UDK 903'1(4)''632'':575.113
Documenta Praehistorica XXXIII (2006)

The Late Glacial ancestry of Europeans: Combining genetic and archaeological evidence

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ABSTRACT – *Chronometric attention in the Late Glacial of Western Europe is turning from the dating of archaeological cultures to studying how the continent was re-populated at the end of the last ice age. We present results from a survey of all available radiocarbon determinations (the S2AGES database) which show that when calibrated, and compared to the GRIP stratotype of climatic events, the data can be interpreted as five population events in the 15ka prior to the onset of the Holocene. The fine-grained climate record provides an opportunity to study the impact of environmental factors on a human dispersal process that not only shaped subsequent European prehistory, but also the genetic makeup of modern Europeans. The population events have implications for archaeologists and molecular geneticists concerning the timing, direction, speed and scale of processes in Western European demographic history. The results also bear on the role of climatic forcing on the expansion and contraction of human populations and in particular the correlation of ice core and terrestrial records for the onset of warming in the North Atlantic.*

IZVLEČEK – *Kronometrična pozornost se v poznem glacialu zahodne Evrope odmika od datiranja arheoloških kultur k proučevanju ponovne poselitve kontinenta ob koncu zadnje ledene dobe. Predstavljamo rezultate pregleda vseh dosegljivih radiokarbonskih sekvenc (podatkovna baza S2AGES), ki kažejo, da lahko datume, potem ko jih kalibriramo in primerjamo z GRIP stratotipom klimatskih dogodkov, interpretiramo kot zaporedje petih populacijskih dogodkov v času 15ka pred pojavom holocena. Podrobno strukturiran klimatski zapis nam omogoča proučevanje vpliva okoljskih faktorjev na proces človekove razselitve, ki je sooblikoval evropsko prazgodovino in genetski zapis modernih Evropejcev. Populacijski dogodki so pomembni za arheologe in molekularne genetike, ki se ukvarjajo s časovnim usklajevanjem, smerjo, hitrostjo in obsegom procesov v zahodnoevropski demografski zgodovini. Rezultati kažejo na pomen klimatskih pritiskov pri širjenju in krčenju človeških populacij in še posebej na korelacijo med lednimi in kopenskimi zapisi ob začetku segrevanja v severnem Atlantiku.*

KEY WORDS – *Radiocarbon; Calibration; Late Glacial; Settlement patterns; mitochondrial DNA; GRIP; Archaeological Taxonomic Unit*

Introduction

A major population expansion occurred in Western Europe during the Late Glacial (15–11.5ka CAL BP) as the OIS2 ice sheets retreated and unglaciated areas in the north became available for re-settlement. Phylogeographic analysis using molecular evidence assigns 60% of the European mitochondrial DNA lineages (*Richards et al. 2000*), and an even higher proportion of West European Y-chromosome lineages (*Semino et al. 2000*), to a population bottleneck prior to an expansion from southwest to northern Europe (*Torroni et al. 1998; Torroni et al. 2001; Achilli et al. 2004; Rootsi et al. 2004; Pe-*

reira et al. 2005). A potential signal of the bottleneck has also been detected in patterns of linkage disequilibrium in the autosomes (*Reich et al. 2001*).

Population estimates (*Bocquet-Apel and Demars 2000*) based on the changing distribution of archaeological sites indicate an increase in the Western European metapopulation, excluding Iberia, from 9000 to 40 000 persons with the corresponding occupied areas augmented from 0.55Mkm² to 1.12Mkm². The demic expansion is associated with the Magdalenian, a time-space archaeological taxonomic unit (ATU), which is found in Western Europe from c.22 to 13ka CAL BP and is known for its abundant cave and mobiliary art. However, the temporal sub-divisions of this ATU, based on artefact type fossils and stratigraphic sequences, remain problematic (*Laville et al. 1980; Thévenin 1995*) such that the timing, direction and pattern of the Late Glacial demic expansion are imprecise. Moreover, estimates of the age of the timing of this expansion derived from a molecular clock model for mitochondrial DNA to be c.16ka BP (*Torroni et al. 2001*) rely upon a number of assumptions and need to be substantiated by independent radiometric means.

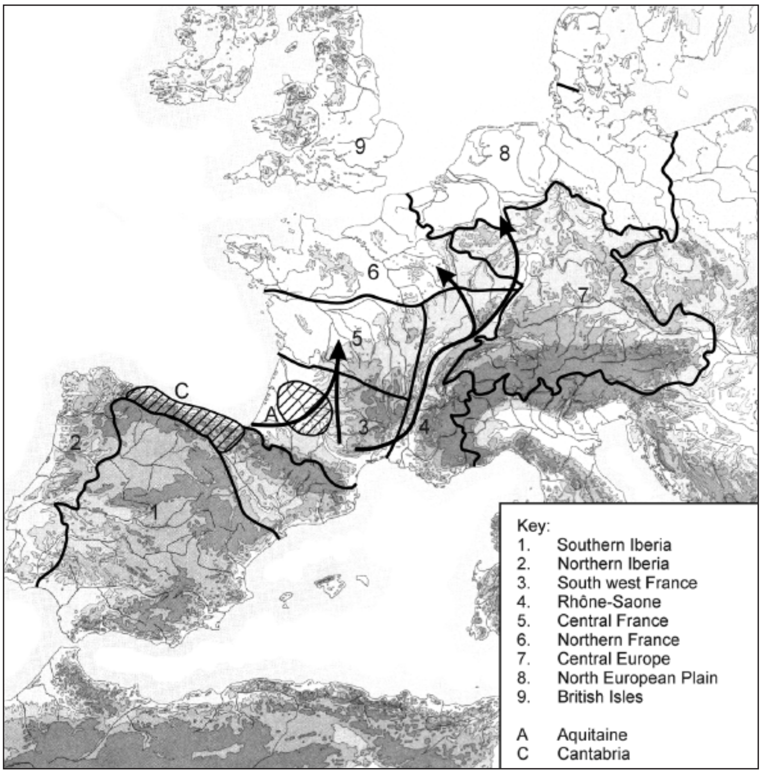

Fig. 1. Late Glacial Western Europe showing sampling regions, the two geographical refugia and probable expansion routes.

To address this imprecision, and to examine the correspondence between archaeological and genetic evidence for a population expansion, we present here results from S2AGES, an OIS2 database of radiocarbon determinations from Europe, the Near East and North Africa. The sub-sample described here comprises 2255 determinations from 1200 archaeological assemblages in Western Europe (Fig. 1) (*Pettitt et al. 2003*). Figure 2 presents, using CALPAL (*Weninger and Jöris 2004*), the calibrated radiocarbon determinations against the GRIP δ^{18} curve for Iberia, France and North Central Europe.

We interpret the changing frequencies of calibrated determinations as a proxy for the timing and direction of demic expansion as well as relative levels of human activity between regions. This method, using dates-as-data, is an established technique to investigate a process such as population dispersal into un-occupied habitats (*Holdaway and Porch 1995; Ross 2001*). We recognise five major population events for Late Glacial Western Europe (Tab. 1).

Population event	Settlement pattern	Dominant settlement type	Phylogeography	GRIP Stratotype	GRIP Ice core years BP
1. Refugium	Dispersed	Sheltered	Low population size	LGM – GS–2c	25ka – 19.5ka
2. Initial demic expansion	Pioneer	Sheltered and Open		GS–2b – GS–2a	19.5ka – 16ka
3.1 Main demic expansion	Residential	Sheltered	Founder effect and expansion	GS–2a	16ka – 14.7ka
3.2 Main demic expansion	Residential	Open		GI–1e	14.7ka – 14ka
4. Population stasis	Nucleation	Open		GI–1d – GS1a	14ka – 12.9ka
5. Population contraction		Open		GS1	12.9ka – 11.5ka

Tab. 1. Late Glacial population history of Western Europe as reconstructed from archaeological, radiocarbon and genetic evidence.

Population event 1: Refugium, 25ka–19.5ka BP

Existing refugium models for Western Europe predict that the lowest metapopulation and the smallest inhabited area co-incided with the last glacial maximum (= LGM 25–21.8ka) (*Soffer and Gamble 1990; Strauss 2000a*). By contrast, refugium is used here to describe the geographical distribution of population (G refugium), and the contraction, irrespective of geographic extent, of the size of the metapopulation (M refugium) within Western Europe.

Iberia, with radiocarbon determinations predominantly from Cantabria and Portugal (*Strauss 2000c*), was the major G refugium into which population contracted throughout the LGM and continued there until GS–2b (Fig. 2). By contrast, human presence was markedly less in France during this long period even though the Southwest, Aquitaine, has often been proposed as a major G refugium (*Jochim 1987; Soffer and Gamble 1990; Demars 1996*). North Central Europe was never entirely abandoned as shown for example by the site of Wiesbaden-Igstadt dated to GI–2 in the Rhineland (*Terberger and Street 2002*) but the calibrated curve indicates a low, probably intermittent, human presence in this region.

When the M refugium is examined using the S2AGES data, we find it lasted much longer than the LGM, sensu stricto and into GS–2b. Moreover, a radiocarbon database compiled for the Stage 3 project (*van Andel et al. 2003*) shows very low human presence in North Central Europe for at least the 10ka preceding the LGM in spite of a further six Dansgaard–Oeschger oscillations in this time interval (*Walker et al. 1999*).

The Solutrean has been proposed as the ATU of the LGM refugium (*Strauss 2000b*) (Fig. 3). The typological differences between the Solutrean and Badegoulian ATUs are regarded by archaeologists as too great to derive the latter from the former (*Djindjian et al. 1999*). As recently demonstrated by Terberger and Street (*2002*) the Badegoulian is most closely related to ATUs in Central and Eastern rather than Western Europe. This suggests the spatially extensive use of the French reindeer steppes by hunting parties with predominantly dispersed settlement patterns and whose population focus lay to the east, rather than the south. The eastern origins of the Badegou-

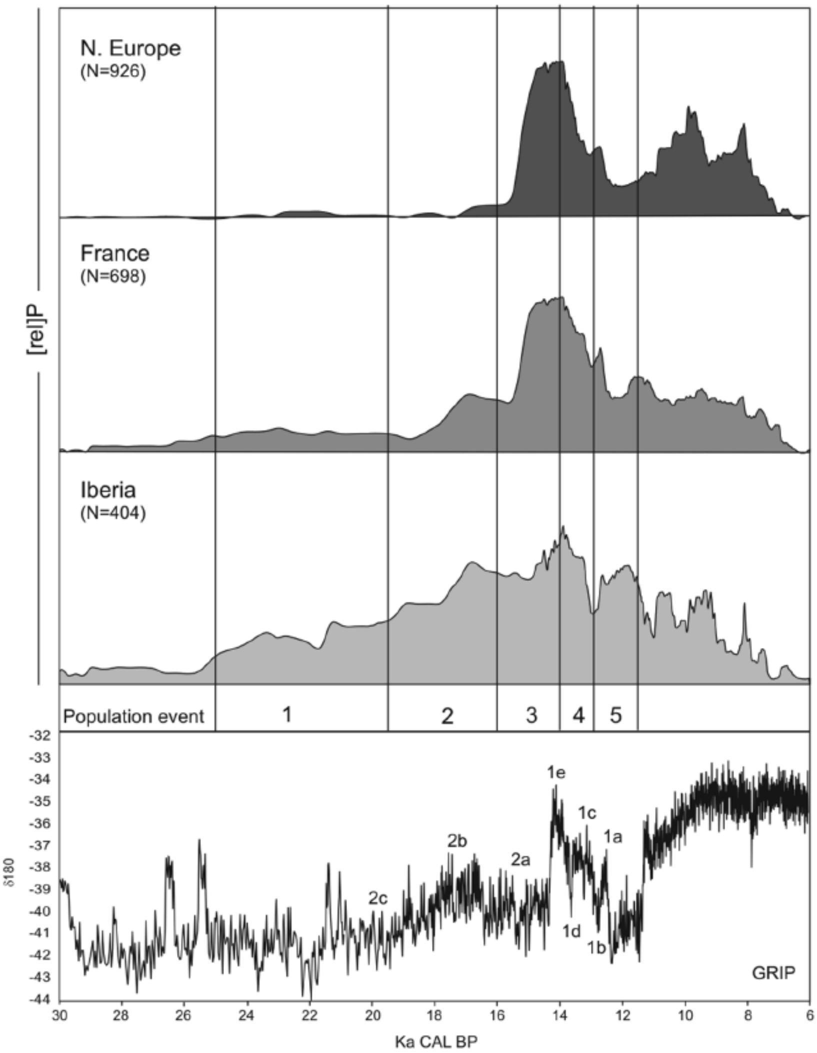

Fig. 2. Overview of Late Glacial radiocarbon dating probabilities for archaeological sites and assemblages, calibrated using CALPAL. The GRIP data form the stratotype for the Late Glacial–Last Termination event based stratigraphy. This recognises, post the Last Glacial maximum (LGM), two warm events (Greenland Interstadials 1 and 2 and two cold events (Greenland stadials 1 and 2). Currently GS–2 is subdivided into three sub-stages and GI–1 into five. In conventional terms GS–1 broadly corresponds to the Younger Dryas, GI–1e to the Bølling and GI–1c–1a to the Allerød interstadials. Other authors follow GISP2 for the period 25–16ka CAL BP. N = number of calibrated radiocarbon determinations in the frequency curve.

lian may be reflected in the distribution of mtDNA haplogroups H and pre-V. These are inferred to have an origin around 20–30ka BP either in eastern Europe or the Near East, and to have re-expanded from southwest Europe circa 16ka BP (*Richards et al. 2000; Torroni et al. 2001; Pereira et al. 2005*). The Y-chromosome cluster R1 shows a similar pattern (*Semino et al. 2000; Kivisild et al. 2003*).

Settlement type in both Cantabria and Southwest France during Population event 1 is dominated by rockshelters as opposed to open sites. Within Population event 1 we include the relatively short lived population expansions from Cantabria (Solutrean) and Central Europe (Badegoulian) into southern France (Fig. 3). We expect that similar demographic pulses were a regular feature of long-term human refugia.

Population event 2: Initial demic expansion 19.5ka–16ka BP

The radiocarbon determinations in Figure 4 form the proxy data to infer significant demographic change during GS-2b and the first half of GS-2a. In all areas this is associated with Magdalenian ATUs (Fig. 4). The change takes the form of an initial step and plateau (Fig. 2) in all regions outside the Cantabrian G refugium before the major rise in the frequency of calibrated determinations during the second half of GS-2a. This occurs during Heinrich Level 1 (17.6–14.9ka BP) when very low summer sea surface temperatures (SST) have been recorded in core MD95-2040 125km off the Portuguese coast (*de Abreu et al. 2003*).

In both France and Iberia Population event 2 corresponds (Fig. 4), to a pronounced peak in directly dated cave art. The number of sites is small (N = 14) but it is noteworthy that an earlier peak in France corresponds to the Solutrean population expansion we have identified (Fig. 3) and which also corresponds to low summer SST in the Iberian Atlantic during HL2 (24.3–23.1ka BP) (*de Abreu et al. 2003*). Therefore, cave art may be associated in some regions with small-scale demic diffusion out of the G refugium. This contrasts with earlier interpretations that linked the appearance of cave art to increased population density as people moved into refugia during the LGM and used art as a means to establish territorial rights to key resources such as salmon runs (*Jochim 1983*).

We favour an alternative, first proposed by Housley et. al. (*1997*), that this small demographic step inferred from the increased number of radiocarbon determinations represents a stage of pioneer settlement in the process of demic expansion as regions

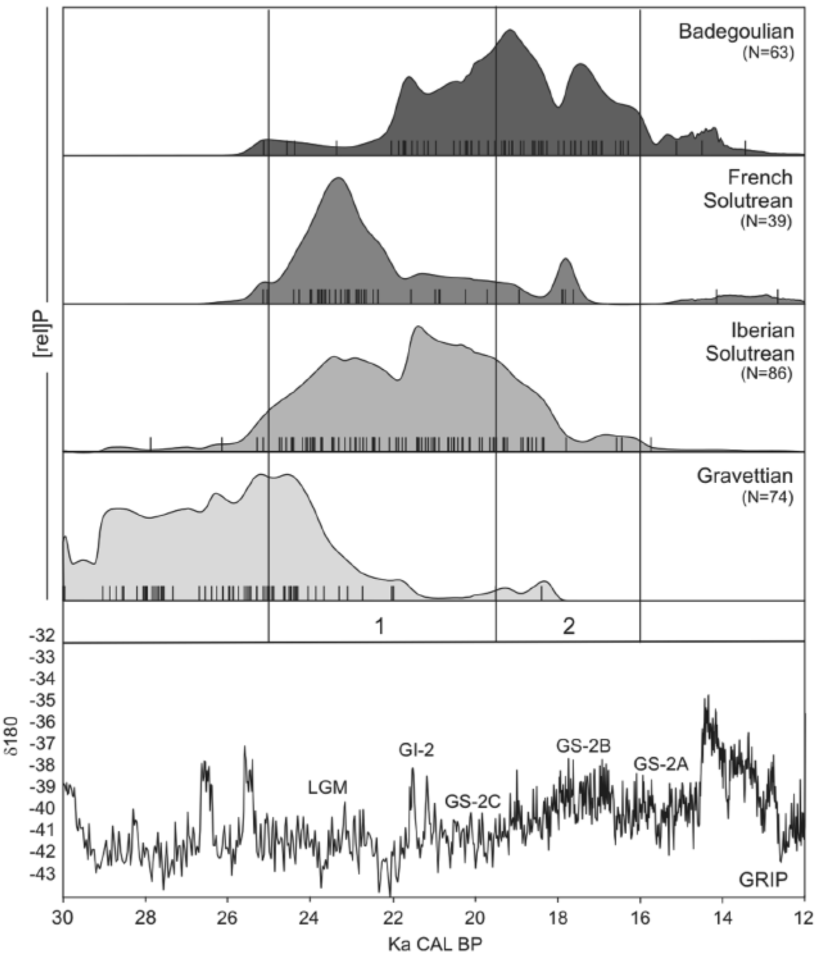

Fig. 3. Population events 1 and 2 (LGM to GS-2b) in Iberia and France. Calibrated curves are shown by ATUs. In Iberia the Solutrean is well represented from the LGM through GS-2c. In France the relative presence of the Solutrean, as indicated by the number of radiocarbon determinations, is substantially less suggesting a small demic diffusion north followed by population contraction back to the Cantabrian refugium. The wider context for the development of the Badegoulian (= Early Magdalenian) is therefore the contraction of population back into Iberia after GI-2.

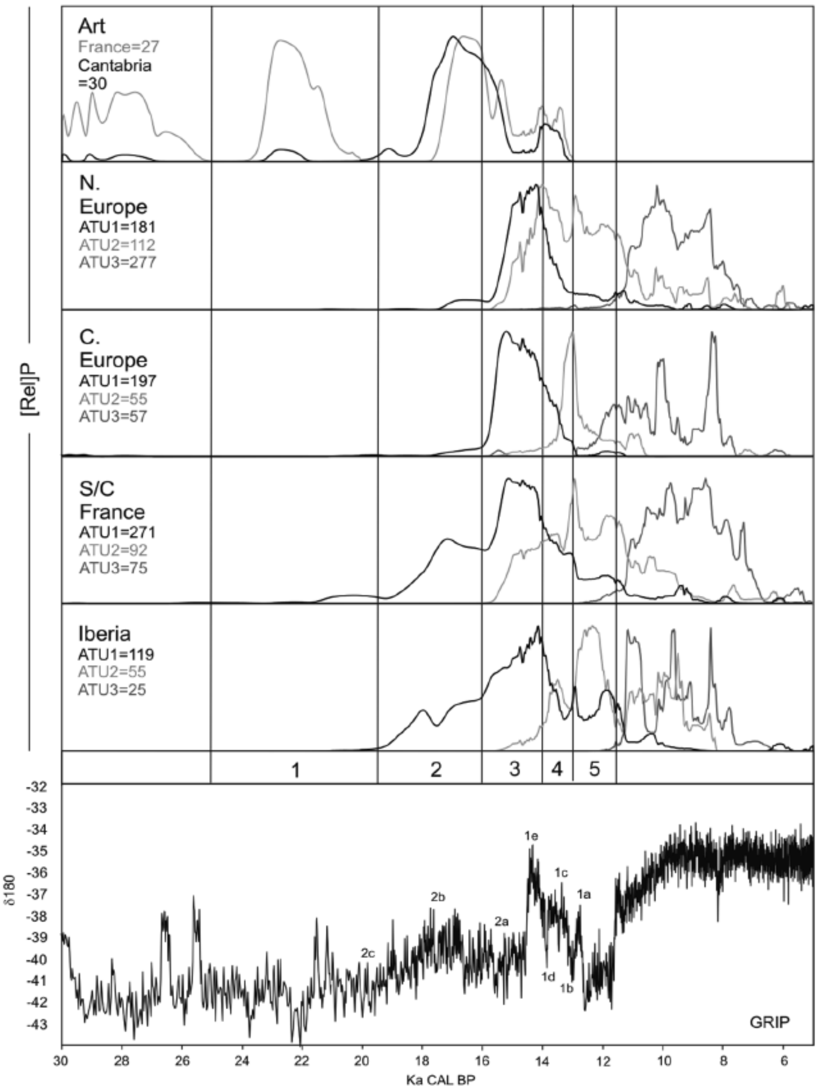

Fig. 4. Population events 3–5 (GS–2b to GS–1) radiocarbon dating probabilities by ATU. Later Magdalenian = ATU1; Epipalaeolithic = ATU2; Mesolithic = ATU3. It is expected that an audit of the dates by precision, accuracy and their archaeological integrity will reduce the outliers in earlier population events (*Pettitt et al. 2003*).

beyond the G refugium were explored, assessed and utilised in a more systematic fashion and on a more regular basis. This settlement pattern occurred over much of Western Europe where the main population focus now included southwest France as well as regions in Iberia outside Cantabria/Portugal. Settlement type now comprises both open and naturally sheltered sites.

Population event 3: Main demic expansion 16ka–14ka BP

The principal Late Glacial demic expansion occurred in two phases in Western Europe (Fig. 5) over a 2000 year period in GS–2a and GI–1e. In phase 3.1 (Tab. 1) there is a significant increase in the number of calibrated determinations in all regions between 16ka and 14.7ka CAL BP. During this 1300 year period the dominant ATU is the Late Magdalenian. Furthermore, the sequence in the radiocarbon curves (Fig. 5) confirm earlier archaeological studies and the interpretation of genetic evidence that within Western Europe demic expansion was from the south to the north and associated with a rapid increase in the metapopulation (*Demars 1996; Housley et al. 1997; Bocquet-Apel and Demars 2000; Strauss 2000a*).

Phase 3.2 of the main demic expansion is represented in two of the three regional radiocarbon curves (Fig. 4) as a plateau that lasts throughout GI–1e (= Bølling interstadial). These 700 years partly coincide with a small plateau in the calibration curve (*Weninger and Jöris 2004*). This is not considered significant because at this time in southern Iberia the frequency of determinations continues to rise (Fig. 5).

Following Housley et al. (*1997*), we describe the archaeological settlement pattern in Population Event 3 as residential. Large-size, open-air campsites are known (*Strauss et al. 1996*) from Lake Neuchâtel and the Neuwied and Paris basins and these are matched by substantial rock shelter occupations in the Rhine-Danube watershed, the uplands of Southern Germany, Thuringia and Belgium. Smaller-scale rock shelter occupations are known from the periphery in the British Isles (*Barton 1999*) and are comparable in site scale to the pioneer settlement of earlier Population event 2. No doubt small open settlements extended into other northern areas, such as Doggerland (*Coles 1998*), now inundated by the North Sea.

Archaeological evidence suggests two dispersal corridors for Population event 3 to the west and east of the Massif Central (*Thévenin 1995*). The eastern corridor following the Rhône-Saône-Rhine rivers is supported by evidence for the long-distance transfer of raw materials including Mediterranean shells and Baltic amber (*Floss 2000*) and is studded with residential settlement sites (*Street et al. 2001*).

Population event 4: Population stasis, 14ka–12.9ka BP

The interpretation of this population event as stasis rather than contraction illustrates the importance of combining radiocarbon determinations, when used as proxy data for past demography, with archaeological information on settlement patterns. The face-value interpretation from the calibrated curves (Fig. 5) is that after 14ka CAL BP population declined in most regions of Western Europe.

However, Figure 6 shows that when the radiocarbon determinations from Northern Europe (Fig.1) are compared for two classes of sites, open and rock shelter/cave, then the reason for the decline in the proxy population curve becomes apparent. Naturally sheltered locations were dominant in both population events 2 and 3. However, this settlement type did not form a significant part of the continuing occupation of the region. On the contrary, open-air campsites continued in importance throughout GI-1 and remained largely unaffected by climate change until the last sub stage GI-1a. We interpret these frequency data as changes in regional settlement patterns, for example from dispersed to nucleated, rather than a decline in the size of the metapopulation.

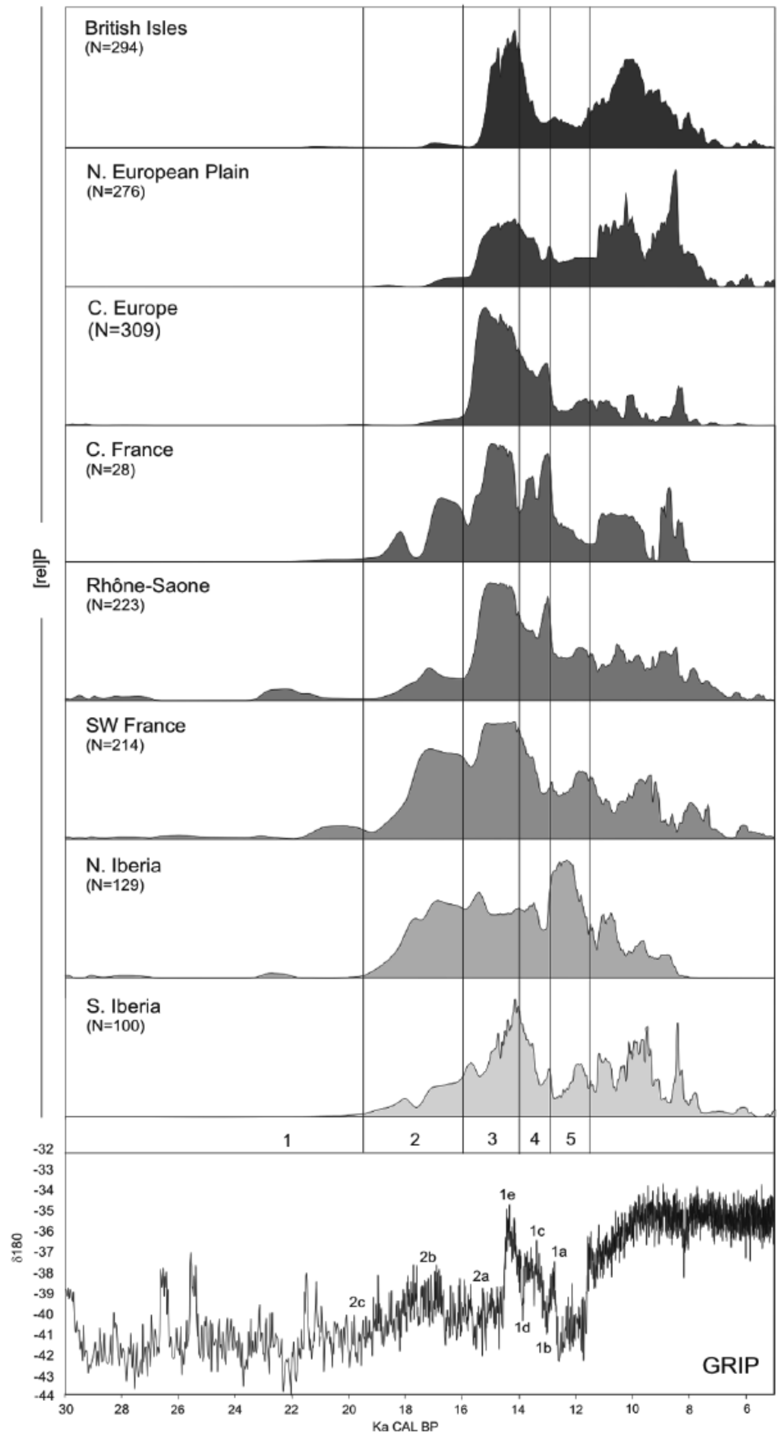

Fig. 5. Population events 3–5 (GS-2b to GS-1) radiocarbon frequencies by region. ATUs represented are Later Magdalenian, Epipalaeolithic and Mesolithic. As in Figure 4 the dates are unaudited.

Population event 5: Population contraction, 12.9ka–11.5 BP

The impact of GS-1 (= Younger Dryas) on population size in northern Europe was considerable (Fig. 6) and is confirmed by archaeological surveys (*Strauss et al. 1996*). However, this northern area was neither abandoned nor used as infrequently as in Population events 1 and 2 (Fig. 2). This suggests a higher metapopulation for Western Europe than the refugium minimum (*Bocquet-Apel and Demars 2000*) and from this deme came the Holocene/Mesolithic recovery and population growth.

Comparison with genetic data and the environmental framework

Phylogeographic analysis of modern Europeans indicates a major founder effect in the Late Glacial (*Richards et al. 2000*), with an age estimated from using the mitochondrial DNA molecular clock to circa 16 000 years ago (*Torroni et al. 2001; Pereira et al. 2005*). The radiocarbon chronology presented here provides the first independent assessment of this estimate with calibrated determinations (Tab. 1, Fig. 2). However, it is not yet possible to be precise about the duration of the constriction itself, except to suggest from the proxy radiocarbon data for regional demography that the neck of the bottle was particularly elongated. Estimates (*Bocquet-Apel and Demars 2000*) that the metapopulation increased from 9000 to 40 000 in the Late Glacial of Western Europe, excluding Iberia, now have to be considered as demographic growth, independent of in-migration, which occurred in Population event 3.1 over an estimated 1.3ka.

The S2AGES proxy data for demic expansion can be considered in the light of two current interpretations of the Greenland ice-core record and its significance for the North Atlantic (*Walker et al. 1999; Lowe et al. 2001*). At issue is the role of climate forcing in the expansion of human populations. Ameliorating climate at the end of the European ice ages is believed to drive the process of northward expansion of many species from southern refuges (*Hewitt 1996; Hewitt 1999; Willis and Whitaker 2000*). For this model to stand for human expansion it is necessary to interpret the radiocarbon and GRIP data as time-transgressive. Multi-proxy environmental evidence from terrestrial locations in northern Europe (*Walker et al. 2003*) suggest this may be the case. These data indicate warming was underway by 15.5ka CAL BP and that a time-transgressive interpretation between palaeoclimate archives at different latitudes is appropriate. If correct, the GRIP δ18 signal lags behind climatic warming and human, plant and animal migration in the oceanically controlled climates of Western Europe. Using Population event 3.1 as indicative of the effect of this warming on the distribution of human populations we can estimate the lag between climate change in Western Europe and its register in GRIP. Cross correlation Corr (τ) of the climate and radiocarbon curves identifies a positive peak only in the Northern Europe and French data. This indicates a significant response in the frequency of radiocarbon determinations some 700 years before climatic warming took place as indicated by GRIP. The width of the peak makes it difficult to ascertain precisely its statistical significance but its simultaneous occurrence in the two regions strongly suggests that it represents the same population event, probably related to biomass changes under climatic amelioration. Furthermore, the Iberian data show a negative correlation with climate change which is consistent with the continued refugium status for this region.

However, an alternative model that expansion is not directly linked to ameliorating climate and that the two records are time-locked is supported by marine evidence. High resolution records from an Iberian ocean core (*de Abreu et al. 2003*) shows in-phase oscillations with GRIP and GISP2 during the last glacial cycle. Significantly Heinrich Level 1 dated 17.6–14.9ka BP represents the coldest sea surface temperatures off Iberia in the last 70ka and coincides with the major human expansion during population events 2 and 3 (Tab. 1). Therefore, environmen-

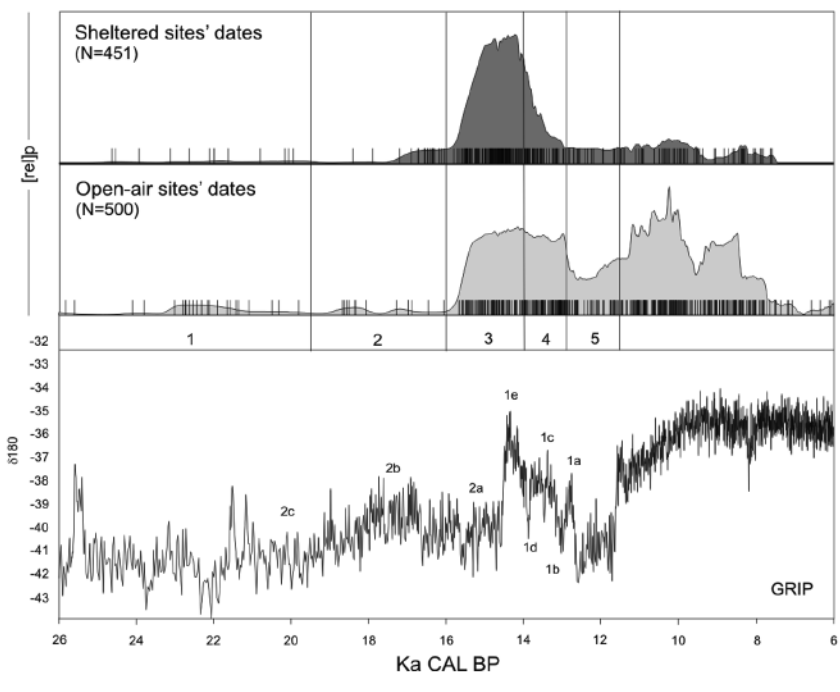

Fig. 6. Open and sheltered sites from northern France and North Central Europe (regions 6–9, Fig. 1) in population events 3–5.

tal forcing on population expansion was linked instead to colder climatic conditions in Western Europe and the earlier Solutrean pulse (Fig. 3) during HL2 confirms this.

One solution to the conflicting evidence over the role of climate in human expansion might rest in the model of southern refuges. Climate modelling using sea surface temperatures (*van Andel et al. 2003*) and evidence from the palaeobotanical (*Willis et al. 2000*) and faunal (*Stewart 2003*) archives points to the existence of cryptic refuges during cold phases north of Europe's continental divide. These refuges may have been small in extent and limited in duration but would have acted as an attractor to human populations with an extensive settlement network.

By comparison to human expansion, the contraction we document in Population event 5 appears in phase with the GRIP stratotype but is not related to any Heinrich Level. This association supports Foley's (*1994*) larger analysis of environmental change and evolutionary events among hominins, where the primary influence of climate is on extinction rather than speciation. We conclude that the expansion and contraction of mobile Late Glacial populations in Western Europe may be responding to fine-scale climate change in similar ways and where, at these smaller temporal and spatial scales, population dispersal and decline are analogous to speciation and extinction (*Gamble et al. 2004*).

ACKNOWLEDGEMENTS

The compilation of S2AGES was supported by a grant from the Leverhulme Trust (F/00180/I). Additional funding from the British Academy for a Research Readership and Research Grant was awarded to CG. Nick Barton, Robert Foley, Mike Walker and Cheryl Ross provided valuable comments.

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