al., 2005); *Zostera marina* (Olsen et al., 2004)), invertebrates (*Carcinus maenas* (Roman and Palumbi, 2004); *Celleporella hyalina* (Gómez et al., 2007); *Idotea balthica* (Wares, 2001); *Pectinaria koreni* (Jolly et al., 2005, 2006); *Macoma balthica* (Luttikhuizen et al., 2003; Nikula et al., 2007); *Pollicipes pollicipes* (Campo et al., 2010); *Semibalanus balanoides* (Wares and Cunningham, 2001)), and teleosts (*Pomatoschistus microps* (Gysels et al., 2004b); *Pomatoschistus minutus* (Larmuseau et al., 2009); *Raja clavata* (Chevolot et al., 2006); *Salmo salar* (Consuegra et al., 2002; Langefors, 2005); *Scomber scombrus* (Nesbø et al., 2000)). Species marked with an asterisk * have been critically reviewed by Maggs et al. (2008). Some of the unusual (and sometimes diverse) genetic signatures in the North Sea and Baltic are speculated to arise from recolonization from east of the Fennoscandian ice sheet and possibly as far as the Pacific Ocean which was ice-free at high latitudes during the LGM (Olsen et al., 2004).
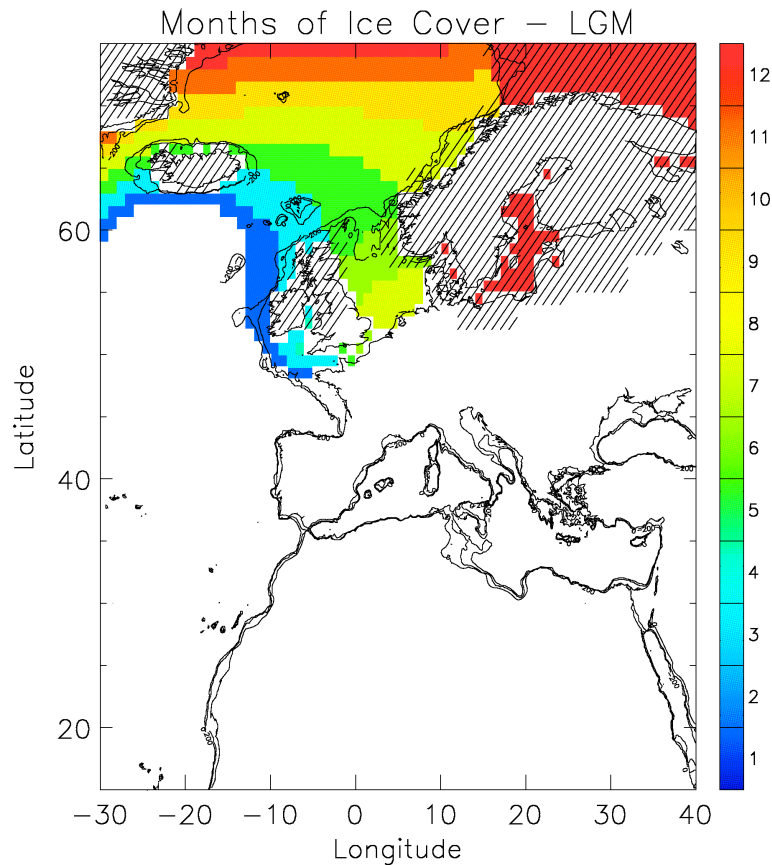
Fig. 8. Months of ice cover from LGM (Paul and Schäfer-Neth, 2003) with glacier template at 21 ka before present indicated by hatching (Peltier, 1994). The LGM bathymetry (sea level and 200 m depth) is derived from the 1° sea level data of Peltier (1994) at 21 ka before present, interpolated to the 5' fields of ETOPO-5. The present-day coastline is indicated on the map.

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