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On the importance of coastal areas in the survival of Neanderthal populations during the Late Pleistocene

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ABSTRACT

This paper examines the distribution of Neanderthal populations across Europe and the Middle East. Key geographical variables are used to identify major population strongholds. Four are identified: southern Iberia, Atlantic Europe, Black Sea-Aegean and coastal Italy. Neanderthal site density in each stronghold was found to correspond closely with the predicted suitability of each area. A strong correlation was found between area suitability and last Neanderthal dates and the process of population fragmentation and extinction was found to affect continental areas first and coastal ones last. Oceanic influence, inter-area connectivity and proximity to coasts were found to be key variables in the Neanderthal extinction process. The functional ecological significance of coastal areas to Neanderthals is discussed.

1. Introduction

The broad geographical distribution of the Neanderthals, stretching from Portugal and the British Isles in the west to southern Siberia in the east, is well established (Finlayson and Carrión, 2007). Often the distribution of the Neanderthals has been represented by the maximum limit of their range and this has caused confusion regarding their biogeographical dynamics (Finlayson, 2004). At the same time traditional views regarding the extinction of the Neanderthals, the result of modern human expansion from the Middle East, persist in the literature (Mellars, 2004) in spite of the absence of evidence in support (Finlayson and Carrión, 2007). The alternative view, that climate change through habitat and resource fragmentation gradually decimated Neanderthal populations across their range (Finlayson et al., 2000), is resisted by some (D'Errico and Sánchez-Goñi, 2003) in spite of their own evidence showing range contraction of Iberian Neanderthals during Heinrich Event (HE) 4 around 35–35,000 years ago (ka bp uncal.). For these authors the subsequent extinction of the last Neanderthals in southern Iberia was caused instead by competition from arriving moderns. Carrión (2004) and Finlayson et al. (2004) have questioned this point of view and Finlayson (2005) has shown that evidence for modern human-Neanderthal competition is non-existent and must be discarded as the global cause of the Neanderthal demise.

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2. Regional setting

The occupation of Mediterranean coastal environments by Neanderthals has been documented in the Middle East (Bar-Yosef, 2000), Greece (Panagopoulou et al., 2002–2004), Italy (Stiner, 1994), France (Boyle, 2000) and the Iberian Peninsula (Finlayson and Giles Pacheco, 2000). Finlayson (2006) and Finlayson and Finlayson (2008) have provided a detailed description of a Mediterranean OIS 3 coastal environment that was exploited by Neanderthals, thus providing a functional basis for our understanding of the importance of such environments as refugia. One such environment, of Gorham's Cave (Gibraltar), is known to have held the last-known population of Neanderthals (Finlayson et al., 2006). It has since been established that rapid climate change was the most probable cause of the extinction of the last Neanderthals on the southern coast of the Iberian Peninsula (Jiménez-Espejo et al., 2007). The aim of this paper is to situate the occupation of coastal areas of the Mediterranean, Atlantic and the Black Sea by Neanderthals in the context of their wider biogeography, making special reference to the importance of such sites within a refugial context.

3. Methods

Fig. 1 is a map of Europe, western Asia and North Africa, showing altitude at three levels: −100 to +300 m, 300–1000 m, and >1000 m. It represents the surface area potentially available to Neanderthal occupation during OIS 3 (Appendix 1). Eight geographical variables were ranked on a scale between 1 and 3, the highest score always being allocated to the

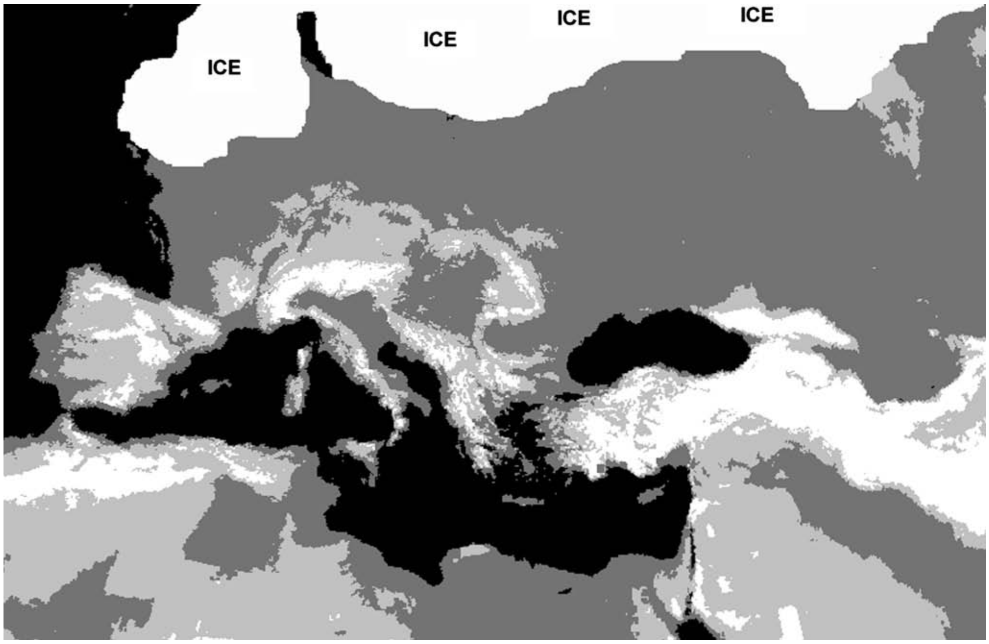

Fig. 1. Map of Europe, western Asia and North Africa. Key (relative to present-day sea level): Black, below −100 m; dark grey, between −100 and 300 m; light grey, between 300 and 1000 m; white, above 1000 m. Approximate position of ice sheets at the Last Glacial Maximum is indicated schematically. Note also that bathymetric lines need not reflect exact position of the coastline, which has been affected, in the Mediterranean for example, by eustasy, glacio-hydro-isostasy and vertical tectonic motion and exhibits considerable spatial and temporal variability (Lambeck et al., 2004). For this reason the map should only be seen as an approximate backdrop that is used in this paper to situate the broad location of Neanderthal populations.

favourable (in terms of potential benefit to Neanderthal survival) end of the spectrum for that variable (Table 1). The region (Fig. 1) was then divided into a series of potential Neanderthal occupation areas and these were categorized by the eight variables.

4. Results

Twenty-three potential Neanderthal occupation areas were established and these were ranked in accordance with their suitability (Table 1). Four major Neanderthal geographical strongholds

Table 1
Suitability of Neanderthal occupation areas

Area	Stronghold number	SURF	ALTD	LATD	OCEA	CONN	COAS	ICEP	DESP	Suitability	Observed last dates	Predicted last dates
SWIBE	1	3	3	3	3	1	3	3	3	22	24	25
SEIBE	1	1	1	3	3	3	3	3	3	20	29	29
INSIBE	1	3	1	3	3	3	1	3	3	20	29	29
EIBE	1	1	1	3	2	3	3	3	3	19	30	31
SWFRA	2	3	3	2	3	1	2	2	3	19	33	31
NWIBE	2	1	2	3	3	3	3	3	3	19	34	31
NWEUR	2	3	3	1	3	2	2	1	3	18	32	33
BLSEA	3	3	3	2	1	1	2	3	3	18	30	33
AESEA	3	2	1	3	1	1	3	3	3	17	34	35
SITA	4	1	1	3	1	2	3	3	3	17	34	35
TUSLAT	4	1	1	2	2	3	3	2	3	17	35	35
NEITA	4	3	1	2	2	2	2	2	3	17	33	35
MEDFRA	1	1	1	2	2	3	3	1	3	16	35	37
INNIBE	2	3	1	2	3	1	1	2	3	16	37	37
MEDTUR	3	1	1	3	1	1	3	3	3	16		37
INTUR	3	3	1	3	1	1	1	3	3	16		37
SETUR	3	3	1	3	1	1	1	3	3	16		37
NWITA	4	1	1	2	2	3	3	1	3	16	40	37
NEUR	2	3	2	1	2	2	1	1	3	15	38	39
BSTUR	3	1	1	2	1	1	3	3	3	15		39
LEVANT	3	1	1	3	1	1	3	3	1	14	44	41
CARP	4	3	1	2	1	1	1	1	3	13	40	43
BALK	4	2	1	2	1	1	1	2	3	13		43

Suitability variables: SURF, available surface area (3 large, 2 intermediate, 1 small); ALTD, proximity to mountains >1000 m (3 far, 2 intermediate, 1 close); LATD, latitude (3 south, 2 intermediate, 1 north); OCEA, proximity to Atlantic (3 close, 2 intermediate, 1 far); CONN, connectivity to suitable areas (3 high, 2 intermediate, 1 poor); COAS, proximity to coast (3 close, 2 intermediate, 1 far); ICEP, proximity to maximum extent of ice sheets (3 far, 2 intermediate, 1 near); DESP, proximity to maximum extent of desert (3 far, 2 intermediate, 1 near). Suitability is the sum of the eight suitability variables and areas are listed in descending order of rank. Area codes: SWIBE, south-western Iberia; SEIBE, south-eastern Iberia; INSIBE, inland southern Iberia; EIBE, eastern Iberia; SWFRA, south-western France; NWIBE, north-western Iberia; NWEUR, north-western Europe; BLSEA, Black Sea; AESEA, Aegean Sea; SITA, southern Italy; TUSLAT, Tuscany/Latium; NEITA, north-east Italy; MEDFRA, Mediterranean France; INNIBE, inland northern Iberia; MEDTUR, Mediterranean Turkey; INTUR, inland Turkey; SETUR, south-eastern Turkey; NWITA, north-western Italy; NEUR, northern Europe; BSTUR, Black Sea Turkey; LEVANT, Levant; CARP, Carpathain Basin; BALK, inland Balkan mountains. For stronghold definition see Fig. 2. Last dates from the literature. Predicted dates from Fig. 3.

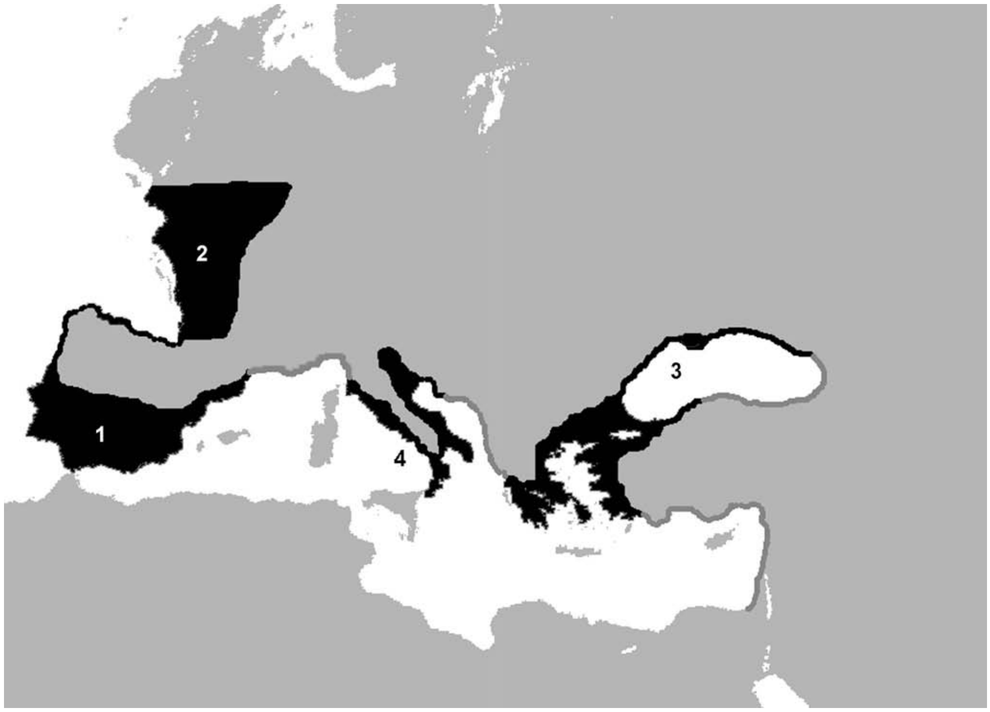

Fig. 2. Four main Neanderthal strongholds (black numbered 1–4). Grey bands show connectivity along the coast between strongholds. Areas not marked black but included in strongholds in Table 3 are considered peripheral areas belonging to the respective stronghold and colonized sporadically.

were identified on the basis of suitability (Fig. 2). These are defined, in order of importance, as follows: (1) Southern Iberia, combining coastal areas of south-western Iberia (SWIBE), south-eastern Iberia (SEIBE) and eastern Iberia (EIBE) along with inland areas of southern Iberia (INSIBE); (2) Atlantic Europe, combining coastal and proximal inland areas of south-western France (SWFRA), coastal north-western Iberia (NWIBE), and coastal and proximal inland areas of Atlantic north-western Europe (NWEUR); (3) Black Sea-Aegean, combining coastal areas along the northern and western coast of the Black Sea (BLSEA) with coastal areas of the Aegean Sea (AESEA); and (4) Coastal Italy, combining coastal areas of Tuscany and Latium (TUSLAT), southern Italy (SITA) and north-eastern Italy (NEITA). To verify that the predicted suitability of areas in Table 1 were meaningful, the individual area scores were regressed against the last-known dates of Neanderthal or Mousterian occupation of each area (Table 1, Fig. 3).

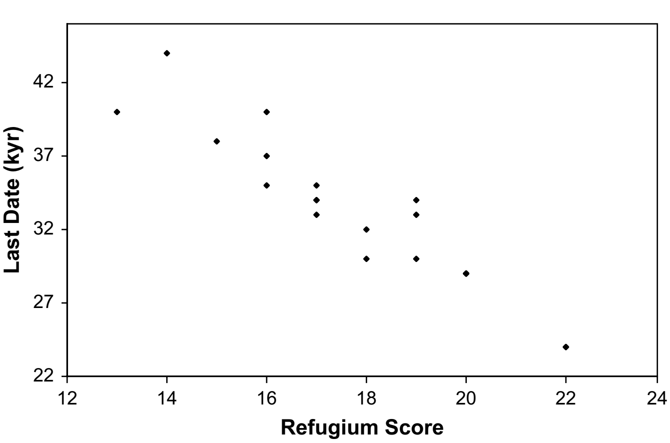

Fig. 3. Regression between Refugium area scores against last observed Neanderthal dates per area (from Table 1). $y = 68.2328 - 1.973x$, $R^2 = 0.88$, $p < 0.00001$.

The results indicate a highly statistically significant relationship, areas with high scores consistently providing younger dates than those with lower scores (Fig. 3). Areas of Asia and northern Africa not covered in the initial analysis and which are known to have been occupied either by Neanderthals or by makers of the Mousterian industry, associated with Neanderthals in Eurasia and with anatomically modern humans (AMHs) in Africa (Finlayson and Carrión, 2007), were scored for the eight geographical variables.

Using the regression equation from Fig. 3, predictions were made as to the last expected dates in each area and these were compared with those available in the literature. There was a close correspondence between the expected and observed dates (Table 2). A database of sites for each area (Appendix 1) was used to compare the predicted suitability of each area with the intensity of use by Neanderthals of each area. Some areas, for example south-western France, north-western Iberia, the Levant and the Carpathian Basin, have been well studied and a large number of sites may reflect sampling intensity. To minimise difficulties related with research intensity, areas were compared within each of the four strongholds. Even so, it should be borne in mind that other factors, e.g. degree of site preservation, may influence site density so that the results have to be viewed with a degree of caution. In spite of these caveats, the results of this analysis (Table 3) do show a very close correspondence between predicted area suitability within each stronghold and site density.

5. Discussion

5.1. The process of Neanderthal extinction

In Fig. 4 the process of fragmentation of Neanderthal populations across Europe and western Asia is plotted on the basis of area suitability and predicted last dates (from Table 1). The fragmentation can be very closely correlated with short and sharp

Table 2
Suitability of occupation areas not covered in Table 1

Area	SURF	ALTD	LATD	OCEA	CONN	COAS	ICEP	DESP	Suitability	Observed last dates[a]	Predicted last dates[b]
SICILY	1	1	3	2	2	3	3	3	18	Unknown	33
CYRENAICA[a]	3	3	3	1	1	3	3	1	18	30–43	33
NWMOR[a]	1	1	3	3	1	3	3	2	17	32	35
NEMOR[a]	1	1	3	2	1	3	3	2	16	35	37
TUNIS[a]	2	1	3	2	1	3	3	1	16	Unknown	37
CENTASIA	3	1	2	1	3	1	3	1	15	39	39
ARABCOAST[b]	1	1	3	1	1	3	3	1	14	Unknown	41
ALTAI	3	1	1	1	3	1	2	1	13	43	43

The presence of Neanderthals is unconfirmed from Sicily.
[a] Sites with Middle Palaeolithic industries (Mousterian, Aterian) attributed to anatomically modern humans (AMHs).
[b] Middle Palaeolithic but taxonomy of hominins is unknown. Last dates from the literature. Predicted dates from Fig. 3.

climatic events (Table 4). There is an initial loss of populations that only affects the eastern strongholds (3 and 4) which is related to HE5 and a DO stadial between 45 and 41 ka. There is then a major break-up of populations affecting continental areas of all strongholds related to a DO stadial so that by 35 ka four isolated nuclei of population remain, in southern and eastern Iberia, the Atlantic coast between Cantabria and the British Isles, the Italian Peninsula, and the coasts of the Black Sea and the Aegean (Fig. 4(c)). The Italian stronghold (4) and the Aegean population are lost with H4 (35–34 ka). This leaves a western population in Iberia, Atlantic France and the British Isles and a remnant Black Sea population at 34 ka (Fig. 4(d)). The Black Sea population, along with the more northerly of the western populations, is lost after a DO (33–32 ka). By 31 ka (Fig. 4(e)) two western, disconnected, nuclei remain, one in south-western France and Cantabria and the other in southern and eastern Iberia. The Atlantic stronghold disappears altogether, along with the eastern Iberian population, after a DO at 30 ka (Table 4). At 30 ka there is only a relict southern Iberian population left (Fig. 4(f)). This population then shrinks towards extinction (Fig. 4(g) and Table 4).

The modelled scenario fits very well with observed regional late Neanderthal dates. It shows that the process of fragmentation broadly followed an east–west pattern that may explain misinterpretations regarding its correlation with an east–west movement of AMHs (Mellars, 2004). The detail of the process is clearly complex and some western populations disappear before some eastern ones and the entire process can be explained solely by climatic factors. The fragmentation process is not linear but instead shows a steep decline between 40 and 34 ka linked with H4 (when it is especially steep) and a preceding DO (Fig. 5), when much of the European population is lost. A further sharp decline around 31–30 ka leaves the southern Iberian population as the last remnant and this slowly dwindles after that (Fig. 5).

5.2. The importance of the coast

The significance of each geographical area is dependent on a combination of the geographical variables examined (Table 1). Certain variables appear, however, to play a major role and this is particularly evident when core stronghold areas are compared with peripheral ones (Table 5). Oceanic influence (OCEA), connectivity (CONN) and proximity to coastline (COAS) stand out as being of particular importance. COAS is a particularly important variable. Only one stronghold area of 12 (8.3%) was distant from the coast and seven (58.3%) were fully coastal. A comparison of last dates for each area (from Table 1) with proximity to coast also shows that there was a clear trend for late Neanderthal sites to be on the coast (Fig. 6). The only exception was inland southern Iberia (INSIBE). It is interesting that this area, apart from its southerly latitude, was surrounded by the two most important areas within stronghold 1 (SWIBE, SEIBE), both of which were coastal.

The importance of coastal areas for Neanderthals has been underplayed in comparison with its significance to AMHs in Africa (Klein, 1999). The exploitation of coastal intertidal resources by

Table 3
Number of Neanderthal/Mousterian sites (see Appendix 1) by stronghold and area

	Area													
Stronghold	SWIBE (*n*)	SWIBE (%)	SEIBE (*n*)	SEIBE (%)	INSIBE (*n*)	INSIBE (%)	EIBE (*n*)	EIBE (%)	MEDFRA (*n*)	MEDFRA (%)				
1. Southern Iberia	122	54.9	40	18.0	31	14.0	14	6.3	15	6.8				
Stronghold	SWFRA (*n*)	SWFRA (%)	NWIBE (*n*)	NWIBE (%)	NWEUR (*n*)	NWEUR (%)	INNIBE (*n*)	INNIBE (%)	NEUR (*n*)	NEUR (%)				
2. Atlantic Europe	367	66.2	114	20.6	28	5.1	13	2.3	32	5.8				
Stronghold	BLSEA (*n*)	BLSEA (%)	AESEA (*n*)	AESEA (%)	MEDTUR (*n*)	MEDTUR (%)	INTUR (*n*)	INTUR (%)	SETUR (*n*)	SETUR (%)	BSTUR (*n*)	BSTUR (%)	LEVANT (*n*)	LEVANT (%)
3. Black Sea-Aegean	38	26.8	42	29.6	6	4.2	10	7.0	12	8.5	2	1.4	32	22.5
Stronghold	SITA (*n*)	SITA (%)	TUSLAT (*n*)	TUSLAT (%)	NEITA (*n*)	NEITA (%)	NWITA (*n*)	NWITA (%)	CARP (*n*)	CARP (%)	BALK (*n*)	BALK (%)		
4. Coastal Italy	20	20.2	21	21.2	20	20.2	10	10.1	24	24.3	4	4.0		

Regression analysis of area suitability (Table 2) against site density (this table) revealed close correspondence between the two variables: 1. Southern Iberia ($R^2 = 0.966$, $p = 0.0001$); 2. Atlantic Europe ($R^2 = 0.43$, $p = 0.0026$); 3. Black Sea-Aegean ($R^2 = 0.794$, $p < 0.00001$); 4. Coastal Italy ($R^2 = 0.863$, $p = 0.0005$). Regression analysis for strongholds 3 and 4 excluded LEVANT and CARP, respectively. These areas may not fall within these strongholds or may reveal a high site density on account of intense research activity. Key to areas as Table 1.

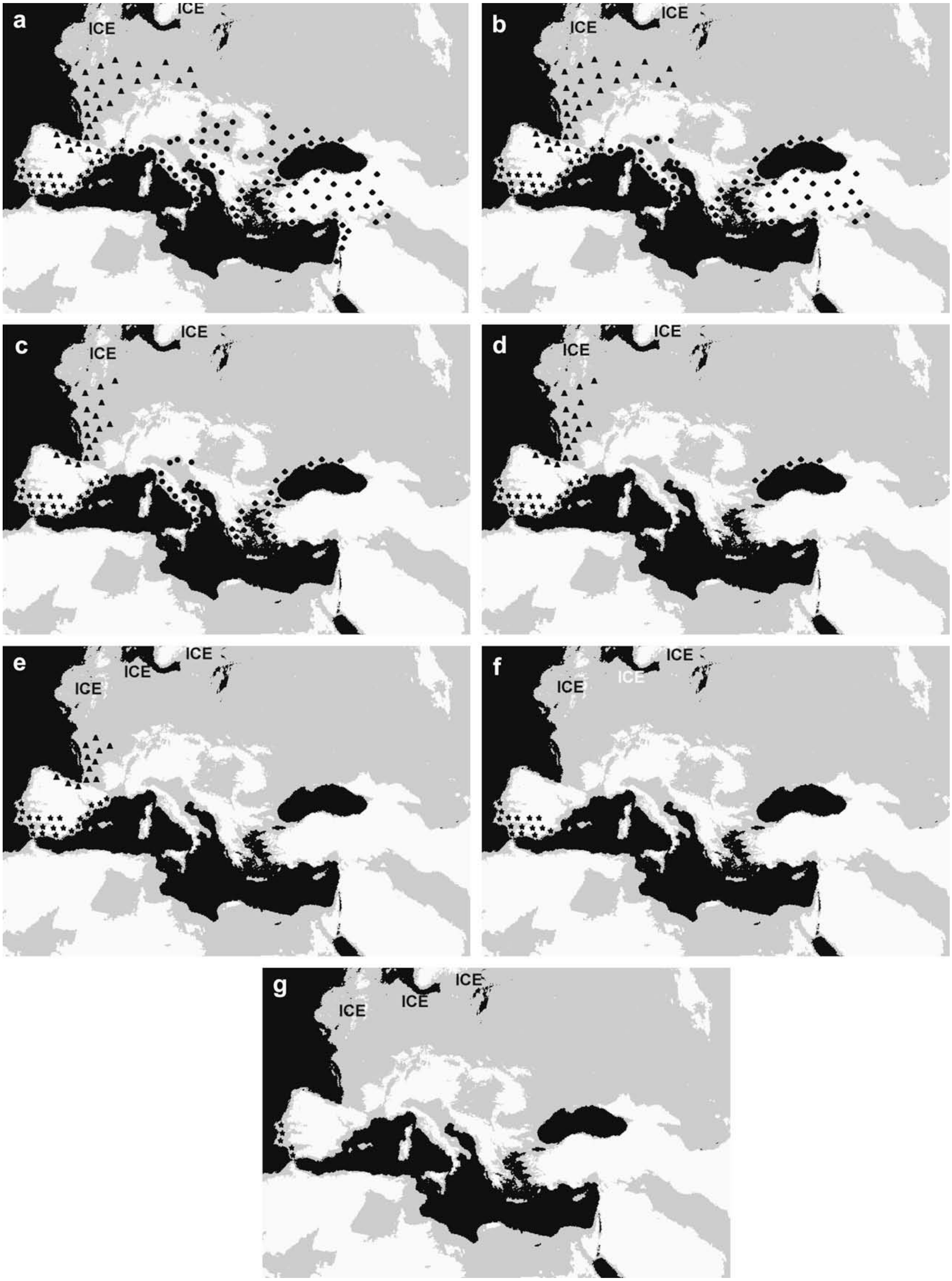

Fig. 4. The process of Neanderthal fragmentation and extinction in relation to major strongholds and predicted regional extinction dates. (a) 46–41 ka; (b) 40–36 ka; (c) 35–34 ka; (d) 34–32 ka; (e) 31–30 ka; (f) 30–28 ka; (g) post-28 ka; see also Table 4. Symbols: ★, stronghold 1; ▲, stronghold 2; ◆, stronghold 3; ●, stronghold 4.

Table 4
Sequence of Neanderthal population fragmentation illustrated in Fig. 4

Map Ref	Time (ka bp)	Climatic event	Population lost
(a)	46		
	45	H5	CARP, BALK
	42–41	DO	LEVANT
(b)	40		
	37–36	DO	BSTUR, NEUR, NWITA, SETUR, INTUR, MEDTUR, INNIBE, MEDFRA
(c)	35		
	35–34	H4	NEITA, TUSLAT, SITA, AESEA
(d)	34		
	33–32	DO	BSEA, NWEUR
(e)	31		
	30	DO	NWIBE, SWFRA, EIBE
(f)	30		
	29–28	DO	INSIBE, SEIBE
(g)	28		
	27–26	H3	
	25	DO	SWIBE

Dates are uncalibrated and timing of Heinrich Events (HE) and Dansgaard-Oeschger Stadials (DO) are from D'Errico and Sánchez-Goñi (2003). Population codes from Table 1.

Table 5
Comparison of stronghold and peripheral areas by geographical variables

VARIABLE	SCORE	STRONGHOLD	PERIPHERAL
SURF	1	5	5
	2	1	1
	3	6	5
ALTD	1	8	10
	2	0	1
	3	4	0
LATD	1	1	1
	2	5	6
	3	6	4
OCEA	**1**	**3**	**7**
	2	**3**	**3**
	3	**6**	**1**
CONN	**1**	**4**	**8**
	2	**3**	**1**
	3	**5**	**2**
COAS	**1**	**1**	**6**
	2	**4**	**0**
	3	**7**	**5**
ICEP	1	1	4
	2	3	2
	3	8	5
DESP	1	0	1
	2	0	0
	3	12	10

Neanderthals has been established in recent years for Israel, Italy and southern Iberia (Stiner, 1994; Stiner et al., 1999, 2000; Stringer et al., 2000; Bailey and Flemming, 2008). There is increasing evidence that Neanderthals in Gibraltar also exploited shallow water marine molluscs (Fa, in press), marine mammals, fish and seabirds (Finlayson, 2006; Finlayson and Finlayson, 2008). A similar pattern is emerging from the coast of Portugal (Bicho and Haws, 2008). Coastal areas are prime ecotones that often combine marine with terrestrial and wetland resources (Finlayson, 2004, 2006). As such they would have always been premium sites for hominins and the Neanderthals were no exception. The richness and diversity of available resources would have enabled Neanderthals in such coastal areas to maintain relatively small home ranges that would be known intimately and exploited systematically during the course of the annual cycle. During the greater part of OIS 3, with lowered sea levels, the coastal shelf would have also permitted connectivity between Neanderthal coastal populations, thus reducing extinction risks associated with isolation.

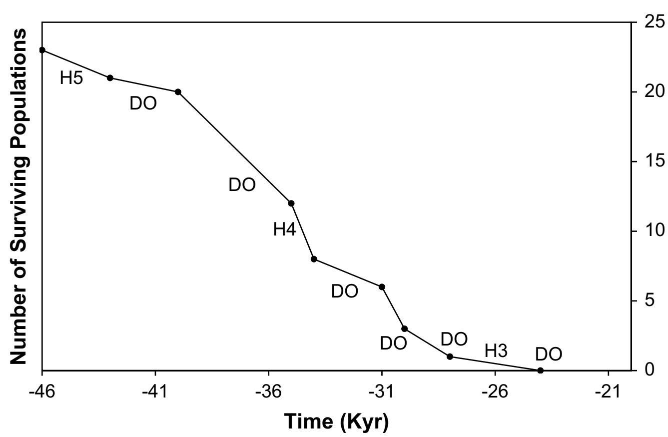

Fig. 5. Decline of the Neanderthal population (from Fig. 4), with HE and DO stadials indicated. Climate markers follow D'Errico and Sánchez-Goñi (2003).

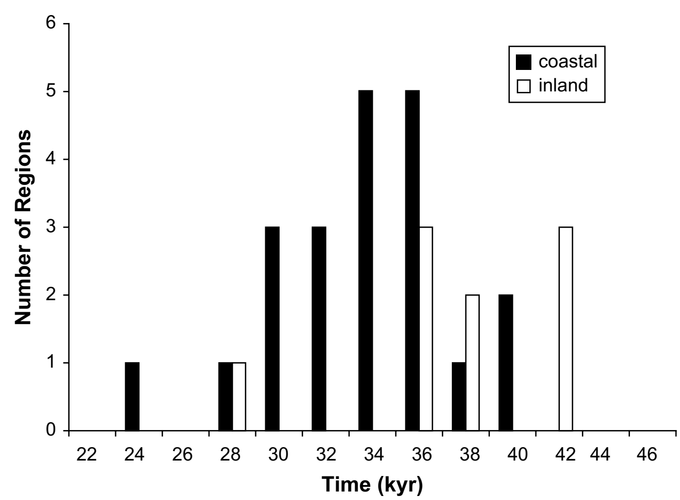

Fig. 6. Distribution of Neanderthal areas by last date, separated into coastal and inland areas.

6. Conclusion

It would seem from the results presented in this paper that this combination of ecological richness and connectivity permitted the survival of Neanderthal populations long after they had disappeared from many continental areas. In addition the oceanic, climate-tempering, influence of Atlantic sites meant that it was here that the last populations survived (Finlayson et al., 2006).

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Appendix 1. Supplementary information

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quascirev.2008.08.033.

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