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A terrestrial record of climate variation during MIS 11 through multi-proxy palaeotemperature reconstructions from Hoxne, UK

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Abstract

A terrestrial (lacustrine and fluvial) palaeoclimate record from Hoxne (Suffolk, UK) shows two temperate phases separated by a cold episode, correlated with MIS 11 subdivisions corresponding to isotopic events 11.3 (Hoxnian interglacial period), 11.24 (Stratum C cold interval) and 11.23 (warm interval with evidence of human presence). A robust, reproducible multi-proxy consensus approach validates and combines quantitative palaeotemperature reconstructions from three invertebrate groups (beetles, chironomids and ostracods) and plant indicator taxa with qualitative implications of molluscs and small vertebrates. Compared to the present, interglacial mean monthly air temperatures were similar or up to 4.0 °C higher in summer, but similar or as much as 3.0 °C lower in winter); the Stratum C cold interval, following prolonged non-deposition or erosion of the lake bed, experienced summers 2.5 °C cooler and winters between 5 and 10 °C cooler than at present. Possible reworking of fossils into Stratum C from underlying interglacial assemblages is taken into account. Oxygen and carbon isotopes from ostracod shells indicate evaporatively enriched lake water during Stratum C deposition. Comparative evaluation shows that proxy-based palaeoclimate reconstruction methods are best tested against each other and, if validated, can be used to generate more refined and robust results through multi-proxy consensus.

Keywords: Hoxnian interglacial period; Middle Pleistocene; Britain; Palaeoclimatology; Palaeotemperature reconstruction; Multi-Proxy Consensus; Micropalaeontology; Palaeontology; MIS11

INTRODUCTION

The Hoxnian interglacial period is of particular interest for its archaeological evidence of human occupation in Britain and its correlation with Marine Isotope Stage (MIS) 11c, 426.6 to 395.9 ka (Ashton et al., 2008; Rodrigues et al., 2011; Candy et al., 2021), a good past analogue for the present warm period (Loutre and Berger, 2003; Candy et al., 2014). Long, continuous, deep marine sequences offer complete records of MIS 11 (duration c. 420 to 360 ka BP; Loutre and Berger, 2003) that include not only the interglacial (MIS 11c) but also post-interglacial intervals (MIS 11b, MIS 11a). In Britain, the Hoxnian interglacial period is well recorded, sometimes together with other MIS 11 intervals, in sequences that are predominantly lacustrine at Hoxne (stratotype), Marks Tey (parastratotype) (West, 1956; Turner, 1970; Thomas, 2001), Barnham (Ashton et al., 1998; 2016) and Elveden (Ashton et al., 2005), terrestrial at West Stow (Preece et al., 2007), and fluvial at Southfleet Road, Ebbsfleet (Wenban-Smith, 2013), Swanscombe (White et al., 2013), Quinton (Coope and Kenward, 2007) and Woodston (Horton et al., 1992) (Fig. 1). At Hoxne (Fig. 1) the Anglian late-glacial is represented by Stratum F and the Hoxnian interglacial (pollen zones Hol to HolIIa) by strata E and D. The lacustrine sediments of strata F (clay with chalk pebbles) and E (unstratified clay) are capped by peat (Stratum D) representing the encroachment of terrestrial vegetation. The absence of pollen zones HolIIb and HolIV and the occurrence of reworked plant material in Stratum C indicate a substantial hiatus between Stratum D and a return to lacustrine deposition (laminated sands, silts and clays) under cold climatic (stadial) conditions in Stratum C (the “Arctic Bed”) (Reid, in Evans et al., 1896; West, 1956; Ashton et al., 2008). Archaeological evidence of human occupation is confined to the succeeding interstadial deposits: fluvial sediments (chalky gravels, sands, silts and clays) of Stratum B and overlying alluvial deposits (gravels, sands and sandy clays) and solifluction gravels of Stratum A (West, 1956; Ashton et al., 2008). Stratum B has yielded a temperate-climate vertebrate assemblage of mammals, birds, amphibians and fish (the last including rudd, *Scardinius erythrophthalmus*, indicative of warm summer water temperatures); the lower part of Stratum A contains a similarly temperate assemblage which may, however, be reworked from Stratum B, and the upper part of Stratum A shows evidence of cold (periglacial) conditions. Ashton et al. (2008) compared the Hoxne sequence with palynological records from key European sites and a marine core off the northwest coast of the Iberian Peninsula, as well as other proxy records from Lake Baikal sediments and an Antarctic ice core, and tentatively suggested that strata C–A at Hoxne might be correlated with one of the cold/warm cycles in the later part of MIS 11 (implying that the hiatus between strata D and C lasted c. 20,000 years). They argued that since the archaeology at Hoxne is associated with the later interstade, rather than the earlier interglacial period, humans were living in a boreal forest environment, with winters significantly colder than during the fully temperate interglacial. This leads to questions about the possible technologies (clothing, shelters, fire) or physiological adaptations that enabled them to survive harsher winters (Ashton et al., 2008; Ashton and Lewis, 2012; Hosfield, 2016).

Quantitative palaeoclimate reconstructions are of key importance in informing such discussion, but so far the available palaeotemperature reconstructions for Hoxne have been limited to those based on beetles for strata F, D and C (Coope, 1993; Ashton et al., 2008), with the addition of an ostracod-based reconstruction of Stratum C palaeotemperatures by Benardout (2015) that disagrees with the beetle-

based reconstruction. Quantitative palaeotemperature reconstructions for the Hoxnian interglacial and post-interglacial intervals of MIS 11 have been published for five other British sites, each based on the application of a single proxy method (Table 1).

In studies of British Pleistocene sites single-proxy quantitative reconstructions have often been accepted uncritically; however, any single proxy method on its own is likely to produce a plausible (though not necessarily accurate) result and there is a pressing need to test, validate and refine reconstructions by means of multi-proxy applications. If the results of two or more proxy methods are correct, then they should have overlapping ranges; in such a case the mutual overlap of the reconstructed palaeotemperatures can be used to identify a narrower range within which all the proxies could have co-existed. If the results from two or more proxies do not overlap, the results must be treated with caution (if not simply rejected) and the reasons for the discrepancy explored. Holmes et al. (2010) cross-checked and combined ostracod and herpetile palaeotemperature reconstructions to validate and refine mean July, January and annual air temperature ranges for MIS 13 at Boxgrove. At Whittlesey, combinations of beetle and ostracod mutual climatic range methods with vertebrate indicator taxa evidence have yielded robust palaeotemperature reconstructions for the MIS 7–6 transition (Langford et al., 2014a), MIS 7 (Langford et al., 2014b) and MIS 5e (Langford et al., 2017). Candy et al. (2014) compiled, compared and discussed published palaeotemperature evidence, based on single-proxy (beetle and ostracod) range reconstruction methods as well as vertebrate and plant indicator taxa, from five British terrestrial sites assigned to MIS 11, and similarly compared evidence from British MIS 11, 9, 7 and 5e interglacial sites, but did not attempt any systematic refinement of the reconstructions. Candy et al. (2016) used reconstructions obtained from beetle- and ostracod-based methods, together with threshold temperatures of vertebrate and plant macrofossils, to determine “most probable” winter and summer palaeotemperature ranges for British Ipswichian/Eemian interglacial period (MIS 5e) sites.

Here we present the first multi-proxy quantitative palaeotemperature range reconstructions for MIS 11 in Britain, using new results from Hoxne that combine beetle-, ostracod- and chironomid-based methods with threshold temperatures of plant indicator taxa and additional evidence from molluscs and small vertebrates. In addition, we present and interpret oxygen and carbon isotope analyses of ostracod shell carbonate from Hoxne Stratum C. We pay critical attention to the likelihood that some components of Stratum C assemblages are reworked from underlying interglacial deposits. We explore the challenges and potential of multi-proxy palaeotemperature reconstructions with the aim of establishing and demonstrating a robust, reproducible approach.

METHODS

A summary column with the main lithostratigraphical units sampled, together with a map showing the locations of sample areas and boreholes, are shown in Fig. 1; stratigraphical locations of samples are shown in Fig. 2.

Comparisons between different proxy methods facilitate the checking, validation and refinement of palaeotemperature reconstructions. We combined three proxy methods based on invertebrate fossils: the Chironomid Transfer Function (CTF) method (e.g., Brooks, 2006), the Mutual Ostracod Temperature Range (MOTR) method (Horne, 2007) and the Beetle Mutual Climatic Range (BMCR) method

(Atkinson et al., 1986). In addition, we took account of plant indicator taxa and considered the qualitative implications of molluscs and small vertebrates. Details of each method are given below; sample processing methods are described in Supplementary Data (SD), Section 1.

For the CTF method a weighted averaging-partial least squares (WA-PLS) 2-component, mean July air temperature inference model (Birks, 1995), was used to reconstruct the mean July air temperature from the fossil chironomid assemblage. This model has a root mean squared error of prediction (RMSEP) of 1.01 °C and a coefficient of variation (r^2) of 0.91, and is based on a modern Norwegian calibration set of 154 lakes covering a mean July air temperature range of 3.5–16.0 °C (Brooks and Birks, 2000, 2001, 2004; Self et al., 2011). Following Larocque (2001), Heiri and Lotter (2001) and Quinlan and Smol (2001), only samples including more than 50 chironomid larval head capsules were used for palaeotemperature reconstruction. Results are presented to the nearest 0.1 °C.

The MOTR method was used to reconstruct mean January and July air temperatures, to the nearest 1.0 °C. Species calibrations are mainly from Horne *et al.* (2012a), based on the NODE (Non-marine Ostracod Distribution in Europe) database and additional records from OMEGA (Ostracod Metadatabase of Environmental and Geographical Attributes; Horne et al., 2012b).

For BMCR application we used previously published species lists: Coope (1993) gave detailed descriptions, interpretations and palaeotemperature reconstructions of beetle assemblages from Stratum F (Anglian late-glacial) and Stratum D (Hoxnian late-temperate), while Stratum C results were first published (partially) by Ashton et al. (2008) and are updated here with the addition of more detail. We provide revised palaeotemperatures for Stratum F and D based on the overall species lists, while Stratum C results are provided sample by sample. Reconstructions of mean January and July air temperatures, to the nearest 1.0 °C, were calculated with the Beetle Mutual Climatic Range (BMCR) method (Atkinson et al., 1987) using the BugsMCR function of the BugsCEP database (Buckland and Buckland, 2012), to calculate the range of T_{max} (July temperature) and T_{min} (January temperature) for each sample/site investigated; T_{range} determines the level of continentality. The technique has undergone several revisions in recent years (Buckland, 2007), providing updated results, while the sample-by-sample analysis for Stratum C provides significant new palaeoclimatic insights.

Pollen and plant macrofossil records of species indicative of threshold temperatures were obtained from West (1956), and are given to the nearest 0.5 °C.

The taphonomic implications and palaeoclimatic significance of non-marine mollusc and small vertebrate fossils are considered qualitatively.

We applied a Multi-Proxy Consensus (MPC) approach using overlapping ranges produced by different proxy methods to determine the narrowest range that agrees with all of the proxy results for that stratum, thus arriving at a “mutual mutual” temperature range (Langford et al., 2014a, 2014b) here termed the Mutual Overlap Range (MOR). Unlike the BMCR and MOTR methods which reconstruct ranges (the actual temperature is considered to have been “somewhere within” that range), the CTF method produces a single “most probable” value with \pm error bars (representing one standard deviation each way), which for multi-proxy comparisons are considered to represent a range. Results of the MPC are presented to the nearest 1.0 °C.

In some cases where, initially, not all proxy results overlapped, improvements were achieved by reconsideration of the assumptions and data on which the reconstructions are based. For example, revision of BMCR results using new

calibrations has removed or reduced gaps that were apparent in our first attempts at multi-proxy reconstruction. Where a gap remains, a “best fit” is obtained by establishing the narrowest temperature range that is in contact with all the proxy results for that stratum, even if this leaves gaps that are not covered by reconstructed values; this is termed a Minimum Gap Range (MGR). Clearly MGRs are much less certain than MORs, since the former, lacking complete sets of mutual overlaps, suggest errors or uncertainties in the method or the data. Such discrepancies highlight limitations of the multiproxy approach but at the same time provide valuable opportunities to reconsider some of the assumptions that underpin the methods. Indeed, we regard the recognition of such limitations as a strength rather than a weakness of the MPC approach because it provides a measure of the reliability of the results.

Stable isotope analyses were carried out on specimens of *Ilyocypris* (“bradyi” - type) and *Cytherissa lacustris* from Stratum C; further details are given in SD, Section 1. The results are expressed in standard δ units on the VPDB scale with a mean standard deviation of measurements of 0.05 ‰ and 0.03 ‰ for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, respectively.

A list of full taxonomic names (genus, species, author, date) is provided in Supplementary Data (SD), Section 7.

RESULTS

Chironomid assemblages

Productive chironomid samples were obtained from strata C and E (Figs 1 and 2); results from those sufficiently abundant to justify further analysis are shown in Fig. 3. Stratum E chironomid assemblages are relatively species-poor, comprising taxa typical of warm, eutrophic waters with submerged aquatic vegetation; low oxygen conditions existed, either in a deep, thermally stratified lake or in a shallow lake containing large amounts of decaying vegetation. Stratum C chironomid assemblages are relatively species-rich, indicative of relatively shallow, well-oxygenated waters with submerged aquatic vegetation, possibly influenced by stream inflow, and dominated by widespread, eurytopic taxa that can occur in both warm and temperate waters; they include cold stenothermic taxa but the overall indications are of cool-temperate rather than cool climate. Further details are given in SD, Section 2.

It is possible that thermophilic taxa present in Stratum C (‘Arctic Bed’) were reworked from earlier sediments deposited during a warmer period (e.g., Stratum E). Indeed West (1956: 313) suggested this possibility when considering the vegetation record at Hoxne, identifying the pollen spectrum of a clay mud pebble from Stratum C as being from Holld (uppermost Early Temperate, within Stratum E; redesignated Hollc by Turner and West, 1968). However, the Stratum E chironomid assemblages, which represent a warm climate, are dominated by *Chironomus plumosus*-type and yet this taxon is hardly present in any of the Stratum C samples, which would be expected if there had been reworking of sediments. Equally, the temperate taxa that are well-represented in the Stratum C sediments, especially *Paratanytarsus penicillatus*-type and *Microtendipes pedellus*-type, are absent from the samples analysed from Stratum E, suggesting these taxa have not been reworked.

CTF method palaeotemperature reconstructions

All reconstructed ranges are mean monthly air palaeotemperatures; the CTF method was used to reconstruct only July temperatures. Results are detailed in Table 2 and illustrated in Figs 3 and 4. Stratum E results are $+19.1\text{ }^{\circ}\text{C} \pm 1.4$ and $+19.3\text{ }^{\circ}\text{C} \pm 1.8$; equivalent to combined range (MOR) of $+17.8$ to $+20.5\text{ }^{\circ}\text{C}$. Stratum C results range from $+13.4\text{ }^{\circ}\text{C} \pm 1.1$ to $+15.0\text{ }^{\circ}\text{C} \pm 1.1$; equivalent to a combined MOR of $+13.9$ to $+14.5\text{ }^{\circ}\text{C}$.

Ostracod assemblages

Ostracod assemblages were recovered from strata F, E, C and B (Figs 1 and 2); details are given in SD, Section 3. The assemblages are composed entirely of typically freshwater taxa (Table 3), although many of those can tolerate slightly brackish waters, and are consistent with lacustrine and (in the case of Stratum B) fluvial depositional environments (SD, Section 3).

MOTR method palaeotemperature reconstructions

All reconstructed ranges are mean monthly air palaeotemperatures. The calibrations used (Table 3) are from Horne *et al.* (2012a), with two exceptions. In the case of *Cytherissa lacustris* an adjustment was made to take account of living records in Lake Biwa, Japan (Smith and Janz, 2009), raising the maxima of its mean January and July ranges by $1\text{ }^{\circ}\text{C}$ and $3\text{ }^{\circ}\text{C}$ respectively. In the case of *Limnocythere suessenbornensis*, found in Stratum F and considered to be extinct in Europe, an unpublished calibration of the living North American species *Limnocythere friabilis* was applied, based on recent work by DJH with Alison Smith (Kent State University, Ohio, USA) that suggests that the two species are synonymous. Extinct species (*Cyclocypris obunca*, *Ilyocypris quinculminata*, *Limnocythere batesi*, *L. falcata*, *Scottia browniana*) are not included in the analyses because they cannot be calibrated. Two living species are not used due to taxonomic uncertainties; attempted calibrations of *Ilyocypris gibba* are considered unreliable because it has frequently been confused with other congeneric species, and there are insufficient living records (only two) of *Paralimnocythere compressa* in NODE and OMEGA to permit its calibration. At least three other species are present in our Hoxne assemblages, lumped together as *Ilyocypris* spp. in Table 3; one of these may be *I. bradyi* Sars, 1890, another *I. decipiens* Masi, 1905, while the third may be a new species, and further study will be necessary before their taxonomy and occurrences are well enough understood to include them in our analyses. All the reconstructions produced 100% overlap of calibrated ranges (i.e., no outliers with non-mutual ranges). Results are illustrated in Figs 4 and 5 and detailed in Table 4.

Stratum F results for each of three samples are provided in Table 4; the MOTR ranges for the combined assemblage being January -8 to $-3\text{ }^{\circ}\text{C}$, July $+16$ to $+23\text{ }^{\circ}\text{C}$. Stratum E results from three separate sample assemblages are likewise given in Table 4, the combined MOTR reconstruction being January -8 to $+3\text{ }^{\circ}\text{C}$, July $+12$ to $+21\text{ }^{\circ}\text{C}$.

High resolution sampling of Stratum C yielded ostracod assemblages from 36 consecutive samples, comprising a mixture of taxa commonly regarded as cold climate indicators (e.g., *L. falcata*, *L. sanctipatricii*, *C. lacustris*) and warm/temperate indicators (e.g., *Metacypris cordata*, *Darwinula stevensoni*). It cannot be ruled out

that at least some of the warm-climate taxa were introduced into Stratum C by reworking from older (interglacial) lake sediments exposed around the margins during times of lowered lake level. However, since all the taxa included in the MOTR analysis do have overlapping, mutual ranges (i.e., they could have co-existed), and there are no reliable criteria (e.g., preservational differences) for distinguishing between *in situ* and reworked specimens, it had to be assumed that they are all *in situ* and thus valid for the MOTR reconstruction; potential problems of reworking are discussed further below. Accordingly, MOTR reconstructions for Stratum C, based on 10 calibrated taxa, are presented in Fig. 5 and Table 4. The sample-by-sample reconstructions appear to demonstrate considerable variation in climatic conditions through the sequence. Since the actual temperatures could be anywhere within the ranges reconstructed, it is possible that they could have stayed between narrower limits throughout the interval, with little or no variation, but comparison with the other proxy results suggests that this is unlikely, as will be discussed further in Section 9. The MOTR ranges for the combined Stratum C assemblage are January -7 to $+1$ °C, July $+14$ to $+19$ °C. The lower extreme of the July MOTR is one degree cooler than the lower extreme of Benardout's (2015) July result for Stratum C ($+15$ to $+19$ °C), a discrepancy that can be explained by our decision not to include *I. decipiens* in our analyses because of taxonomic uncertainties within the genus *Ilyocypris*. Also worthy of note are the occurrences of three extinct taxa with palaeoclimatic significance: *Leucocythere batesi*, *Limnocythere falcata* and *I. quinculminata*. The first two are considered to be cold-climate indicators by association with other taxa (Whittaker and Horne, 2009). *Ilyocypris quinculminata* was considered to be a warm indicator by association with other taxa (Whittaker and Horne, 2009), so its sporadic occurrence in Stratum C (and absence from the other strata) seemed anomalous. Since it is extinct, its temperature ranges cannot be calibrated, but two occurrences for which MOTR results have been published more recently offer an insight into its palaeotemperature tolerances. At Boxgrove (MIS 13) it was found in an assemblage that provided palaeotemperature reconstructions, based on a combination of MOTR and herpetile-MCR methods, of -4 to $+4$ °C (January) and $+15$ to $+20$ °C (July), which in comparison with modern temperatures for that vicinity are consistent with similar summers but suggest colder winters (by at least 2 °C) than today (Holmes *et al.*, 2010). In MIS 11 at Ebbsfleet (Southfleet Road) it occurred in association with extant ostracod taxa that together yielded MOTR values of -4 to -1 °C (January) and $+17$ to $+21$ °C (July) (Whittaker *et al.*, 2013), which for that region suggests warmer summers but colder winters (by at least 4 °C) than today (a more continental climate). We conclude, tentatively, that *I. quinculminata* may be regarded as an indicator of a temperate/cool continental climate similar to that of northern Germany and Poland today, with (in comparison with the maritime / oceanic climate of present-day England) warmer summers and colder winters.

Stratum B1 ostracods were sparse, yielding wide-ranging MOTR results from two samples (Table 4); the combined MOTR reconstructions are January -8 to $+13$ °C, July $+10$ to $+25$ °C.

Beetle assemblages

Productive beetle samples were obtained from strata C, D, E and F (Figs 1 and 2). The beetle assemblage of Stratum F was obtained and described by Coope (1993) from a single sample of laminated drift mud collected at the base of the sequence in

West's (1956) section 100 (Fig. 1). Stratum F yielded 82 taxa of which 69 could be named to species, the assemblage being dominated by cold-adapted species (e.g. *Pycnoglypta lurida*, *Holoboreaphilus nordenskiöldi*, *Tachinus caelatus*, *Simplocaria metallica*). There were also more temperate and less cold-adapted species present such as *Bembidion guttula* and *Colymbetes fuscus*, although the ranges of both of these extend north of the Arctic Circle in Fennoscandia at the present day.

Stratum E beetle samples from BH02/1 (Figs 1, 2) yielded only sparse assemblages, likely due to small sample size. The Stratum D beetle assemblage, originally published by Coope (1993), is from a single block of woody peat taken from Cutting XXIII of the 1971–1974 excavations (Wymer, 1993) (Fig. 1); it is very diverse and clearly associated with temperate conditions.

Stratum C beetle assemblages were obtained from Area VII samples (Figs 1, 2) and first published by Ashton et al. (2008). Table 5 shows critical species from Stratum C which have significance because none of them lives in Britain today. Two climatically significant species in this assemblage are not represented in the MCR database; *Hippodamia arctica* is a high boreal species living in Fennoscandia and northern Russia with an outpost in the Caucasus mountains (Brundin, 1934), where it is found on *Betula nana*-rich *Empetrum* heath, while *S. metallica* is a boreo-alpine species, ranging from Greenland and Fennoscandia and the high mountains of central Europe (Horion, 1953), that feeds exclusively on mosses.

It is interesting to note the presence in Stratum C of a few species that also occur in the underlying Stratum D, suggesting the possibility of reworking. It is noteworthy that the lowermost assemblages of Stratum C (374 and 373; Table 6) are cool temperate, indicating warmer summer conditions than the rest of the sequence, but still very cold winter conditions; there is a small assemblage of wood/tree-associated species (3.6% of the terrestrial fauna) as well as a number of dung beetles and species associated with open ground (4.5% of the terrestrial fauna). The abundance of individuals and diversity of taxa in these samples is more typical of cool temperate conditions, including a range of ground beetles, hydrophilid and staphylinid beetles, leaf beetles and weevils. A wide and diverse range of aquatic and semi-aquatic vegetation is indicated by the reed beetles, not seen again higher in the sequence. These include *Donacia dentata* which is found on *Sagittaria sagittifolia* and occasionally *Potamogeton* spp. (Hyman, 1992); it is not an alpine taxon and its distribution in Britain today is largely southern (Hyman, 1992; Koch, 1992); similarly, *Plateumaris affinis* is not an alpine species and along with *Donacia thalassina* is found on club rushes and sedges (*Carex* spp., *Scirpus* spp.) (Hyman, 1992; Koch, 1992). *Donacia semicuprea* is found on *Glyceria* spp. (Bullock, 1993). *Donacia aquatica* cocoons on *Ranunculus lingua*, *Sparganium simplex*, *Glyceria* spp., *Carex* spp. (Stainforth, 1944), similar habitat for *Donacia cinerea*. This rich waterside vegetation fauna is also found in Stratum D, although in a more abundant and diverse assemblage. There are also, however, several species that indicate very cold winter conditions, including *Boreaphilus henningianus* and *Holoboreaphilus nordenskiöldi*.

The other species common to strata C and D is the saproxylic *Stenoscelis submuricatus*, which appears in both lowermost samples from Stratum C. Today, it lives in the sapwood of *Populus* and *Salix*, but also on *Alnus*, *Fraxinus* and *Fagus* (Koch, 1992). It is clearly a temperate species that has been found in other Hoxnian sites (e.g., Nechells, Warwickshire) as well as MIS 7, 9 and 5e sites. It was very abundant at the top of Stratum D. Its presence in Stratum C may seem anomalous but is not necessarily inconsistent with the assemblage, since its ability to live on a

variety of tree hosts (including *Salix*, notwithstanding that *S. polaris* is a tundra shrub rather than a tree) may have allowed it to be more tolerant of cool conditions. The original view, based on research by Gaunt et al. (1972) and Hoffman (1954), was that this is a Mediterranean species, but more recent records show that it can also be found in western and eastern Europe across to Switzerland, Austria (Folwaczny, 1983), Hungary (Szenasi, 2014), montane regions of France and the Pyrenees (Hoffman, 1954), and northern coastal France (GBIF, 2018). A review by Whitehouse (2006) of many non-British Holocene fossil cossinine weevils, a group to which *Stenoscelis submuricatus* belongs (note that some authors prefer to assign the species to the genus *Rhyncolus*) suggests their modern distribution is more likely to be influenced by availability of quality habitat rather than temperature *per se*. Recent species distribution models of *Rhyncolus* and other saproxylic taxa (Whitehouse et al. unpublished data) suggest that many appear responsive to continental conditions and are especially adversely impacted by wetter conditions rather than cold or warm temperatures *per se* (see further discussion on *Rhyncolus*, below). They are, however, always associated with tree habitats. Several other species attest to the presence of trees, including *Agrilus* sp., whose larvae develop under the bark or wood of deciduous trees, whilst *Eledona agricola* lives on various fungi growing on deciduous trees, principally *Polyporus sulphureus* on species of *Salix*. There are, therefore, grounds for re-considering whether *Stenoscelis submuricatus* signifies warm conditions; its biology and ecology could be more in keeping with the rest of the faunal assemblage, indicative of cooler summer temperate conditions and cold winter conditions. There are three species typical of northern boreo-montane conditions, including *P. lurida*, *Helophorus obscurellus* and *S. metallica* (the first two not now living in the British Isles). *Simplocaria metallica* is found in montane and alpine areas of Central Europe (Koch, 1989), while *P. lurida* is found as far south as Denmark, Germany and Poland (Koch, 1989; Gusarov, 1995) and *H. obscurellus* is an Asiatic species, found as far West as the Kanin Peninsula, Russia (Coope, 1994). None is associated with high arctic conditions and all have been found associated with late glacial deposits during cooler interstadial periods; *P. lurida*, for instance, can be found in summer warmth up to +24.5 C ° and winter temperatures as mild as -0.4 C ° (Table 5). They are not inconsistent with cooler temperate conditions indicated by the rest of the assemblage, suggesting continental conditions of cold winters but moderately warmer summers during the early stages of Stratum C, compared with later samples of the stratum.

In summary, despite some ecological similarities between Stratum C samples 374–373 and Stratum D, on balance those from Stratum C appear to constitute a coherent *in situ* assemblage, rather than one contaminated with reworked material, indicating cold winter temperatures and cool summer temperatures of sufficient spring and summer warmth to allow some tree growth, perhaps in the form of *Salix* and other cool tolerant species (e.g., *Betula*) in the basal portions.

Additional notes on selected climatically significant species from strata F and C (none of which occurred in strata E or D) are given in SD, Section 4.

BMCR method palaeotemperature reconstructions

The BMCR results are illustrated in Figs 4 and 5 and summarised in Table 6.

Previously published BMCR results for Stratum F, based on 24 species, were January -26 to -9 °C, July +10 to +12 °C (Coope, 1993). To explain the mixture of taxa (warm and cold) from this interval Coope (1993) discussed the possibility that

some were reworked, but considered it likely that the mixture was due to fairly rapid climate change in the interval represented by Stratum F, with July temperatures initially about +10 °C but quickly rising to +15 °C. However, re-running Coope's (1993) list in BUGCEP (36 species, 89% overlap, which means 11% had outlier palaeotemperature ranges that were not mutual with the 89%) produced revised reconstructions suggesting substantially warmer climate (January -11 to -4 °C, July +15 to +16 °C). Failure to find 100% overlap likely supports the idea that this interval encompassed a period of rapid climate change, such that the sampled assemblage does not represent a single snapshot of stable climate.

Stratum E yielded only nine beetle species from four small samples of the lacustrine sediments and because so few predatory or scavenging species were found, no MCR reconstruction could be made. However, they include several species, not in the MCR database, which indicate that the temperatures at the time were at least as warm and possibly warmer than those of the present day and likely to be reasonably continental. Notable amongst these is the non-British *Rhyncolus elongatus*, a saproxylic species associated with decaying, rotting pine (Koch, 1992). Its distribution is today in central and eastern parts of northern and central Europe up to southern Fennoscandia (Whitehouse, 1997, 1999). Recent exploratory research on this species and other members of this genus by Whitehouse et al. (unpublished data), using the Maxent software maximum-entropy approach for modeling species niches and distributions, with 18 bioclimatic variables, supports the idea that its predicted climatic niche based on modern distributions is largely in eastern Europe and southern Sweden. Temperature seasonality appears to be the strongest driver of its predicted climatic niche, followed by mean diurnal range and minimum temperatures of the coldest month. This suggests that while seasonality is an important determinant of the distribution of *R. elongatus*, it is also sensitive to day-time temperature extremes and winter cold. Another species in the assemblage supports temperate conditions: the Deathwatch beetle *Xestobium rufovillosum* is not found in its natural environment represented by present climate in northern Britain (Alexander, 1994).

The originally published BMCR results for Stratum D (Coope, 1993; Ashton et al., 2008) were January -10 to +6 °C, July +15 to +19 °C. The revised results, based on 25 species, are January -10 to +1 °C, July +16 to +19 °C (96% overlap), showing a July lower limit that is 1 °C higher, and a January upper limit 5 °C lower than the original ones. The sub-optimum overlap is likely due to minor in-sequence climate change (although there is no obvious evidence for this in the species list) and/or that the full climate range of one or more species has not been fully captured (Milne, 2016).

Stratum C reconstructions using BUGSCEP are presented on a sample-by-sample basis (Fig.5; Table 6), as well as overall (Fig. 4) using the combined assemblages to represent Stratum C. Using 23 species of predatory or general scavenging beetles, combined BMCR results are January -16 to -2 °C, July +12 to +14 °C (82.6% overlap), indicative of somewhat warmer (though still markedly colder than present-day) summer conditions than quoted by Ashton et al. (2008) (July at or <10 °C) but consistent with their winter reconstruction (January about -15 °C). The fact that 100% overlap was not achieved suggests that climate variation occurred during the times represented by the relatively coarse sampling interval and this is borne out by the BMCR sample-by-sample reconstructions (Fig. 5) and supported by evidence from the high-resolution ostracod results described above.

The sample-by-sample reconstruction for Stratum C (Fig. 5; Table 6) demonstrates clear differences in climatic conditions through the sequence. Working up from the base of the sequence, where summer temperatures were only slightly cooler (+13 to +15 °C in sample 374) than today's, we see cooling to +9 to +11 °C (sample 369), a mean July temperature drop of at least 2 °C alongside a slight amelioration of winter temperatures through the same interval, with the upper limit of the January range rising from -13 °C (sample 374) to -9 °C (sample 369). Also noteworthy is the step between the reconstructions for samples 373 and 372, which show no overlap of their reconstructed temperature ranges, indicating a significant and relatively rapid change involving summer cooling and winter warming, and suggesting a transition from continental to oceanic climate. It must also be noted, however, that the size of the winter envelopes is large for these samples and extends to very low values. The coldest envelopes are particularly controlled by two species that can tolerate extremely cold winters, *Boreaphilus hennigianus* and *H. nordenskiöldi*, both of which are recorded as being associated with winter temperatures as low as -34 and -35 °C, respectively (Table 5). It is impossible to determine where exactly within an envelope the true temperature was situated, but it seems likely that, since these species also occur in adjacent assemblages that give slightly warmer reconstructed temperatures, conditions were never as cold as the lowest limits that the reconstructions might imply. The upper samples provide reconstructions that suggest climatic warming, with ranges of January -16 to 0 °C and July +10 to +14 °C indicated by the topmost assemblage (sample 328). Note that combining the sample-by-sample results to obtain overall representative ranges for Stratum C produces Minimum Gap Ranges (January -13 to -12 °C, July +11 to +13 °C) that differ from those obtained by applying the BMCR method to the combined assemblage from all of the Stratum C samples (January -16 to -2 °C, July +12 to +14 °C) which produced an overlap of only 82.6%; this demonstrates that low sampling resolution may have merged short-term climatic changes to which the beetle taxa responded, resulting in gaps between the calibrated ranges of some included taxa and thence a lower overlap percentage for the whole assemblage.

Importantly, this BMCR reconstruction does not use plant-associated species and is therefore independent of (as well as consistent with) the overall beetle assemblage qualitative evidence (section 5.1). The diversity of wood-loving taxa evident in Stratum D is absent from the rest of Stratum C and conditions are cooler than Stratum D, indeed becoming increasingly cooler over time (although *Stenoscelis submuricatus* re-appears again in the upper portions of the sequence); therefore, the Stratum C assemblages represent an increasingly cooling community that is largely distinct from the temperate community represented by Stratum D.

In summary, the sample-by-sample reconstruction suggests a previously unknown summer cooling event coincident with winter amelioration within Stratum C. However, its registration within winter temperatures is much less clear due to the much larger envelope sizes generated by the present BUGSCEP MCR package. New envelopes that have recently been developed and tested independently using modern modeling techniques (Milne, 2016) suggest that the current envelopes tend to over-estimate winter cold and summer warmth, when compared against 12 modern test sites and species lists. The new envelopes are not yet fully operational, so are not used here.

Finally, the types of species used for each sample BMCR suggest the reconstructions are robust. A common assumption of the BMCR methodology has been that increasing the number of taxa used in a reconstruction will give a more

precise (i.e., narrower) temperature range (T. Atkinson, pers. comm., 2013). Modern testing work has shown that there is no discernible relationship between number of taxa used in the BMCR reconstruction and the obtained BMCR temperature ranges for summer or winter (Milne, 2016), but that understanding species niche traits is crucial. As Russell Coope highlighted both vocally and in print ‘species should not be treated merely as ciphers in some purely mathematical model.’ (Coope, 2010: 1511); thus, simply including more beetles in a reconstruction will not necessarily produce a better result. What may be more pertinent is whether the species are eurytherms (climate generalists) or stenotherms (climate specialists): the type of species used in a reconstruction has huge importance for the output. It is thus vitally important that users of any reconstruction system understand the climatic and ecological conditions associated with the taxa used, in order to understand the robustness of a reconstruction. In this reconstruction, a high number of stenotherms have been used, increasing the confidence levels of the reconstruction.

Palaeoclimatic implications of flora

Several plant indicator taxa recorded at Hoxne (West, 1956) are indicative of threshold temperatures (Figs 4 and 5). Of the pollen taxa, *Hedera* (assumed to be *H. helix*; West, 1956) requires mean air temperatures of $-1.5\text{ }^{\circ}\text{C}$ or higher in January and $+13\text{ }^{\circ}\text{C}$ or higher in July (Iversen, 1944; West, 1956). *Ilex* (assumed to be *I. aquifolium*; West, 1956) requires mean January temperature of at least $-0.5\text{ }^{\circ}\text{C}$ or $0\text{ }^{\circ}\text{C}$ (the latter value is used herein) (Iversen, 1944; West, 1956; Walther et al., 2005). *Typha latifolia* needs mean July temperature of $+13\text{ }^{\circ}\text{C}$ or above (Isarin and Bohncke, 1999). All three taxa occur in strata C, D and E at Hoxne, with the last-mentioned being found additionally in Stratum F (West, 1956). Minimum mean July air temperature requirements of four plant macrofossil species were obtained from Isarin and Bohncke (1999): *Betula nana* ($+7\text{ }^{\circ}\text{C}$), *Ceratophyllum demersum* ($+13\text{ }^{\circ}\text{C}$), *Miriophyllum spicatum* ($+10\text{ }^{\circ}\text{C}$) and *Sanguisorba officinalis* ($+9\text{ }^{\circ}\text{C}$). All four occur in Stratum C and *C. demersum* occurs additionally in strata D, E and F (West, 1956).

Another potentially significant plant taxon, the water fern *Azolla filiculoides*, was commented on by West (1956) who found it commonly in Stratum C (but suggested that it may have been reworked from older strata), abundantly in Stratum D and occasionally in the middle and upper parts of Stratum E. He considered its palaeoclimatic value doubtful, as it is widely distributed in the Americas and has an “erratic” behaviour in western Europe, and he noted that it survives under ice but is killed by winter frosts. On the other hand Hall (Appendix A in Coxon, 1985) noted the occurrence of *Azolla* megaspores at nearby Athelington as being of particular interest as it is typical of Hoxnian zones II and III, and because he considered it indicative of somewhat higher summer temperatures than at the present day. Experimental evidence has shown that adult plants survive at $-2\text{ }^{\circ}\text{C}$ but were killed at $-4\text{ }^{\circ}\text{C}$ in the laboratory, but they can survive air temperatures (or being encased in ice) of $-5\text{ }^{\circ}\text{C}$ or even lower in the wild, given the right microclimatic conditions (Janes, 1998). It apparently grows best at $+15$ to $+20\text{ }^{\circ}\text{C}$ and high irradiance (Janes, 1998) although its optimum temperature for nitrogen fixation and oxygen evolution is $+25\text{ }^{\circ}\text{C}$ (Wong et al., 1987). Populations in Poland have been observed to survive frosts down to $-22\text{ }^{\circ}\text{C}$ (Szczęśniak et al., 2009). In the light of this evidence its status as a thermophile in the context of the British Quaternary is questionable, to say the least; consequently, we have not included it in our analyses.

Mollusc assemblages

Non-marine molluscs were obtained from the same samples processed for other proxies as part of the AHOB excavations (Ashton et al., 2008), from strata E, D, C and B2 (Figs 1 and 2); see SD, Section 1, for further details. The first analysis of non-marine molluscan remains spanning the complete Hoxne sequence was undertaken by White (2012) and relevant data are published here for the first time (Table 7). Stratum F data from the quantified faunal list of Sparks (1956) have been included to complete the Hoxne molluscan succession, but it should be noted that they came from a more marginal part of the lake than the other material.

The Stratum F freshwater assemblage is dominated by gastropods, namely *Gyraulus laevis* (35.8%) and *G. crista* (34.4%) with subordinate numbers of *Valvata piscinalis* (8.0%) and *Radix balthica* (7.8%). *Hippeutis complanatus* is also well represented (3.9%). Several other gastropod taxa were recorded at low frequencies. Bivalves, predominantly *Pisidium nitidum*, account for only 9.8% of the overall assemblage. The molluscan evidence from Stratum F is indicative of a relatively shallow lacustrine environment, rich in aquatic vegetation and inhabited by species tolerant of colder conditions (White, 2012).

Assemblages from the overlying sediments of Stratum E are dominated by the freshwater gastropod *Valvata piscinalis*, which constitutes over 90% of most samples and is indicative of a relatively deep-water habitat. Also present at low frequencies throughout Stratum E is the extinct bivalve *Pisidium clessini*, which occurs in several Middle Pleistocene interglacial periods and is a member of the 'Rhenish suite' of aquatic molluscs characteristic of Hoxnian pollen substage Hollb (White et al., 2013). None of the molluscan taxa present within Stratum E are obligate thermophiles, but all are compatible with the temperate climate indicated by the Hoxne pollen record (West, 1956; Turner, 1970).

The molluscan assemblage of Stratum D includes *Valvata piscinalis*, *Bithynia tentaculata*, *Anisus leucostoma* and indeterminate species of *Pisidium* (Fig. 6). The shells from this part of the sequence were in relatively poor condition, with a distinctive dark stain indicative of the peaty sediments from which they were recovered. It is not clear whether this assemblage represents an *in situ* fauna or material derived from the underlying lacustrine deposits. Only the early part of the period represented by Stratum D, during which lake water levels were still reasonably high (cf. Coope, 1993), would have provided a suitable habitat for *V. piscinalis* and *B. tentaculata*.

Mollusc shells recovered from Stratum C in Area VII were relatively poorly preserved and a large proportion could not be identified to species level, leading to under-representation of species. The assemblages from Stratum C contain no obligate cold-adapted species but can be easily distinguished from the underlying temperate faunas from the earlier parts of the Hoxne sequence by the dominance of various species of *Pisidium* and the reduced abundance of *V. piscinalis* (Fig. 6). Similar bivalve-dominated faunas have been reported from other British cold-stage localities, such as Beetley (Preece, in West, 1991) and in modern situations such as Scandinavian lakes (Kuiper et al., 1989, Økland, 1990). Shells representing species common in the underlying sediments, such as *Valvata cristata* and *Bithynia tentaculata*, were probably reworked from older deposits, although alternative interpretations are possible (see below). However, several bivalve species present in Stratum C, notably *Pisidium amnicum* and *P. henslowanum*, can be regarded as part

of an *in situ* fauna because, with the exception of single specimens of the latter recorded in Stratum F and the basal sample of Stratum E, they are absent from the earlier part of the Hoxne sequence (Fig. 6).

In the fluvial deposits of Stratum B2 the molluscan assemblages include a more diverse gastropod fauna dominated by *V. piscinalis* and *B. tentaculata*, and are broadly similar to the temperate fauna encountered in Stratum E (Fig. 6).

Calculation of the ratio of *Bithynia* shells to opercula has proved to be a useful means of assessing the energy dynamics of depositional environments (e.g., potentially discriminating between lacustrine and fluvial conditions) and can contribute to assessment of reworking. At Hoxne, the ratio of *Bithynia* shells to opercula within strata F and E is balanced at close to 1:1 in most samples, indicative of minimal post-mortem sorting and suggestive of a low-energy depositional environment consistent with a lake. In contrast, ratios of 1:3 and 1:4 typify samples recovered from Stratum C and may be considered to support the idea that *Bithynia* is a reworked element in these assemblages. Stratum C Samples in which only opercula are represented might indicate some decalcification of the sediments. It is also possible, however, that the *Bithynia* in Stratum C are *in situ* but were subject to post-mortem sorting in the lake environment. Alexandrowicz (1999) described a process whereby shells of dead *Bithynia* float for a more prolonged period of time than the opercula, which detach more quickly and sink, while the shells are driven shorewards by wind and wave processes. In the fluvial Stratum B2 evidence for higher-energy conditions is provided by *Bithynia* shell:opercula ratios of 1:10 (White, 2012). The above interpretations should be treated cautiously as the numbers on which the shell:opercula ratios are based are generally very low (20 specimens or fewer) in samples from strata E, D and C, although many of the assemblages from Stratum B2 are big enough (>50) for the ratios to be considered more reliable.

Climatic significance of the molluscan assemblages

The molluscan record from Hoxne does not provide strong evidence for significant climatic variation due to the relatively broad tolerances of most of the taxa represented. Moreover, as noted above, several features of the record provide critical evidence relating to the potential for re-working and the taphonomic integrity of assemblages from Stratum C.

The most climatically significant taxon present in Stratum F is the gastropod *Gyraulus laevis*, which is characteristic of late-glacial or early post-glacial molluscan faunas. It is common in the 'Arctic Fresh-water Bed' at Ostend, Norfolk (Parfitt et al., 2010) and a fauna dominated by *G. laevis* was reported in association with an early post-glacial pollen profile at Tottenhill (Ventris, 1996). Similar freshwater assemblages dominated by *G. laevis* and *G. crista* have been documented from both late Anglian/early Hoxnian and late Devensian/early Holocene sequences (Kerney, 1977). Given that the molluscan evidence from Stratum F is derived from a single bulk sample, it is difficult to compare with the data provided by the beetle faunas from this part of the Hoxne sequence, but they are not incompatible.

In the overlying temperate lacustrine deposits of Stratum E there are no obligate cold- or warm-adapted species that would place significant constraints on palaeoclimatic reconstructions. One species that provides some evidence for prevailing temperatures is *Valvata cristata*, which is not known from any Pleistocene cold-stage deposits. However, it occurs only as a rare element of the molluscan

assemblages from Stratum E due to the deep-water environment represented by this unit, which is suboptimal for *V. cristata*. The limited molluscan fauna preserved in the Stratum D sediments provides little in the way of climatic information.

The molluscan assemblages from Stratum C contain no obligate cold-adapted species but can easily be distinguished from the preceding parts of the Hoxne sequence by the dominance of various species of the bivalve genus *Pisidium*. Similar faunas have been reported from other cold-stage localities such as Beetley (Preece, in West, 1991) and in modern habitats such as Scandinavian lakes (Kuiper et al., 1989; Økland, 1990). The presence of *V. cristata* in Stratum C at higher frequencies than the underlying Stratum E deposits has been attributed to re-working (cf. White, 2012), although the rarity of this species in the upper part of the Stratum E deposits suggests that these shells might have been derived from sediments now missing from the sequence (i.e., the hiatus between Strata D and C). Alternatively, if they are genuinely part of the Stratum C fauna, their occurrence together with cold-tolerant taxa requires explanation. Another gastropod species known only from interglacial and interstadial sequences in Britain is *Bithynia tentaculata*; this taxon is primarily represented in Stratum C by opercula, suggestive of re-working although, as noted above, other explanations are possible.

The assemblages from Stratum B2 are very similar to those from Stratum E, indicating a return to temperate climatic conditions. The similarity of the assemblages in these units is somewhat surprising, given the marked sedimentological differences indicative of lacustrine (Stratum E) and fluvial environments (Stratum B2). The absence of *Pisidium henslowanum* from Stratum B is noteworthy, given that it is a common species within Stratum C and prefers moving water environments.

Small vertebrate assemblages from Stratum C

Small vertebrates were obtained from successive samples through Stratum C (Figs 1 and 2); additional specimens were extracted from larger subsamples collected for insect remains (see SD, Section 1, for further details). A summary of the small vertebrates and other fossils recovered from the sieved samples is given in Table 8 and in Fig. 7. Bone fragments are not distributed uniformly through the sequence, with concentrations of bones in some horizons separated by samples that are virtually devoid of vertebrate material. Fish remains are the most abundant component with identified specimens that include scales of *Perca fluviatilis* (perch), a tooth of *Esox lucius* (pike), pharyngeal teeth of cyprinids (carp family) and the distinctive spines of *Pungitius pungitius* (nine-spined stickleback). The bulk samples processed for insects yielded tiny pharyngeal bones of *Alburnus alburnus* (bleak) and *Phoxinus phoxinus* (minnow). Taken together, the general composition, low diversity of identified species and relatively small size of the fishes imply a small waterbody, such as a pool or backwater.

Only a few small mammal specimens were recovered from Stratum C. Among the more complete specimens, the presence of *Dicrostonyx* sp. (collared lemming) was determined from a molar fragment (sample 304) and a second upper molar (M²) fragment (sample 301). At least one other microtine rodent (vole) is represented by material too fragmentary to identify more precisely. For further details and discussion see SD, Section 5.

Taphonomy and environmental implications of the Stratum C vertebrates

Taking the assemblage as a whole, the vertebrate species recovered from Stratum C appear to be climatically coherent. The assemblage includes *Dicrostonyx*, a cold-indicating lemming of tundra and mammoth steppe (Guthrie, 1968), together with fish species (*Perca fluviatilis*, *Esox lucius*, *Pungitius pungitius*) that have geographical ranges that today extend above the Arctic Circle. The cyprinids could also belong to the same cold stage assemblage. Although many cyprinid species are restricted in their ability to colonise the far north due to insufficiently high summer water temperatures in order to spawn successfully (Wheeler, 1977), other cyprinids (including bleak, *Alburnus alburnus*, and minnow, *Phoxinus phoxinus*, both found in Stratum C) can survive for long periods in ice-covered water and are found in rivers and lakes in the tundra, some as far north as the Arctic Ocean. The closest region to Hoxne where the geographical ranges of these taxa overlap today is located at the southern limit of the tundra south of the Kanin Peninsula. At the present day, this area is characterized by extremely cold winters (mean air temperatures of the coldest month between -14 and -8 °C) and summers with temperatures of the warmest month between $+7$ and $+14$ °C. Whether these estimates can be applied to Stratum C, however, depends on two critical assumptions; first that the vertebrate assemblage represents animals that lived in the vicinity of the site during the period of accumulation of Stratum C, and second that conditions didn't change significantly during the deposition of this unit.

The first of these assumptions was investigated by examining the stratigraphical occurrence of different elements of the fossil assemblages recovered from the bulk samples (Fig. 7). Sedimentologically, Stratum C consists of silty muds interspersed with thin layers of organic detritus and, in its upper part, lenses of chalky gravel and sand. These coarser horizons represent episodic pulses of erosion and redeposition of older sediments exposed on the margins of the basin. These sediments contain a mix of fossil material, some of which (Mesozoic corals, ostracods and foraminifera, and Cenozoic marine molluscs) have undergone multiple cycles of transportation and redeposition, with initial erosion from the bedrock, transportation by glacial processes and winnowing prior to burial at the depositional site. Plio-Pleistocene 'crag' and glacial deposits (Lowestoft Till and 'Corton beds') at the edge of the Hoxne basin (Lord, 2012) provide a probable source for these reworked fossils. The horizons in Stratum C containing reworked pre-Quaternary fossils also correspond to peaks in the abundance of Quaternary fish, small mammals and plant macrofossils, the latter including well-preserved seeds and wood fragments up to 5 cm in diameter. This mix of debris appears to have been transported by pulses of higher-energy currents that washed the detritus into the basin. Marginal exposures of the Hoxnian lake muds provide a possible source for the Quaternary plant macrofossils (Stratum D) and fish remains (Stratum E). However, there is no obvious difference in the state of preservation (colour differences, weathering, abrasion) of the vertebrate remains that identifies a reworked component in the Quaternary assemblage. With respect to taphonomy, while a few fish specimens in the Stratum C assemblage may be reworked from the interglacial deposits, the dominance of taxa (pike, perch, nine-spined stickleback) that are otherwise rare in the earlier lake muds suggests that the Stratum C accumulation reflects an essentially indigenous fauna. Similarly, the lemming teeth are unlikely to have been reworked from the interglacial sediments, and their

presence in Stratum C plausibly indicates severe climatic conditions, at least during the deposition of the upper part of that unit.

Stable isotopes

Details of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measurements of ostracod (*Ilyocypris* and *Cytherissa*) shells from Stratum C are shown in Fig. 5 and Table 9. The oxygen-isotope composition of lacustrine carbonate is controlled by the temperature and isotopic composition of lake water. The isotopic composition of lake water, in turn, is determined by the composition of rainwater and inputs from groundwater or surface runoff, catchment effects (*sensu* Gat and Lister 1995) and any evaporative enrichment. For ostracod shells, there is generally a positive offset from oxygen-isotope equilibrium that is taxon-specific (e.g., von Grafenstein et al., 1999; Decrouy, 2012). For *Cytherissa lacustris*, the offset is well characterised as $+1.2 \pm 0.23$ ‰ (von Grafenstein et al., 1999). For *Ilyocypris*, the other genus analysed here, there is no published offset. Moreover, we do not have sufficient numbers of paired analyses from Hoxne in order to be able to estimate the effect with confidence. However, values for paired analyses of *Candona neglecta*, which has a well-established vital offset, and *Ilyocypris bradyi* in Belis and Aritztegui (2004) have a mean difference of -1.78 ± 0.80 (n = 5), indicating that the vital offset for the latter is smaller than that for the former. We used a bootstrap technique (Efron and Tibsharini, 1993) to estimate the mean of the vital effect for *Ilyocypris* as $+0.41 \pm 0.31$ ‰. The fact that the $\delta^{18}\text{O}$ values for *Cytherissa lacustris* are more positive than those for *Ilyocypris* for the two levels at Hoxne for which we have values for both species is at least consistent with this result.

The carbon isotope composition of lacustrine carbonates is strongly controlled by the $\delta^{13}\text{C}$ of dissolved inorganic carbon (DIC): fractionation of carbonate isotopes between carbonate and DIC is minimally affected by temperature and, for ostracod shells, appears to be an equilibrium process (Keatings et al., 2001). The isotopic composition of DIC is, in turn, controlled by the $\delta^{13}\text{C}$ of groundwater inputs, exchange with atmospheric CO_2 and processes occurring in the lake, especially the preferential uptake of ^{12}C during aquatic photosynthesis and the return of ^{13}C -depleted organic matter from plants as a result of decay (Talbot, 1990).

The $\delta^{18}\text{O}$ values for *Ilyocypris* fall within a fairly narrow range of -2.47 to -1.08 ‰, which equates to -2.88 to -1.49 ‰ at oxygen-isotope equilibrium. Owing to taxonomic uncertainties and limited information on life cycles, it is difficult to be precise about the calcification season of the *Ilyocypris* specimens that were analysed. However, given that reconstructed temperatures were lower than present day during the deposition of Stratum C, especially during winter, it seems reasonable to assume that the ostracods were more likely to have reached adulthood during the warm season: this is supported for *Ilyocypris* sp. by limited evidence from Lake Geneva (Decrouy, 2009). If this is correct, the calculated $\delta^{18}\text{O}$ for Hoxne lake water during Stratum C times (based on reconstructed July temperature of 14 °C) would have been -2.3 ‰, substantially higher than precipitation. Present-day precipitation of Eastern England has a $\delta^{18}\text{O}$ value of around -7 ‰ (Darling et al., 2003) and values during the colder climate of Stratum C times may have been even lower. Higher reconstructed $\delta^{18}\text{O}$ values for the Hoxne Lake are best explained by evaporative enrichment. The limited number of $\delta^{18}\text{O}$ values for *C. lacustris* provide partial support for these conclusions (Fig. 5; Table 9). For two of the levels, they yield similar results to those derived from analyses of *Ilyocypris* assuming warm-season calcification, whereas for the remaining two, values are much more negative. However, even for

the most negative values, reconstructed $\delta^{18}\text{O}$ values for lake water (around -5.5‰) are higher than those for precipitation. Whether these values reflect variations in the lake environment during the formation of Stratum C remains unclear. Our assumption that temperatures remained constant during this interval is also questionable in view of the MOTR evidence for variation. However, substantially lower temperatures would be required for the ostracods to have calcified in water with a $\delta^{18}\text{O}$ value close to the likely values of contemporary rainfall. We therefore conclude that Hoxne lakewater was subject to evaporative enrichment throughout much or all of the time represented by Stratum C.

The carbon isotope values are more difficult to interpret, since they are controlled by a number of variables, as discussed above, and we have limited constraint on any one of these. Our conclusions must therefore remain speculative. Carbon supply to DIC in the Hoxne lake could have come from chalk, soil CO_2 (ultimately derived from catchment vegetation) and aquatic vegetation, and potentially modified by aquatic photosynthesis and equilibration with atmospheric CO_2 . Carbon in groundwater would have $\delta^{13}\text{C}$ value in the range -16 to -10.5‰ assuming a 50:50 mixture of carbon from chalky till ($\delta^{13}\text{C}$ for Upper Chalk = $+2$ to $+3\text{‰}$; Jarvis et al., 2006) and soil organic matter ($\delta^{13}\text{C} = -24$ to -24‰ in areas of C3 vegetation: Smith and Epstein, 1971; Deines, 1980). Ostracod shells that calcified in equilibrium with this DIC would have $\delta^{13}\text{C}$ values between -15 and -9.5‰ . However, ostracods from Hoxne Stratum C have $\delta^{13}\text{C}$ values between -3.1 and -5.7‰ , indicating that other sources of carbon and/or processes must have affected DIC composition. The addition of ^{13}C -depleted carbon to the DIC pool from respiration or decay of aquatic plants would decrease the $\delta^{13}\text{C}$ of DIC. However, the uptake of ^{12}C by aquatic plants for photosynthesis and equilibration with atmospheric CO_2 both have the potential to increase $\delta^{13}\text{C}$ values (e.g., Talbot, 1990). Without further evidence, it is difficult to be certain which was the dominant process, although partial equilibration with atmospheric CO_2 , which is a slow process, is consistent with a relatively long residence time for the lake, a condition that would favour evaporative enrichment of water isotopes, which is consistent with the oxygen-isotope values and some of the faunal assemblage data.

Multi-Proxy Consensus palaeotemperature reconstructions

The acronyms used in this section are explained in the Methods section, but for convenience a summary look-up table is here provided (Table 10). The MPC approach produced MORs for stratum C (July) and strata D, E and F (all January and July), while Stratum C (January) required acceptance of the only MGR result. Only a single proxy method (MOTR) was available for Stratum B, and no proxies useable for quantitative palaeotemperature reconstruction were available from strata A and G. These results are presented here in chronological order from bottom to top and illustrated in Fig. 4. For comparison, present-day mean monthly air temperature values for the vicinity of Hoxne are $+3.0\text{ °C}$ for January and $+16.5\text{ °C}$ for July.

Stratum F. Overlap of the January BMCR and MOTR ranges gives an MOR of -8 to -4 °C . The BMCR and MOTR ranges together produced a July MOR of $+16\text{ °C}$ (i.e., a single value rather than a range), consistent with plant threshold values. July mean air temperature was thus very close to that of today, but January was at least 7.0 °C colder, consistent with the suggestion (West, 1956; Ashton et al., 2008) that lake deposition began in the Anglian late glacial period.

Stratum E. No BMCR could be obtained from Stratum E but the CTF results for July fall within wider ranges indicated by the MOTR method, with an MOR of +18.0 to +20.5 °C (rounding up the upper and lower extremes to the nearest half degree). This is consistent with the evidence of three plant taxa that require a mean July temperature of +13.0 °C or higher, and of two beetle taxa (*Rhyncolus elongatus* and *Xestobium rufovillosum*) that indicate warmer than present-day climate, suggesting a full interglacial climate with summers between 1.5 and 4.0 °C warmer than today. Mean January air temperatures in Stratum E were similar to those of today or up to 3 °C colder, as indicated by the 0 to +3.0 °C MOR of the MOTR results combined with two plant indicators.

Stratum D. The January MOR of the BMCR and plant thresholds is 0 to +1 °C, indicating winters that were 2 to 3 °C colder than those of today. The MOR result for July (+16.0 to +19.0 °C) is based on the BMCR method and plant indicator taxa, consistent with an interglacial climate with summer temperatures not dissimilar to those of today, but possibly up to 2.5 °C warmer.

Hiatus. A missing interval of unknown (but substantial) duration is represented by the erosion surface at the base of Stratum C, to the extent that pollen zones HolIb and HolV are absent (Turner, 1970; Ashton et al., 2008).

Stratum C. The January reconstruction uses a combined BMCR overlapping the MOTR to produce an MOR of -7 to -2 °C, indicating winters between 5 and 10 °C colder than today's. However, accommodating the two floral indicator taxa, which have minimum thresholds higher than the upper limit of the MOR by 0.5 °C (*Hedera helix*) and 2.0 °C (*Ilex aquifolium*), results in an MGR of -2 to 0 °C, indicating winters between 3 and 5 °C colder than today's. This gap is accommodated within the variability apparent in the high-resolution record from Stratum C (discussed below). Whether the MOR or the MGR is accepted, the indications are clear that Stratum C summers and winters were definitely colder than during the interglacial period. The upper limit of the combined BMCR for July coincides with the lower limit of the MOTR, producing an MOR of precisely +14 °C indicating summers 2.5 °C cooler than today's. All three CTF ranges and the floral indicator taxa for Stratum C are consistent with this result.

In the other sedimentary units it has necessarily been assumed that the sampled interval is representative of the unit as a whole, but in the case of Stratum C, high-resolution sampling has produced a detailed ostracod record that reveals variability within the unit. Reconstructed July palaeotemperature ranges from beetles and chironomids (neither of which were sampled at the same high resolution as the ostracods) show some overlap and some gaps when mapped onto the detailed MOTR results (Fig. 5; Table 11). The gaps may be the result of a lack of exact equivalence (both geographic within the Hoxne site and stratigraphic within Stratum C) in sampling for the different proxies, in view of the possibility of climate variation within this interval as shown by the high-resolution MOTR results. We cannot rule out the possibility that at least some of the variation in the MOTR results may be due to "noise" attributable to low numbers of taxa recovered from some samples (the maximum number of species used for the MOTR analysis in a single sample was nine, but in a few cases only one or two could be used and inevitably produced very wide ranges), nor can we completely rule out contamination of the assemblages with reworked specimens. The BMCR results, although based on samples mostly of coarser stratigraphical resolution than the MOTR data and covering only parts of the succession, similarly show variation within Stratum C. However, the July results from the BMCR and CTF methods show a general correspondence with the minimum

curve of the July MOTR results; similarly the January BMCR results mostly fall around the minima of the January MOTR results although in the lowest samples there are gaps, the BMCR method indicating colder temperatures than the MOTR method. This suggests that the January and July MOTR minima may offer the best representation of the actual palaeotemperatures. The occurrences of the extinct ostracod *I. quinculminata*, which we consider to be possibly indicative of continental climate with warmer summers and colder winters than today, correspond to some extent with some of the warmer July intervals with cooler January temperatures.

The maxima of the January BMCR results generally fall substantially below the threshold temperature indicated by pollen taxa *H. helix* and *I. aquifolium*, but in one case (a beetle sample equivalent to ostracod samples 343–345) the BMCR maximum matches the pollen taxa thresholds. Unfortunately, we have no way of determining precisely from West's (1956) pollen data the equivalence of his Stratum C samples with ours; his pollen diagrams for Stratum C (op. cit., figs 22–24) show sporadic rather than continuous occurrences of the two pollen taxa. Molluscs and vertebrates recovered from Stratum C are generally consistent with the quantitative reconstructions; *Dicrostonyx* is indicative of tundra and mammoth steppe, while the temperature ranges of the suggested modern analogue region for the fish assemblage has a July maximum that matches our July MOR and although its January maximum is 6 °C colder than the low end of our January MGR, this is easily accommodated within the variability shown by the high-resolution MOTR and BMCR results.

Stratum B. Only wide-ranging MOTR results are available for Stratum B (January –8 to +13 °C, July +10 to +25 °C), not inconsistent with the climatic amelioration suggested by mammalian and fish fauna (Ashton et al., 2008), but also not ruling out the possibility of a significantly warmer or colder climate.

Stratum A. No palaeotemperature reconstructions are available for Stratum A, but its vertebrate assemblage suggests a transition from warm to cold climate (Ashton et al., 2008).

DISCUSSION

Reworking in Stratum C assemblages

Discrepancies between proxy-based palaeotemperature reconstructions at some levels could be explicable by reworking of certain “warm” taxa from exposed marginal deposits of the larger interglacial lake into the smaller Stratum C lake, an issue already discussed in the individual proxy results sections above. It is possible that some Stratum C thermophilic chironomids were reworked from earlier warm period sediments; we consider this unlikely for well-represented temperate taxa that were not also found in Stratum E assemblages, but we cannot rule the possibility that they were derived from material subsequently eroded and represented by the hiatus. The Stratum C beetle and pollen assemblages contain both warm and cold elements, suggestive of an admixture of material eroded from older interglacial deposits, but the beetle assemblages can be interpreted as *in situ* rather than contaminated with reworked material. Some degree of reworking of ostracods cannot be ruled out but is not required to explain the results, due to the 100% overlap of taxa used in the MOTR reconstructions. The vertebrate assemblage is consistent with a cold climate. While reworking of some vertebrate fossils from older deposits cannot be ruled out,

taphonomic considerations suggest that dominant fish taxa represent an indigenous fauna, as does the presence of lemming which may be regarded as indicating severe climatic conditions, at least during the deposition of the upper part of Stratum C. There are no obligate cold-climate mollusc taxa but no component of the mollusc assemblage is incompatible with cold climate; the absence of some species in the underlying lacustrine part of the sequence identifies them as *in situ* elements of the Stratum C fauna. The gastropod *Bithynia tentaculata*, usually found only in interglacial and interstadial deposits in Britain, has usually been considered a probable reworked element of Stratum C assemblages. However, its *in-situ* presence is not necessarily ruled out by its modern distribution, since it has been recorded in Scandinavia at least as far north as the Gulf of Bothnia and Finland as well as northwestern Russia in Karelia and the area between St Petersburg and Archangelsk (Alexandrowicz, 1999). Present-day mean January and July air temperatures in this region are between -13 to -4 and +14 to +17 °C respectively, ranges that are not inconsistent with our MPC results for Stratum C.

Combined ostracod palaeoecology and oxygen stable-isotope analyses confirm the Stratum C early cold phase and allow the tentative suggestion that warmer and/or more evaporatively enriched conditions prevailed at the beginning and end of the interval represented by these sediments; this is consistent with the evidence of the sample-by-sample BMCR results. Taking account of sedimentological and stratigraphical evidence for reworking of older lake strata into Stratum C, West (1956: 334) considered that the pollen in Stratum C is “to a large extent derived from the older deposits, as must be many of the macrofossils”. If this is the case, we might be justified in ignoring our MGR for Stratum C January, which is necessitated by two pollen taxa (with assumed species-level identifications) and accepting the MOR result that shows winters 5 to 10 °C colder than those of today. However, as already discussed above for various proxies, invoking reworking is more a matter of interpretation than of hard evidence. West argued that the contemporary flora of Stratum C characterised an arctic or sub-arctic climate, with *Salix herbacea*, *Salix myrsinites*, *Salix polaris* and *Betula nana* growing around the lake. *Betula nana* indicates mean July air temperature of +7 °C or higher. According to West’s view we should probably consider the persistent presence (but low abundance) of *Typha latifolia* in Stratum C to be the result of its reworking from older lake sediments exposed around the margins during an interval of lower lake level; certainly, it is relatively abundant in parts of Stratum D. However, if considered as an *in situ* component of the lake flora during Stratum C times, *T. latifolia* indicates mean July air temperatures of at least +13 °C, consistent with the July MOR of +14 °C and with the indications of the small vertebrates assemblage (warmest month between +7 and +14 °C).

Comparisons with other sites and records

Ashton et al. (2008) suggested that the Hoxne climate intervals could be correlated with those evident in the SPECMAP stack (e.g., Tzedakis et al., 2001): the Hoxnian interglacial with MIS 11c, the Arctic Bed / Stratum C stadial with MIS 11b and the Stratum B interstadial with MIS 11a. They noted, however, that other correlations might be possible, for example with isotopic events seen in more detailed deep ocean records. Multi-proxy evidence from deep Atlantic Ocean sediment cores has shown that the inception of the MIS 10 glacial period was complex, with a series of cold/warm climatic oscillations following the MIS 11

interglacial period (Desprat et al., 2005; Martrat et al., 2007; Voelker et al., 2010; Rodriguez et al., 2011; Candy et al., 2014). Off the Iberian Peninsula these are evident in (for example) terrestrial pollen record and pollen-derived air-temperature reconstructions (Desprat et al., 2005), in alkenone-derived sea surface temperatures (Rodriguez et al., 2011), and in planktonic foraminiferal $\delta^{18}\text{O}$ and lithic abundance interpreted primarily as ice rafted debris (Voelker et al., 2010). Similar climatic oscillations are evident in the Lake Baikal biogenic silica record (Prokopenko et al., 2010).

There is disagreement in the literature as to how the marine isotope substages and isotopic events should be correlated (Candy et al., 2014). Some authors, with reference to SPECMAP, have considered the possibility that the MIS 11b stadial and MIS 11a interstadial equate to events 11.22 and 11.1 respectively (e.g., Ashton et al., 2008) while others have matched MIS 11b with 11.24 and then place 11.23 – 11.1 in MIS 11a (e.g., Voelker et al., 2010). Desprat et al. (2005) identified four post-interglacial cold intervals within MIS 11: the first (oldest) they equated with isotopic event 11.24, the second forms a short cold episode within the 11.23 interstadial, while the third was assigned to 11.22. Subsequently Voelker et al. (2010; fig. 6) identified the same four cold intervals as stadials (numbered I – IV in decreasing order of age) separated by three interstadials; the first (oldest) stadial was placed in MIS 11b which they equated with isotopic event 11.24, separating the 11.23 interstadial from the MIS 11c interglacial period, while the remaining three stadials were assigned to MIS 11a. Thus, MIS 11b has been centred around 375 ka BP (e.g., SPECMAP stack: Imbrie et al., 1984) or around 390 ka BP (e.g., Voelker et al., 2010).

Figure 8 shows a possible correlation of our Hoxne palaeotemperature reconstructions with examples of the above-mentioned palaeoclimate records (locations shown in Fig. 9). We cannot tell how long an interval is represented by the hiatus between Stratum D and Stratum C at Hoxne. The erosion of strata deposited between the lowest (remaining) part of Stratum D and the beginning of Stratum C might have removed a record of climate oscillations that is now represented only by material that has been reworked, mixed and incorporated into Stratum C or removed entirely from the basin; this could have included not only the late part of the interglacial but also post-interglacial cold and/or warm intervals. Nevertheless, although the possibility of contamination of Stratum C assemblages with reworked material cannot be entirely ruled out, the simplest solution is to correlate Stratum C / Stratum B with the first post-interglacial cold/warm oscillation of Voelker et al. (2010), 11.24/11.23. Human occupation at Hoxne therefore likely occurred during the 11.23 interstadial, represented by Stratum B. It is unfortunate that our reconstructed palaeotemperature ranges for this interval are wide and inconclusive, allowing for both summers and winters to have been colder or warmer than those of the present day; perhaps the evidence of boreal forest suggests a greater likelihood that temperatures were nearer the cooler ends of the reconstructed ranges, although this may be difficult to reconcile with the mammal and fish evidence of climatic amelioration (Ashton et al., 2008). Another possibility is that Stratum B represents a warm 11.23 interval punctuated by a short cold interval, as is evident in the pollen record off the Iberian Peninsula (Desprat et al., 2005) and the Lake Baikal biogenic silica record (Prokopenko et al., 2010). The lesson of Stratum C, discussed above, may be pertinent: the integration of proxy evidence into a single virtual sample representative of the whole unit, blurring any record of such a short climate oscillation, could explain the wide MOTR results and other conflicting evidence. Similarly, the

lack of high-resolution continuous sampling through Stratum E at Hoxne precludes any attempt to recognise an abrupt cold-climate episode within MIS 11c, identified at Marks Tey in Essex and ODP 980 in the North Atlantic by Candy et al. (2021) who correlated the two occurrences by means of a single tephra layer. On the other hand, dynamic fluvial depositional environments are generally far less capable of preserving high-resolution archives of environmental change than are lacustrine depositional settings, so even high-resolution sampling of Stratum B might be unlikely to yield any record of such short-term changes.

Two other British terrestrial MIS 11 sites may record post-interglacial cold/warm oscillations that could be correlatives of the Stratum C / Stratum B interval at Hoxne. One is Quinton in the West Midlands where a cold interlude was recognised in BMCR results although the pollen record at the site shows no equivalent response (Coope and Kenward, 2007). The other is West Stow in Suffolk where the lower part of the sequence represents the early part of the interglacial period while the upper part (Bed 7), separated from the lower interval by a hiatus, contains cold-climate indicators (including ostracods, molluscs and mammals) as well as thermophilous mammals and fish (Preece et al., 2007), the mixture being suggestive of a similar situation to that discussed above for Stratum B at Hoxne. The MOTR results for Bed 7 at West Stow (January -7 to -1 °C, July $+15$ to $+21$ °C) suggest a more continental climate with winters at least 4 °C colder than today's and are quite similar to those for Stratum C at Hoxne (Benardout, 2015). It is possible that the cold intervals at the different sites each correlate with a different isotopic episode in the deep ocean record, but it is worth considering that, given their occurrence within a relatively small geographical area, it is not unreasonable to expect that all three experienced the same climatic variations capable of influencing their sedimentary and fossil records in similar ways. The similarities between these three British records thus hint at equivalence and a common cause reflecting a regional climatic oscillation worthy of further investigation at other British MIS11 sites, for example Marks Tey in Essex where there is a substantial lacustrine succession overlying the Hoxnian interglacial deposits (Horne et al., 2014; Tye et al., 2016).

CONCLUSIONS

The multi-proxy comparisons of BMCR, MOTR and CTF results, combined with threshold temperatures for indicator taxa, produce consistent and well-constrained palaeotemperature ranges with few disagreements.

The results confirm and constrain two post-Anglian temperate phases at Hoxne (the first, represented by strata F, E and D, being the Hoxnian interglacial period; the second represented by strata B and A) separated by a cold episode (Stratum C), tentatively correlated with MIS 11 substages. Multi-Proxy Consensus palaeotemperature reconstructions (°C), for January and July respectively, were as follows: Stratum F, -8 to -4 °C and $+16$ °C; Stratum E, 0 to $+3.0$ and $+18.0$ to $+20.5$; Stratum D, 0 to $+1$ and $+16.0$ to $+19.0$; Stratum C, -7 to -2 and $+14$. For Stratum B a single-proxy reconstruction of January -8 to $+13$ and July $+10$ to $+25$ was obtained; no reconstruction was possible for Stratum A.

Discrepancies between proxy methods may be explicable in terms of (1) local reworking of older (interglacial strata E/D) deposits into the younger (Stratum C) lake, (2) lack of precisely equivalent samples for different proxies and (3) differences in sampling resolution between the proxies.

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Author contributions

David J. Horne: coordination, editing, preparation of figures, MOTR reconstructions, pollen and plant macrofossil palaeoclimate indications.

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Ginny Benardout: ostracod analyses and interpretation, MOTR reconstructions.

Stephen J. Brooks: chironomid analyses and interpretation, CTF reconstructions.

G. Russell Coope: beetle analyses and interpretation, MCR reconstructions.

Jonathan A. Holmes: isotope analyses and interpretation.

Simon G. Lewis: site context and stratigraphy.

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Tom S. White: mollusc analyses and interpretation.

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All authors contributed to the Multi-Proxy Consensus reconstructions as well as discussion of reworking and comparisons with other sites and records.

Competing interests statement

We have no competing interests to declare.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at

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Table 1. Summary of published quantitative palaeotemperature reconstructions for British MIS 11 sites. MOTR = Mutual Ostracod Temperature Range; BMCR = Beetle Mutual Climatic Range.

Site	Interval	Proxy method	January	July	Reference
Ebbsfleet (Southfleet Road)	Early interglacial	MOTR	-4 to -1	+17 to +21	Whittaker et al., 2013
Hoxne	Stratum C (post-interglacial)	MOTR	-7 to +1	+15 to +19	Benardout, 2015
Hoxne	Stratum C (post-interglacial)	BMCR	about -15	≤ +10	Coope, 1993; Ashton et al., 2008
	Stratum D (mid-interglacial)	BMCR	-10 to +6	+15 to +19	
	Stratum F (early interglacial)	BMCR	-26 to -9	+10 to +12	
Quinton	post-interglacial	BMCR	-20 to -11	+9 to +11	Coope and Kenward, 2007
	late interglacial	BMCR	-12 to +4	+15 to +19	
	cold interlude	BMCR	-27 to -10	+9 to +11	
	mid- interglacial	BMCR	-10 to +8	+15 to +22	
Swanscombe	Lower Middle Gravel (mid-interglacial)	MOTR	-7 to +3	+15 to +21	White et al., 2013
	Lower Loam (early interglacial)	MOTR	-3 to +4	+15 to +19	
West Stow	Bed 7 (post-interglacial)	MOTR	-7 to -1	+15 to +21	Benardout, 2015
	Beds 3 & 4 (interglacial)	MOTR	-8 to +7	+12 to +23	
Woodston	interglacial	MOTR	-4 to +1	+16 to +19	Horne, 2007; Horne et al., 2012a

Table 2. Chironomid Transfer Function palaeotemperature reconstructions. See Figs 1 and 2 for locations and stratigraphical context of samples.

Stratum	Chironomid samples	Mean July air temperature (°C)	Mean July air temperature range (°C)
C	Core B, 5–10 cm	+13.6 ± 1.1	+12.5 to +14.7
C	Core G, 5–10 cm	+15.0 ± 1.1	+13.9 to +16.1
C	Area VII, sample 366	+13.4 ± 1.1	+12.3 to 14.5
C	Combined (MOR)		+14 to +15
E	Core S, 40–47 cm	+19.3 ± 1.8	+17.5 to +21.1
E	Core AA, 0–5 cm	+19.1 ± 1.4	+17.7 to +20.5
E	Combined (MOR)		+18 to +21

Table 3. Summary of ostracod occurrences recorded from MIS 11 strata at Hoxne, with calibrations used in the MOTR method where available; * denotes extinct species.

Species	Strata						Mean monthly air temperature range (°C)			
	A	B	C	D	E	F	January min.	January max.	July min.	July max.
<i>Candona</i> and/or <i>Fabaeformiscandona</i> spp juveniles			x				-	-	-	-
<i>Candona candida</i>			x				-40	+9	+6	+26
<i>Cyclocypris</i> sp.					x	x	-	-	-	-
* <i>Cyclocypris obunca</i>			x				-	-	-	-
<i>Cyclocypris ovum</i>			x				-32	+14	+7	+27
<i>Cypridopsis vidua</i>			x				-32	+17	+9	+34
<i>Cytherissa lacustris</i>			x			x	-34	+4	+4	+26
<i>Darwinula stevensoni</i>			x		x		-31	+14	+12	+30
<i>Fabaeformiscandona levanderi</i>			x				-40	+1	+11	+19
<i>Fabaeformiscandona protzi</i>			x		x	?	-40	+3	+11	+21
<i>Herpetocypris reptans</i>		x			x	x	-8	+15	+10	+25
<i>Ilyocypris gibba</i>		x	x			x	-	-	-	-
* <i>Ilyocypris quinculminata</i>			x				-	-	-	-
<i>Ilyocypris</i> spp..		x	x		x	x	-	-	-	-
* <i>Leucocythere batesi</i>			x				-	-	-	-
* <i>Limnocythere falcata</i>			x				-	-	-	-
<i>Limnocythere sanctipatricii</i>			x				-40	+7	+7	+24
<i>Limnocythere suessenbornensis</i> (syn. <i>L. friabilis</i>)						x	-15	-3	+16	+23
<i>Metacypris cordata</i>			x				-7	+7	+14	+24
<i>Neglecandona neglecta</i>		x	x		x	x	-10	+13	+7	+27
<i>Paralimnocythere compressa</i>			x				-	-	-	-
<i>Pseudocandona</i> sp.					x		-	-	-	-
<i>Pseudocandona</i> sp. juveniles			x				-	-	-	-
* <i>Scottia browniana</i>			x		x		-	-	-	-

Table 4. Mutual Ostracod Temperature Range results from Hoxne. See Figs 1 and 2 for locations and stratigraphical context of samples.

Stratum	Ostracod samples	Mean January air temperature range (°C)	Mean July air temperature range (°C)
B1	Column 1	-8 to +13	+10 to +25
B1	Column 2	-10 to +13	+7 to +27
B1	Combined assemblages	-8 to +13	+10 to +25
C	332	-10 to +3	+11 to +21
C	333	-10 to +7	+7 to +24
C	334	-40 to +7	+7 to +24
C	335	-40 to +3	+11 to +21
C	336	-31 to +7	+12 to +24
C	337	-32 to +14	+7 to +27
C	338	-32 to +14	+7 to +27
C	339	-32 to +7	+7 to +24
C	340	-31 to +9	+12 to +26
C	341	-30 to +6	+12 to +27
C	342	-10 to +13	+12 to +27
C	343	-32 to +1	+11 to +19
C	344	-32 to +14	+7 to +27
C	345	-10 to +13	+7 to +27
C	346	-10 to +1	+14 to +19
C	347	-31 to +1	+14 to +19
C	348	-10 to +4	+14 to +26
C	349	-7 to +4	+14 to +24
C	350	-10 to +13	+12 to +27
C	351	-10 to +4	+7 to +26
C	352	-31 to +4	+12 to +26
C	353	-7 to +1	+14 to +19
C	354	-10 to +13	+12 to +27
C	355	-10 to +4	+7 to +26
C	356	-10 to +4	+7 to +26
C	357	-10 to +1	+12 to +19
C	358	-10 to +4	+12 to +26
C	359	-10 to +1	+12 to +19
C	360	-7 to +1	+14 to +19
C	361	-10 to +1	+12 to +19
C	362	-10 to +1	+12 to +19
C	363	-7 to +1	+14 to +19
C	364	-7 to +1	+14 to +19
C	365	-10 to +4	+12 to +24
C	366	-10 to +13	+7 to +27
C	367	-10 to +4	+12 to +24
C	Combined assemblages	-7 to +1	+14 to +19
E	BH02/1	-10 to +3	+11 to +21
E	Area IV Column 1 (39, 40)	-8 to +13	+12 to +25
E	Area IV Column 2 (2, 3)	-10 to +3	+12 to +21
E	Combined assemblages	-8 to +3	+12 to +21
F	BH03/1 (46.0–47.5 cm)	-8 to -3	+16 to +23
F	BH03/1 (47.8–50.0 cm)	-8 to +13	+10 to +25
F	BH02/1 (core EE 20.0-25.0 cm)	-10 to +4	+7 to +26
F	Combined assemblages	-8 to -3	+16 to +23

Table 5. Calibrated present-day mean monthly temperature ranges of selected beetle taxa from Stratum C, Hoxne. Temperatures in °C. Data based on BUGSCEP envelopes with the exception of *P. lurida* and *O. boreale* which are based on updated envelopes generated using GBIF, which demonstrate improved winter temperature envelope values (Milne, 2016). Only a restricted number of revised envelopes are available via this source.

Species	Mean monthly air temperature range (°C)			
	January min.	January max.	July min.	July max.
<i>Bembidion hasti</i>	-31	0	+5	+15
<i>Bembidion mckinleyi</i>	-36	-1	+5	+13
<i>Colymbetes dolabratus</i>	-40	+4	+3	+13
<i>Helophorus obscurellus</i>	-40	-10	+3	+20
<i>Pycnoglypta lurida</i>	-24.5	-0.4	+9.8	+24.5
<i>Olophrum boreale</i>	-24.5	-7.5	+6.5	+19.4
<i>Boreaphilus hennigianus</i>	-35	-2	+6	+13
<i>Holoboreaphilus nordenskiöldi</i>	-34	-9	+6	+11
<i>Simplocaria metallica</i>		Not calibrated		
<i>Hippodamia arctica</i>		Not calibrated		

Table 6. Beetle Mutual Climate Range results from Hoxne. The % overlap indicates the proportion of calibrated species in the assemblage that have mutual (i.e., overlapping) temperature ranges. See Figs 1 and 2 for locations and stratigraphical context of samples.

Stratum	Beetle samples	Mean January air temperature range (°C)	Mean July air temperature range (°C)
C	328	-16 to 0	+10 to +14
C	329	-18 to -10	+10 to +13
C	368	-27 to -2	+9 to +13
C	369	-27 to -9	+9 to +11
C	370	-12 to -10	+10 to +11
C	371	-12 to -9	+10 to +11
C	372	-12 to -9	+10 to +11
C	373	-17 to -12	+12 to +15
C	374	-17 to -13	+13 to +15
C	Combined beetle samples (MGR)	-13 to -12	+11 to +13
C	Combined beetle samples (82.6% overlap)	-16 to -2	+12 to +14
D	Cutting XXIII (96% overlap)	-10 to +1	+16 to +19
F	Section 100(89.0% overlap)	-11 to -4	+15 to +16

Table 7: Freshwater Mollusca from Hoxne, Suffolk; relative abundance (%) values used to plot Fig. 6. Data from Sparks (1956) and White (2012). See Figs 1 and 2 for locations and stratigraphical context of samples.

N.B. This table is in two parts, designed to be laid out (portrait) across facing pages

Stratum	Location	Sample	<i>Valvata cristata</i>	<i>Valvata piscinalis</i>	<i>Bithynia tentaculata</i>	<i>Galba truncatula</i>	<i>Stagnicola palustris</i> agg.	<i>Lymnaea stagnalis</i>	<i>Myxas glutinosa</i>	<i>Radix ballifera</i>	<i>Planorbis planorbis</i>	Planorbidae	<i>Bathymphalus contortus</i>	<i>Gyraulus crista</i>	<i>Gyraulus laevis</i>	<i>Hippelitis complanatus</i>	
A2	Area IV	94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
A2	Area IV	96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
A2	Area IV	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	25	-	+	+	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	27	-	+	-	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	29	-	+	-	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	30	-	+	+	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	31	-	+	-	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	34	-	83.3	8.3	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	36, 38	-	+	-	-	-	-	-	-	-	-	-	-	-	-	
B2	Area III	40, 42-44	0.3	87.7	7.4	0.9	0.1	0.3	0.1	0.6	0.3	-	-	0.4	-	-	
B2	Area III	45, 48, 49	0.9	91.7	4.9	-	-	0.6	0.0	-	0.4	-	-	0.2	-	-	
B2	Area III	50	2.4	87.4	2.4	0.6	-	-	0.2	-	0.6	-	-	1.7	-	-	
B2	Area III	55, 58	1.1	90.5	4.2	0.2	-	0.2	-	0.3	0.8	-	0.2	0.2	-	-	
B2	Area III	64	-	94.1	4.5	-	-	0.6	-	-	0.4	-	-	-	-	-	
B2	Area III	66, 67	-	39.1	39.1	-	-	2.2	-	13.0	-	-	-	-	-	-	
B2	Area III	68, 71	0.6	89.1	5.9	-	-	0.2	-	0.2	0.2	-	-	1.0	-	-	
B2	Area III	74-78	2.0	78.7	8.7	0.1	0.1	0.9	0.4	0.3	1.1	-	-	2.4	-	-	
B2	Area III	79, 81, 82	0.6	84.1	6.4	0.2	-	0.2	0.2	0.8	0.8	-	-	2.8	-	-	
B2	Area III	83-88	2.4	87.3	3.8	-	0.5	-	-	0.9	-	-	-	1.9	-	-	
C	Area VII	301	-	+	-	-	-	-	-	-	-	-	-	-	-	-	
C	Area VII	302	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
C	Area VII	303	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
C	Area VII	304	-	-	-	+	-	-	-	-	-	-	-	-	-	-	
C	Area VII	305	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
C	Area VII	306	-	41.7	8.3	-	-	-	-	16.7	-	-	-	-	-	-	
C	Area VII	307	-	23.9	-	1.5	-	-	-	7.5	-	-	-	-	-	-	
C	Area VII	308	2.3	23.3	7.0	-	-	-	-	4.7	-	-	-	-	-	-	
C	Area VII	309	-	12.4	3.8	-	-	-	-	1.9	-	-	-	-	-	-	
C	Area VII	310	-	15.4	-	-	-	-	-	5.8	-	-	-	-	-	-	
C	Area VII	311	1.9	29.2	2.8	-	-	-	0.9	13.2	-	-	-	-	-	-	
C	Area VII	312	-	49.6	7.0	0.8	-	-	2.3	7.8	-	-	-	-	-	-	
C	Area VII	313	-	8.3	4.2	-	-	-	-	8.3	-	-	-	-	-	-	
C	Area VII	314	5.2	41.5	14.8	-	-	-	-	5.2	-	0.7	-	0.7	-	-	
C	Area VII	315	-	10.9	17.4	-	-	-	-	6.5	-	-	-	-	-	-	
C	Area VII	316	-	7.4	-	-	-	-	-	-	-	-	-	-	-	-	
C	Area VII	317	-	16.7	-	-	-	-	-	4.2	-	-	-	-	-	-	
C	Area VII	318	-	23.3	-	-	-	-	-	2.2	-	-	-	-	-	-	
C	Area VII	319	1.1	14.3	-	-	-	-	-	-	-	-	-	-	-	-	
D	Area III	91	-	+	-	-	-	-	-	-	-	-	-	-	-	-	
D	Area III	89	-	60.0	30.0	-	-	-	-	-	-	-	-	-	-	-	
E	Area I	9	-	97.3	1.5	-	-	-	-	-	-	-	-	-	-	-	
E	Area I	10	-	94.1	1.4	-	-	-	-	-	-	-	-	-	-	-	
E	Area I	11	-	93.9	3.8	-	-	-	0.2	-	0.2	-	-	-	-	-	
E	Area I	12	-	94.5	2.5	-	-	-	-	-	-	-	-	-	-	-	
E	Area I	13	-	94.2	3.6	0.4	-	-	-	0.9	-	-	-	-	-	-	
E	Area I	14	0.7	95.1	4.2	-	-	-	-	-	-	-	-	-	-	-	
E	Area I	15	1.4	91.7	2.1	1.4	-	-	-	1.4	0.7	-	-	-	-	-	
E	Area I	16	-	95.3	1.7	-	-	-	-	-	-	-	-	0.6	-	-	
E	Area I	18	-	89.0	1.9	-	-	-	-	-	0.6	-	-	-	-	-	
F	Section 100	Sparks (1956)	-	8.0	0.1	0.2	0.1	-	-	7.8	-	-	-	34.4	35.8	3.9	continued...

Stratum	Location	Sample	<i>Anisus leucostoma</i>	<i>Ancyclus fluviatilis</i>	<i>Sphaerium comeum</i>	<i>Pisidium amnicum</i>	<i>Pisidium casertanum</i>	<i>Pisidium clessini</i>	<i>Pisidium subtruncatum</i>	<i>Pisidium henslowianum</i>	<i>Pisidium milium</i>	<i>Pisidium obtusale</i>	<i>Pisidium nitidum</i>	<i>Pisidium molitessierianum</i>	<i>Pisidium tenuilineatum</i>	<i>Pisidium</i> spp.	Total countable
A2	Area IV	94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
A2	Area IV	96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
A2	Area IV	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
B2	Area III	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
B2	Area III	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
B2	Area III	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
B2	Area III	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
B2	Area III	31	-	-	-	-	-	-	+	-	-	-	-	-	-	-	2
B2	Area III	34	-	-	-	-	-	-	8.3	-	-	-	-	-	-	-	12
B2	Area III	36, 38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
B2	Area III	40, 42-44	-	-	0.1	-	-	0.5	1.3	-	-	-	-	-	-	-	781
B2	Area III	45, 48, 49	-	0.2	-	-	-	0.2	0.9	-	-	-	-	-	-	-	469
B2	Area III	50	-	-	0.2	-	-	-	3.5	-	-	-	0.2	-	-	0.9	540
B2	Area III	55, 58	-	0.2	0.2	-	-	0.3	1.2	-	-	0.5	-	-	-	-	645
B2	Area III	64	-	-	-	-	-	0.4	-	-	-	-	-	-	-	-	488
B2	Area III	66, 67	-	-	-	-	-	-	-	-	-	-	-	-	-	6.5	46
B2	Area III	68, 71	-	0.2	0.6	-	-	0.6	1.3	-	-	-	-	-	-	-	478
B2	Area III	74-78	-	0.3	1.0	-	-	1.1	2.0	-	-	0.7	-	-	-	-	698
B2	Area III	79, 81, 82	-	-	0.2	-	-	1.8	0.8	0.2	-	0.6	-	-	-	-	503
B2	Area III	83-88	-	-	0.5	-	-	0.5	0.9	0.9	-	-	-	0.5	-	-	212
C	Area VII	301	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
C	Area VII	302	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
C	Area VII	303	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
C	Area VII	304	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
C	Area VII	305	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
C	Area VII	306	-	-	-	-	-	-	-	-	-	-	-	-	-	16.7	12
C	Area VII	307	-	-	-	-	-	-	-	1.5	-	-	-	1.5	-	64.2	67
C	Area VII	308	-	-	-	9.3	-	-	-	-	-	-	-	-	-	53.5	43
C	Area VII	309	-	-	-	4.8	-	-	2.9	2.9	-	-	-	-	-	71.4	105
C	Area VII	310	-	-	-	-	-	-	-	26.9	-	-	-	-	-	51.9	52
C	Area VII	311	-	-	-	4.7	-	-	-	0.9	-	0.9	-	-	-	45.3	106
C	Area VII	312	-	-	1.6	-	1.6	0.8	13.2	0.8	-	-	-	4.7	0.8	9.3	129
C	Area VII	313	-	-	-	-	-	-	-	8.3	-	-	-	-	-	70.8	24
C	Area VII	314	-	-	2.2	-	-	-	-	2.2	-	0.7	-	-	-	26.7	135
C	Area VII	315	-	2.2	2.2	-	-	-	-	13.0	-	-	-	-	-	47.8	46
C	Area VII	316	-	-	-	-	-	-	-	7.4	-	-	-	-	-	85.2	27
C	Area VII	317	-	-	-	-	-	-	4.2	33.3	-	-	4.2	-	-	37.5	24
C	Area VII	318	-	-	1.1	-	-	-	21.1	8.9	-	-	11.1	-	-	32.2	90
C	Area VII	319	-	-	-	-	-	-	16.5	5.5	-	6.6	5.5	-	-	50.5	91
D	Area III	91	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
D	Area III	89	5.0	-	-	-	-	-	-	-	-	-	-	-	-	5.0	20
E	Area I	9	-	-	0.5	-	-	-	0.7	-	-	-	-	-	-	-	405
E	Area I	10	-	0.2	0.7	-	-	0.2	2.4	-	-	-	0.7	-	-	0.3	573
E	Area I	11	-	-	0.6	-	-	0.4	0.4	-	-	-	0.4	-	-	-	477
E	Area I	12	-	-	1.8	-	-	1.2	-	-	-	-	-	-	-	-	163
E	Area I	13	-	-	0.4	-	-	0.4	-	-	-	-	-	-	-	-	223
E	Area I	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	142
E	Area I	15	-	-	0.7	-	-	0.7	-	-	-	-	-	-	-	-	145
E	Area I	16	-	-	0.6	-	-	0.6	-	-	0.6	-	-	-	-	-	172
E	Area I	18	-	-	0.6	-	-	0.6	4.5	0.6	-	-	1.9	-	-	-	154
F	Section 100	Sparks (1956)	0.1	-	1.5	-	0.1	-	0.6	0.1	0.7	1.2	5.7	-	-	-	1622

Table 8. Small vertebrate remains from Stratum C, Area VII sample column, Hoxne, See Figs 1 and 2 for locations and stratigraphical context of samples.

Sample	Vertebrate taxa										
	Pisces							Mammals			
	Cyprinidae gen. et sp. indet. (Carp family)	<i>Esox lucius</i> (Pike)	<i>Pungitius pungitius</i> , (Nine-spined stickleback)	Gasterostidae gen. et sp. indet. (Stickleback)	<i>Perca fluviatilis</i> (Perch)	<i>Gymnocephalus cernua</i> / <i>Perca fluviatilis</i> (Ruffe / Perch)	Pisces indet. (fish)	<i>Alburnus alburnus</i> (bleak)	<i>Phoxinus phoxinus</i> (minnow)	<i>Dicrostonyx</i> sp. (lemming)	Microtinae indet. (vole)
301										+	
302											
303	+										+
304	+					+				+	
305	+										
306											
307	+			+							
308	+			+							
309				+							
310											
311				+							+
312	+	+	+			+					
313					+	+					
314			+		+						+
315				+							
316											
317											
318											
319				+							
Beetle samples											
369							+				
370			+				+				+
371							+	+	+		
372							+				
373							+				
374							+				

Table 9. Carbon and Oxygen stable isotope results (‰) from Stratum C ostracod shells, Hoxne. See Figs 1 and 2 for locations and stratigraphical context of samples.

Sample	<i>Ilyocypris</i>		<i>Cytherissa</i>	
	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
327*	-5.71	-2.23	-3.06	-1.67
332	-5.23	-1.62	–	–
335	-5.11	-2.02	–	–
336	-5.09	-1.76	–	–
346	-5.22	-2.47	–	–
353	-4.12	-2.47	–	–
355	–	–	-5.62	-4.05
356	–	–	-5.62	-4.69
361	-4.6	-1.95	–	–
363	-5.24	-2.26	-4.18	-0.81
364	-5.09	-1.08	–	–
365	-5.71	-2.2	–	–

* 327 is a test sample from same level as 362

Table 10. Look-up table of method acronyms used in the Multi-Proxy Consensus palaeotemperature reconstructions section of the text.

Acronym	Full name
MPC	Multi-Proxy Consensus
MOR	Mutual Overlap Range
MOTR	Mutual Ostracod Temperature Range
BMCR	Beetle Mutual Climatic Range
MGR	Minimum Gap Range
CTF	Chironomid Transfer Function

Table 11. Stratum C individual proxy-based palaeotemperature reconstructions and Multi-Proxy Consensus (MOR in bold, MGR in italics) results. For sample locations and equivalents see Figs 1 and 2; for acronyms see Table 10.

Ostracod samples	Reconstructed mean January air temperature range (°C)			Reconstructed mean July air temperature range (°C)			
	MOTR	BMCR	MPC MOR/MGR	MOTR	BMCR	CTF	MOR/MGR
332	-10 to +3			+11 to +21			
333	-10 to +7			+7 to +24			
334	-40 to +7			+7 to +24			
335	-40 to +3			+11 to +21			
336	-31 to +7			+12 to +24			
337	-32 to +14			+7 to +27			
338	-32 to +14			+7 to +27			
339	-32 to +7			+7 to +24			
340	-31 to +9			+12 to +26			
341	-30 to +6			+12 to +27			
342	-10 to +13			+12 to +27			
343	-32 to +1		-16 to 0	+11 to +19			+11 to +14
344	-32 to +14	-16 to 0	-16 to 0	+7 to +27	+10 to +14		+10 to +14
345	-10 to +13		-10 to 0	+7 to +27			+10 to +14
346	-10 to +1		-10	+14 to +19			<i>+13 to +14</i>
347	-31 to +1	-18 to -10	-18 to -10	+14 to +19	+10 to +13		<i>+13 to +14</i>
348	-10 to +4		-10	+14 to +26			<i>+13 to +14</i>
349	-7 to +4			+14 to +24			
350	-10 to +13			+12 to +27			
351	-10 to +4			+7 to +26			
352	-31 to +4	<i>-27 to -2</i> <i>-27 to -9</i>	-27 to -2 -27 to -9	+12 to +26	<i>+9 to +13</i> <i>+9 to +11</i>		+12 to +13 <i>+11 to +12</i>
353	-7 to +1			+14 to +19			
354	-10 to +13			+12 to +27		+12.5 to +14.7	+13 to +15
355	-10 to +4			+7 to +26			
356	-10 to +4			+7 to +26			
357	-10 to +1			+12 to +19		+13.9 to +16.1	+14 to 16
358	-10 to +4	<i>-12 to -10</i> <i>-12 to -9</i>	-10 -10 to -9	+12 to +26	<i>+10 to +11</i> <i>+10 to +11</i>		<i>+11 to +12</i> <i>+11 to +12</i>
359	-10 to +1			+12 to +19			
360	-7 to +1		<i>-9 to -7</i>	+14 to +19			<i>+11 to +14</i>
361	-10 to +1	-12 to -9	-10 to -9	+12 to +19	+10 to +11		<i>+11 to +12</i>
362	-10 to +1		-10 to -9	+12 to +19			<i>+11 to +12</i>
363	-7 to +1		<i>-12 to -7</i>	+14 to +19			+14 to +15
364	-7 to +1	-17 to -12	<i>-12 to -7</i>	+14 to +19	+12 to +15		+14 to +15
365	-10 to +4		<i>-12 to -10</i>	+12 to +24			+12 to +15
366	-10 to +13	-17 to -13	<i>-13 to -10</i>	+7 to +27	+13 to +15	+12.3 to +14.5	+13 to +15
367	-10 to +4		<i>-13 to -10</i>	+12 to +24			+13 to +15

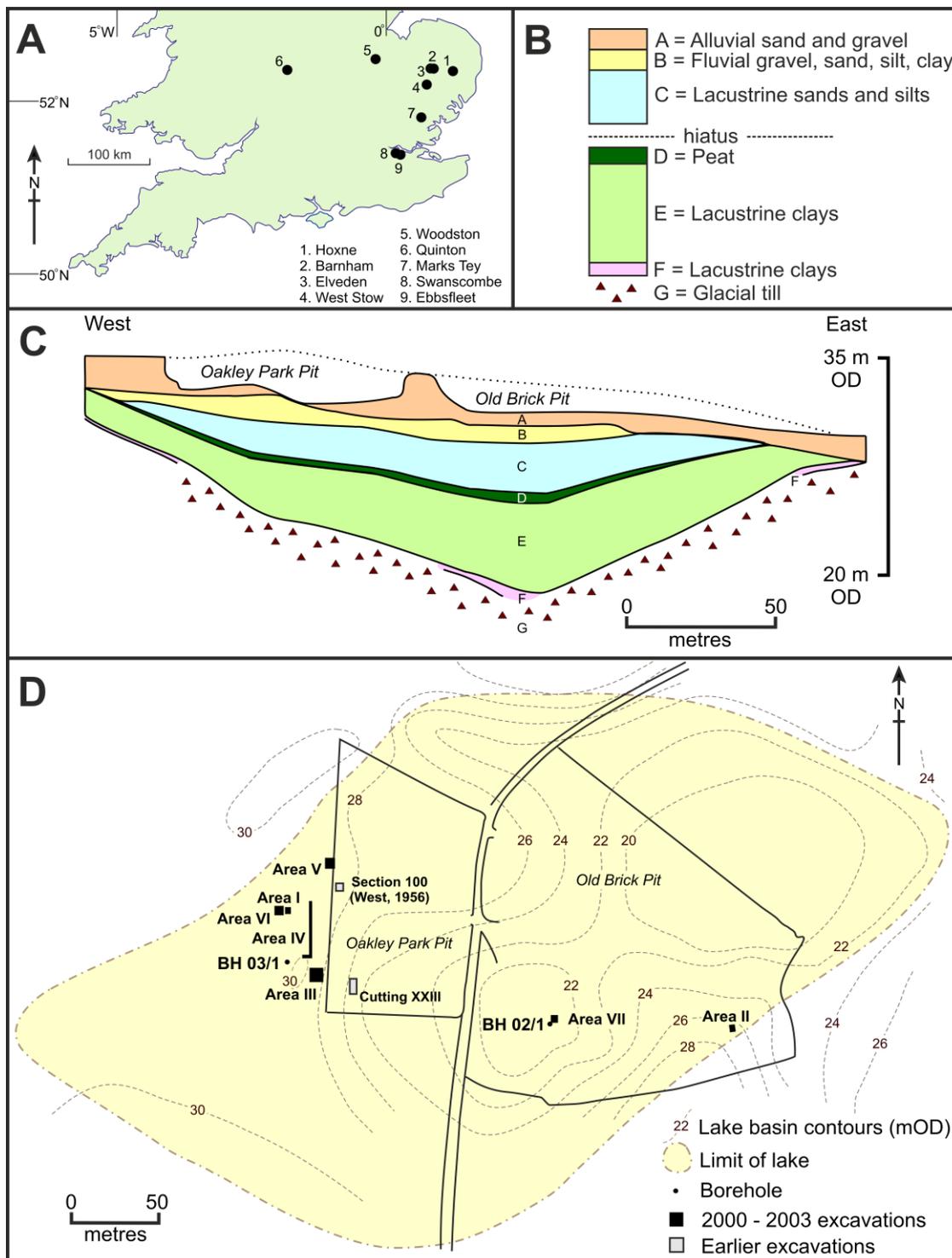


Fig. 1. A: Location of British MIS 11 sites mentioned in the text and Table 1; B: summary succession of MIS 11 deposits at Hoxne; C: Schematic cross-section of the Hoxne lake basin; D: map of the Hoxne lake basin showing sampling locations referred to in the text and in Supplementary Data. C and D modified from Ashton et al. (2008).

Molluscs	Area IV samples		Ostracods	Molluscs
	Stratum A 1 Stratum A2 (i)			
	Stratum A2 (iii)	Stratum A2 (ii)		
Area III	Stratum B2	Stratum B1	Area IV	Area IV

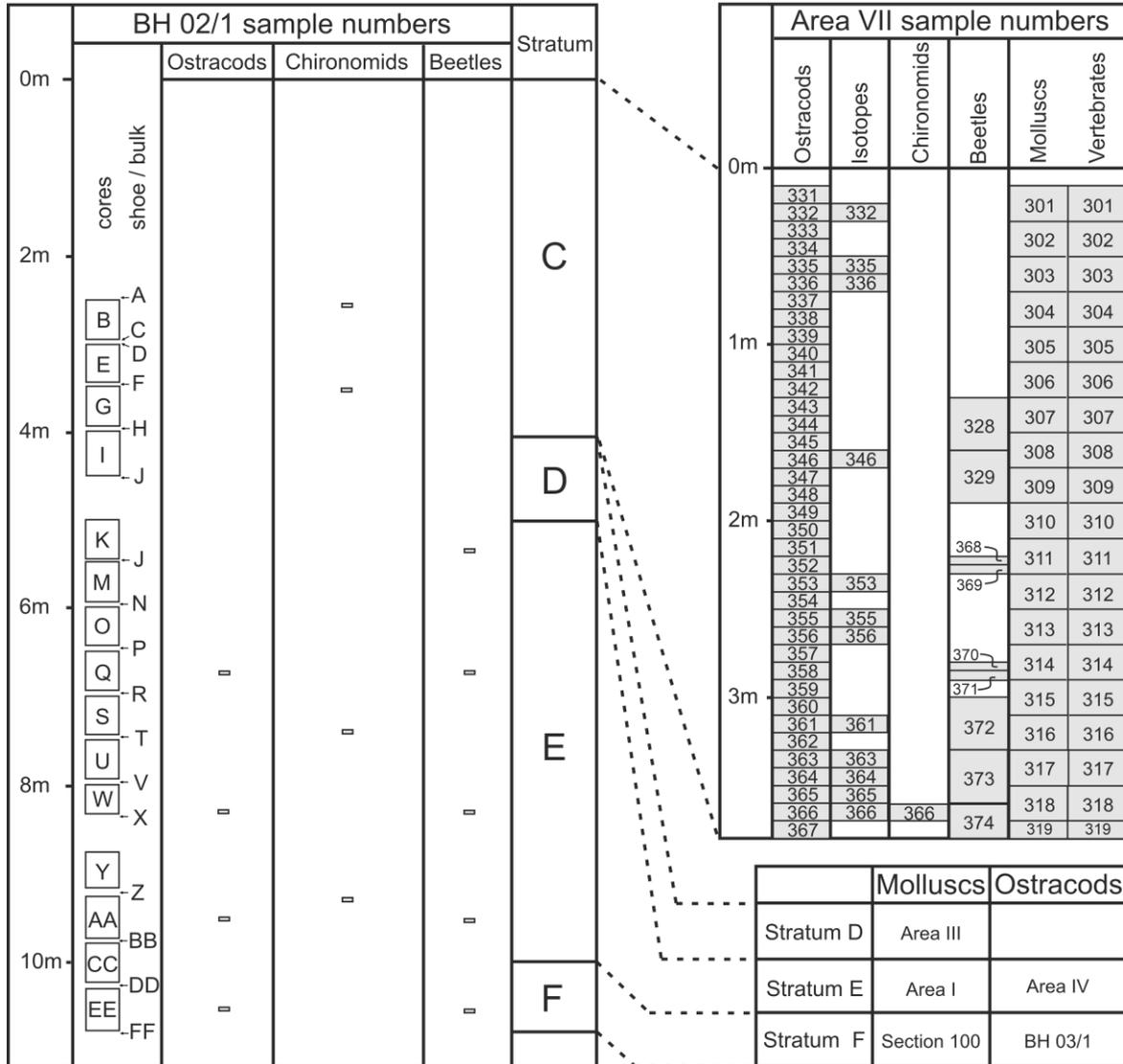


Fig. 2 Stratigraphical context of samples from Hoxne referred to in the text and in Supplementary Data; see Fig. 1 for geographical locations.

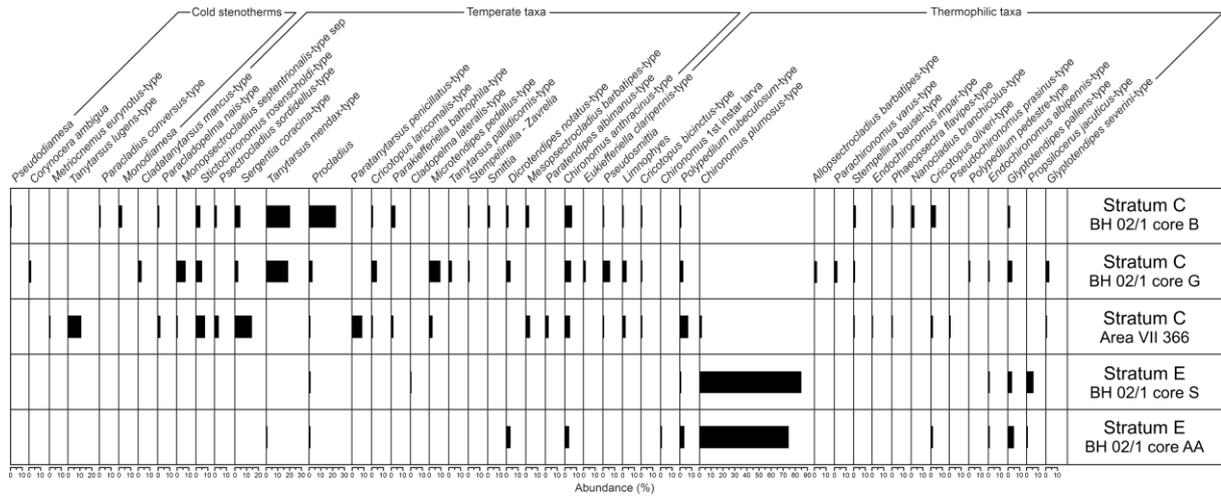


Fig. 3. Summary of chironomid occurrences recorded from MIS 11 strata at Hoxne.

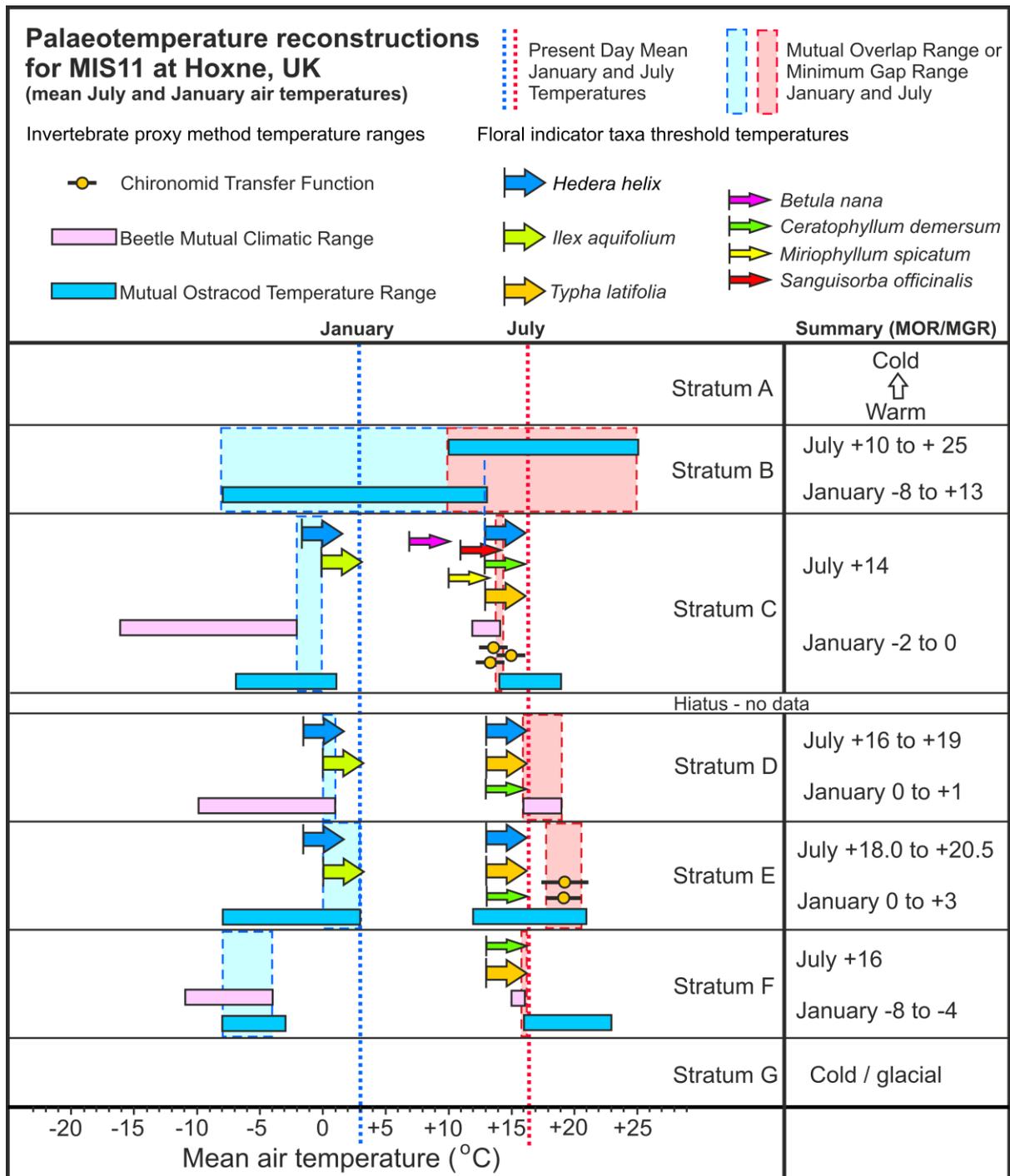


Fig. 4. Multi-proxy palaeotemperature reconstructions for MIS 11 at Hoxne.

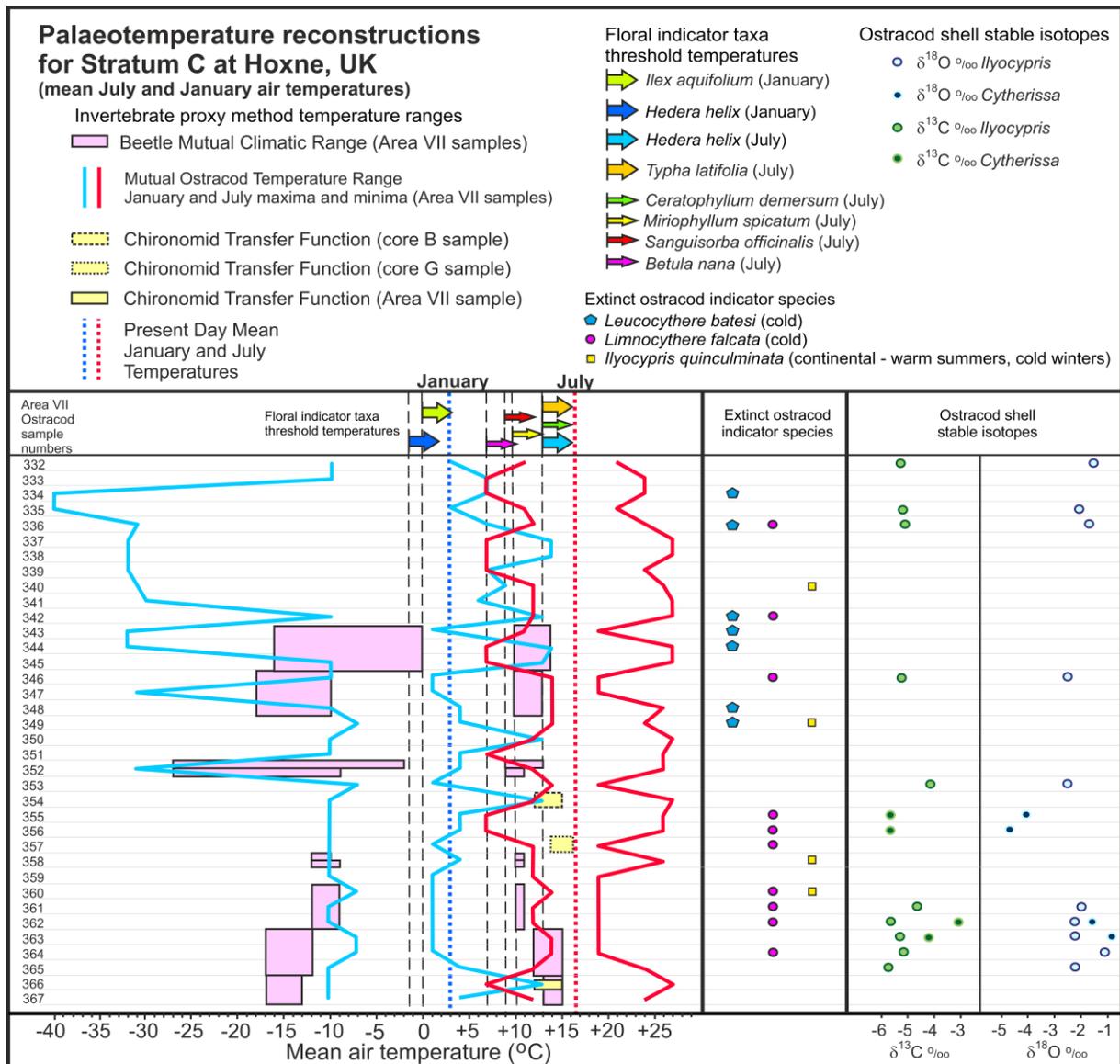


Fig. 5. Stratum C, Hoxne: palaeotemperature reconstructions from MOTR, BMCR and CTF methods with the addition of plant threshold temperatures, and ostracod shell $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measured in shells of *Cytherissa* and *Ilyocypris*. Note that the BMCR and CTF sample intervals were determined from a different numbering sequence matched to the equivalent ostracod sample numbers shown on the left of the figure (See Fig. 2 for details).

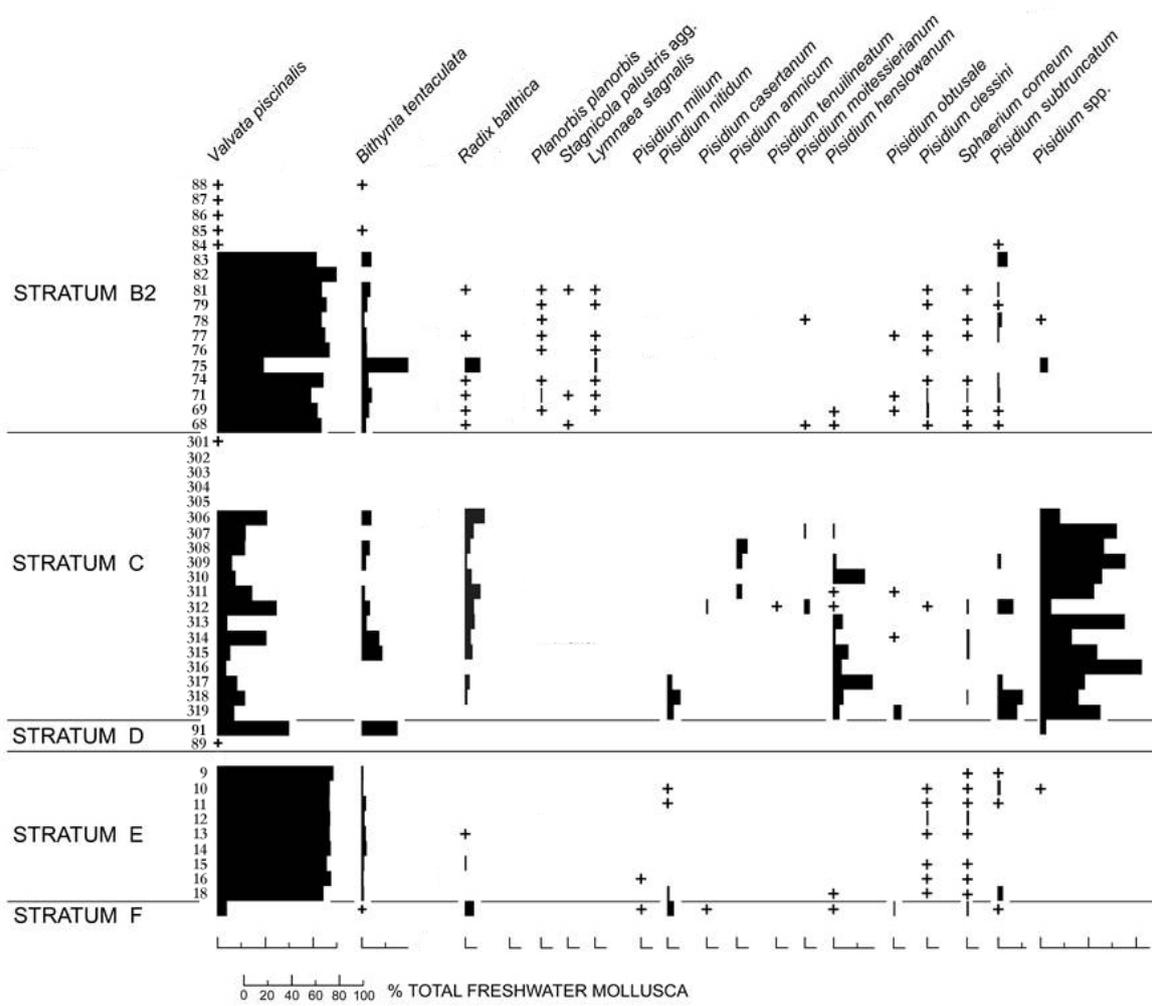


Fig. 6. Selected freshwater Mollusca from Hoxne strata F to B.

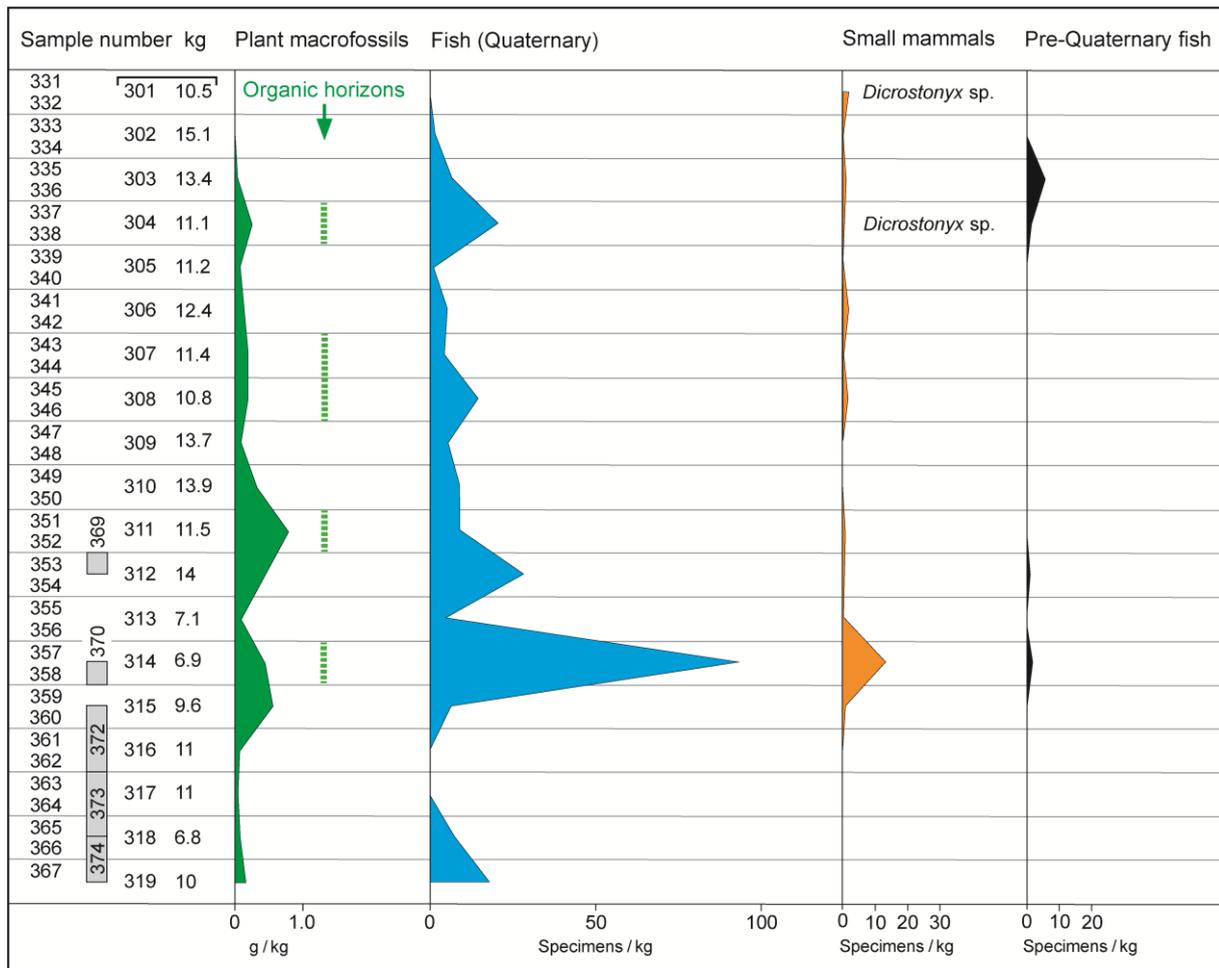


Figure 7. Abundance of small vertebrate and other fossil remains in Stratum C (Area VII). Conspicuous organic seams correspond to peaks in the abundance of plant and other fossils remains in samples 314, 311, 308–307 and 304. Chalk stringers and lenses of chalky and gravelly sand occurring towards the top of the sequence (equivalent to samples 304–301) are associated with reworked Chalk fossils (corals, ostracods), pre-Quaternary fish remains and marine molluscs. Occasional Mesozoic ostracods and foraminifera are also found in the lower organic-rich horizons.

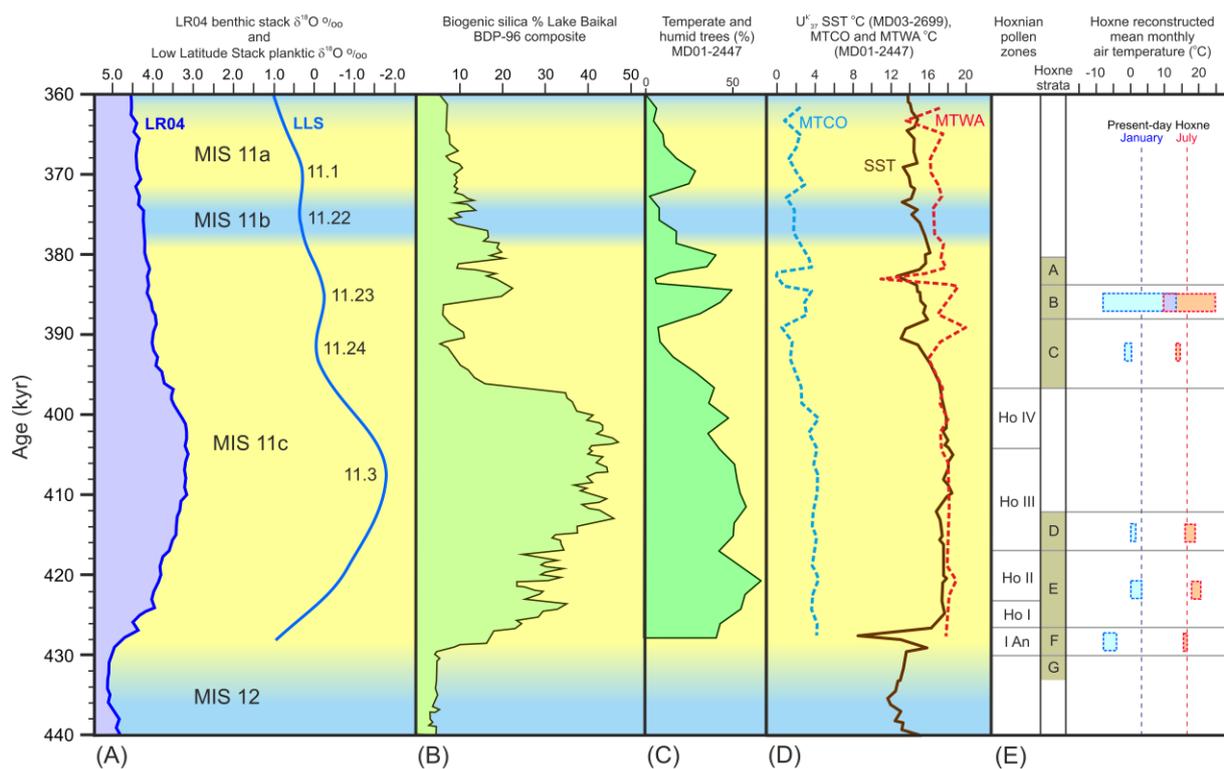


Fig. 8. Comparison of records of MIS 11 climatic variability; from left to right: (A) Structure and sub-division of MIS 11 in the LR04 benthonic $\delta^{18}\text{O}$ stack (Lisiecki and Raymo, 2005) and the planktonic $\delta^{18}\text{O}$ Low Latitude Stack (Bassinot et al., 1994); (B) Lake Baikal BDP-96 composite record of biogenic silica, a proxy for lacustrine productivity (Prokopenko et al., 2010); (C) pollen record of temperate and humid trees from North Atlantic oceanic core MD01-2447 off northwestern Iberia (Desprat et al., 2005); (D) alkenone-derived Sea Surface Temperature from North Atlantic oceanic core MD03-2699 off western Iberia (Rodrigues et al., 2011) and pollen-derived mean air temperature of coldest (MTCO) and warmest (MTWA) months from North Atlantic oceanic core MD01-2447 off northwestern Iberia (Desprat et al., 2005); (E) Hoxne pollen zones, strata and reconstructed January and July air temperature ranges (herein). Site locations are shown in Fig.9.



Fig. 9. Map showing locations of sites in Fig. 8.

Supplementary Material

1. Sample processing

Ostracod samples were first oven-dried, then soaked for several hours in hot water with a little sodium carbonate, and finally washed through a 75 µm sieve with hand-hot water, the retained residues being dried in an oven and ostracods picked from them under a low-power stereo-microscope. Identification and environmental preferences are based on Meisch (2000) and other sources cited in the text. Samples of monospecific ostracod shells (7 to 10 valves of *Ilyocypris* ("bradyi"-type) or 4 to 6 valves of *Cytherissa lacustris*) destined for stable isotope analysis were brush-cleaned and air dried before loading into Labco glass Exetainer® tubes. Oxygen and carbon isotope analyses were performed on CO₂ produced by reaction with phosphoric acid at 45°C in a ThermoFisher Gasbench II connected to a Delta V mass spectrometer. The results were expressed in standard δ units on the VPDB scale with a mean standard deviation of measurements of 0.05 ‰ and 0.03 ‰ for δ¹⁸O and δ¹³C, respectively.

Chironomid samples were prepared using the paraffin flotation method of Coope (1986) but, instead of a 200 µm mesh sieve, the float was passed through a 90 µm sieve to retain the smallest chironomid taxa. Identification and ecological assessment of the assemblage was made following Brooks et al. (2007).

Beetle data were taken from previously published species lists, e.g. in Coope (1993), where (pp. 156 and 158) sample preparation methods were summarised as follows: "Insect remains were extracted by the standard technique of wet-sieving in the laboratory, kerosene concentration and hand sorting, as described by Coope (1986)... Identification was by direct comparison of the fossils with well-authenticated modern material... The nomenclature is that of *Die Käfer Mitteleuropas* (Lucht, 1987)."

Small vertebrates were obtained from a series of 19 samples (319–301), each between ~7 and 15 kg (totalling 211 kg), from successive 20 cm levels through Stratum C in Area VII. Additional vertebrate specimens were extracted from larger subsamples collected for insect remains (369–374). Samples were wet-sieved and all vertebrate specimens retained by a 1 mm sieve were picked and counted. A note was made of the distribution of reworked Chalk fossils and pre-Quaternary fish remains, and plant remains (seeds and woody fragments) were weighed; ostracods and insect remains were also picked.

Non-marine molluscs were obtained from the same samples processed for other proxies as part of the AHOB excavations (Ashton et al., 2008).

2. Chironomid assemblages

Stratum E chironomid assemblages were analysed from BH02/1 core S, 40.0–47.0 cm (61.75 g sediment; 116 heads; 8 taxa) and BH02/1 core AA, 0–5.0 cm (38.32 g sediment; 86 heads; 11 taxa). They are dominated by *Chironomus plumosus*-type (75–85% of the assemblage). The chironomid assemblage is relatively species-poor and all taxa present are typical of warm, eutrophic waters containing submerged aquatic vegetation. The high dominance of *C. plumosus*-type suggests low oxygen conditions, either in a deep, thermally stratified lake or in a shallow lake containing large amounts of decaying vegetation. The presence of *Cricotopus oliveri*-type, *Dicrotendipes*, *Glyptotendipes pallens*-type and *Polypedilum nubeculosum*-type are indicative of the presence of submerged aquatic vegetation and a warm-temperate climate.

Stratum C chironomid assemblages were analysed from borehole BH02/1 core B, 5.0–10.0cm (28.3 g of sediment processed; 73 heads; 26 taxa) and core G, 5.0–10.0 cm (10.1 g sediment; 69 heads; 25 taxa), and from Area VII sample 366 (19.83 g sediment; 81 heads; 28 taxa). They are relatively species-rich. Samples from BH02/1 cores B (5.0–10.0cm) and G (5.0–10.0cm) are dominated by *Tanytarsus mendax*-type (25%) and *Procladius* (20%). These two taxa are widespread and eurytopic: they can occur in both warm and temperate waters. However, *Tanytarsus mendax*-type is absent from Area VII

sample 366 and *Procladius* is uncommon (< 5%) in the assemblage, which does, however, include the cold stenotherm *Tanytarsus lugens*-type (10%) and the temperate taxon *Paratanytarsus penicillatus*-type (10%), which are both absent from cores B and G. The cold stenothermic taxa *Sergentia coracina*-type (15%) and *Stictochironomus rosenschoeldi*-type (10%) are present in all three Stratum C samples. The presence of *Eukiefferiella*, *Limnophyes*, *Pseudosmittia*, *Smittia* and *Metriocnemus hygropetricus* in Stratum C samples are indicative of relatively shallow waters and/or the influence of a stream inflow. The absence or rarity of *C. plumosus*-type also suggests the waters in this interval were relatively shallow and well-oxygenated. *Tanytarsus lugens*-type typically occurs in deep lakes but can also occur in shallow water in cold lakes. The presence of submerged aquatic vegetation is suggested by the presence of *Cricotopus oliveri*-type, *Dicrotendipes*, *Glyptotendipes pallens*-type and *Polypedilum nubeculosum*-type. These taxa are typical of temperate and warm lakes. Many taxa indicative of cool climatic conditions are present in Area VII sample 366 and core B, including *Paracladius*, *Monodiamesa*, *Pseudodiamesa*, *Paracladopelma*, *Sergentia coracina*-type, *Stictochironomus rosenschoeldi*-type, *Corynocera ambigua* and *Tanytarsus lugens*-type. Of these taxa, only *Sergentia coracina*-type, *Stictochironomus rosenschoeldi*-type and *Corynocera ambigua* are present in core G. The assemblages of all three Stratum C samples are not dominated by cold stenothermic taxa, however, and the presence of many temperate taxa in similar abundance suggests the climate was cool-temperate rather than cool.

3. Ostracod assemblages

Stratum F ostracods were recovered from boreholes BH03/1 (46–47.5 cm and 47.8–50.0 cm) and BH02/1 (core EE, 20.0–25.0cm). Although labelled "Stratum G", the lower of the two above-mentioned BH03/1 samples was taken immediately below the lowermost Stratum F sample; since Stratum G is actually the underlying Anglian till, this sample is here considered to belong to Stratum F.

Stratum E results are from borehole BH02/1 (core Q, 20.0–30.0cm; core W, 25.0–30.0cm; core AA, 20.0–25.0cm) and Area IV trench Column 1 (samples 39, 40) and Column 2 (samples 2, 3).

Stratum C ostracod assemblages were obtained from continuous sampling in Area VII.

Stratum B results were obtained from Area IV trench Column 1 (sand/silt filled fluvial channel; samples 63, 61, 64) and Column 2 (fluvial channel; samples 13, 14).

Notes on the palaeoenvironmental and palaeoclimatic significance of selected species are given below, based on Meisch (2000) except where other works are cited (* denotes extinct species).

Candona candida occurs in a wide range of waterbody types, with a preference for permanent fresh waters, and tolerates brackish water up to around 6 ‰; it has a shorter life-cycle in high latitudes than in low latitudes and is considered to be adapted to the climate of arctic regions.

Cyclocypris ovum is found in almost every kind of freshwater habitat including temporary as well as permanent waterbodies; it is common in the littoral zone of lakes and tolerates salinity up about 6 ‰.

Cypridopsis vidua lives in a wide range of freshwater environments with a preference for vegetated permanent habitats such as the littoral zone of lakes and is also found in temporary ponds and in springs; tolerant of salinities up to 8 ‰.

Cytherissa lacustris is usually regarded as a cold stenothermal freshwater form, found in sublittoral to profundal depths of lakes with a preference for oligo-mesotrophic waters, but is also found in the shallower parts of lakes and in ponds where it experiences warm summer temperatures, so it is probably best considered as a eurythermal species with a preference for cold water; it tolerates slightly brackish water up to 1.5 ‰.

Darwinula stevensoni inhabits a wide variety of permanent freshwater environments including lakes (to depths of about 12m), ponds and rivers; it tolerates brackish water up to 15 ‰.

Fabaeformiscandona levanderi lives in freshwater lakes and ponds (found at a depth of 62m in Lake Constance) and is tolerant of slightly brackish waters up to 6 ‰. Wetterich et al. (2005) recorded fossils of this species on the Bykovsky Peninsula bordering the Laptev Sea (approx. 72°N, 129°E) in deposits of the Karginian Interstadial (48-34 ka BP), considered to be a warm and dry interval; the habitat was small, cold, oligotrophic pools located in ice-wedge polygon centres or thermokarst depressions, set in a landscape with shrubby tundra vegetation experiencing dry and relatively warm summers. They considered it to be suggestive of arid climatic conditions with higher evaporation rates than today in this region. Wetterich et al. (2009) found it in Eemian Interglacial assemblages in NE Siberia.

Fabaeformiscandona protzi is an inhabitant of permanent freshwater bodies (lakes, ponds, swampy and muddy ditches, dead arms of rivers) and is tolerant of slightly brackish water (up to about 6 ‰); it is considered to be a cold stenothermal species.

Herpetocypris reptans inhabits a wide variety of freshwater environments but shows a preference for richly vegetated permanent waters and muddy bottoms, and in lakes it is usually restricted to the littoral but has been recorded down to 15 m depth (it is also known from springs, swamps and temporary waterbodies); it can tolerate brackish waters up to 6 ‰.

**Leucocythere batesi* and **Limnocythere falcata* are considered to be a freshwater cold-climate indicator by association with other taxa (Whittaker and Horne, 2009). The latter species was recorded in Late Quaternary assemblages of the Siberian Arctic by Wetterich et al. (2005), in association with ostracod taxa characteristic of European cold-stage lake deposits. They found it on the Bykovsky peninsula bordering the Laptev Sea (approx. 72°N, 129°E) in deposits of the Karginian Interstadial (48-34 ka BP), considered to be a relatively warm and dry interval, where it inhabited small, cold, oligotrophic pools located in ice-wedge polygon centres or thermokarst depressions, set in a landscape with shrubby tundra vegetation experiencing dry and relatively warm summers. In the same area they also found it in late Holocene deposits (3 ka BP) considered to be representative of cool, wet climate reflecting recent conditions of the Arctic tundra. Wetterich et al. (2009) found it very common in Eemian Interglacial assemblages of Oyogos Yar in NE Siberia.

Limnocytherina sanctipatricii inhabits oligotrophic lakes and small permanent ponds and ditches, is tolerant of slightly brackish water up to 3 ‰ and was found down to 250m depth in Lake Constance (Meisch, 2000). Löffler (1975) considered it to be a cold-water indicator but Meisch (2000) questioned this because it has also been reported from the littoral zone which warms up in summer. Wetterich et al. (2005) found this species to be abundant in deposits of the Zyrianian Stadial (58-53 ka BP), interpreting it as indicative of cold, arid conditions (associated pollen and plant macrofossils indicated an open, treeless landscape with cold, dry summers). Habitat was small, shallow, cold, oligotrophic pools in thermokarst or ice-wedge polygon depressions, which warmed in the summer. They considered it to be an indicator of arid climatic conditions with higher evaporation rates than present day in this region. Wetterich et al. (2009) recorded it in Eemian Interglacial deposits of Oyogos Yar in NE Siberia.

Neglecandona neglecta inhabits a wide range of freshwater environments, both permanent and temporary, with a preference for relatively cold waters, and is tolerant of brackish waters up to at least 15 ‰.

Metacypris cordata lives among aquatic macrophytes in freshwater meso- to eutrophic lakes and ponds, showing a preference for ion-rich waters with pH >7.

4. Beetle assemblages

Notes on selected climatically significant species from strata F and C (none of which occurred in strata E or D) are given below (* indicates species not now living in the British Isles). It is striking that many are common together in later mid-Devensian and late glacial assemblages from the British Isles (e.g. *Diacheila polita*, *Bembidion hasti*, *Pycnoglypta lurida*, *Olophrum boreale*, *Oreodytes alpinus*, *Colymbetes dolabratus*, *Helophorus obscurellus*, *Boreaphilus hennigianus*, *Tachinus caelatus*, *Notaris aethiops*).

**Diacheila polita* is a terrestrial ground beetle found usually on peaty soils in either rather dry places or occasionally at the margins of pools with *Carex*; its true habitat is the present-

day tundra (Lindroth, 1961). In arctic Fennoscandia it is found exclusively on the tundra but in northeastern Russia and Siberia its range also includes the northern fringe of the taiga (Böcher, 1995; Lindroth, 1945). In Alaska and the Northwest Territories of Canada it is similarly found on the open tundra. It occurred in Stratum F.

**Bembidion mckinleyi* is a small terrestrial ground beetle that occurs on gravelly or sandy banks in the mountains where it lives beside very cold water often emanating from glaciers (Lindroth, 1963). It is known only from northernmost Fennoscandia and from North-west North America (Lindroth, 1985). It occurred in both Stratum F and Stratum C.

**Bembidion hasti* is often found in company with the previous species and in similar habitats. Its range is circumpolar. In Fennoscandia it is widespread in the far north but usually confined to alpine areas further south (Lindroth, 1985). It occurred in both Stratum F and Stratum C.

Agonum chalconatum (formerly *sahlbergi*) is a riparian species, living at the edges of sandy banks and stones (Hyman, 1992). Today, it is likely a glacial relict, being found on banks of the Clyde and elsewhere in Scotland (Hyman, 1992), but also eastern Fennoscandia and the White Sea coast of Siberia (Lindroth, 1986). It occurred in Stratum F.

Oreodytes alpinus is a Palearctic small predatory water-beetle that was only added to the British Isles species list in 1986 (Foster and Spirit, 1986), where it occurs on wave washed shores of base-rich lochs in the extreme north-east of Scotland (Caithness and Sutherland) (Foster, 2000). In Fennoscandia, it is widespread in the north but is most common in western Lapland; eastwards it ranges as at least as far as north-western Siberia (Böcher, 1995). It is likely that it also occurs in North America but under a different name. It occurred in Stratum F.

**Colymbetes dolabratus* is a moderately large predatory water-beetle with a circumpolar distribution at all high latitudes ranging across Eurasia to North America and Greenland (Lindroth et al., 1973). Its main habitat is shallow pools above the tree line. It occurred in Stratum C.

**Helophorus obscurellus* has (in contrast to most of the species of this genus which are aquatic) terrestrial adults, living in sandy places under stones and vegetation where they probably feed on decomposing plant matter (Angus, 1970). Its geographical range is northern and montane; in Europe is only known from the northern coast of the Kanin Peninsula in arctic Russia (Coope, 2004). It is widespread in eastern Asia from the Tibetan plateau to the north of Siberia (Angus, 1970). It occurred in both Stratum F and Stratum C.

**Pycnoglypta lurida* is found mostly in damp locations under plant debris such as *Salix* leaves (Bocher, 1995); it is a circumpolar species, widespread in northern Europe, Asia and North America. In Fennoscandia it has been found chiefly in the northern areas though reaching as far south as Denmark (Böcher, 1995; Gusarov, 1995). It occurred in both Stratum F and Stratum C.

**Olophrum boreale* is a hygrophilous species associated with damp decaying vegetation, widespread in the northern half of Fennoscandia and northern Asia (Böcher, 1995). It has a relict outpost in the High Tauern Mountains of Austria (Koch, 1989). It occurred in Stratum C.

**Boreaphilus hennigianus* is another small predator with a wide distribution across northernmost Fennoscandia, Norway, north Russia and northern Siberia (Mani 1968; Ostbye and Hagvar, 1966). There is a relict population in the Rhön Mountains of central Germany (Koch, 1989). Its habitat requirements are similar to those of the previous species. It occurred in both Stratum F and Stratum C.

**Holoboreaphilus nordenskiöldi* is another small predator with a circumpolar geographical distribution. Its nearest locality today is on Novaya Zemlya from where it ranges eastward to northern Alaska. It is found under moss and stones (Coope, 1982). It occurred in both Stratum F and Stratum C.

**Tachinus caelatus* is a predator, known today only from Mongolia where it lives in the mountains near Ulan Bator and is found under moss and leaves in the birch woodland at altitudes between 1150m and 2000m (Ullrich, 1975). This species has been found as a fossil in a variety of Quaternary deposits in both Britain and Switzerland - mostly early Devensian and Late glacial in date - and always in company with arctic beetle species. Its present-day

restricted distribution may thus not reflect the full climatic potential of this species. It occurred in Stratum F.

**Simplocaria metallica* is a species that feeds exclusively on tightly matted mosses on sandy-granular soils in boreal and alpine habitats (Böcher, 1995). It has a boreo-montane distribution in Europe, being widespread in the far north of Fennoscandia but also living on the high mountains of central Europe. It is also recorded from Greenland (Böcher, 1995). There may be some confusion between this species and other similar northern species such as *Simplocaria elongata* Sahl. As a fossil it is frequently abundant in Quaternary deposits where it is always associated with numerous other northern species. It occurred in both Stratum F and Stratum C.

**Hippodamia arctica* is a ladybird that feeds on aphids on small *Salix* or *Betula nana* bushes (Brundin, 1934). It lives today in northern Fennoscandia and northern Russia (Pechora) (Brundin, 1934). There is a subspecies in the Caucasus Mountains. It occurred in Stratum C.

Notaris aethiops is a boreo-montane weevil that feeds on reedy vegetation in marshy habitats beside ponds (Koch, 1992). Its wide geographical range covers northernmost Europe, including northern Britain and it also extends across northern Asia to Alaska (Lindroth, 1957). It is also found in the mountains of central Europe (Koch, 1992). It is very common fossil in Quaternary beetle assemblages (frequently: Devensian and late glacial) where it is found with numerous other northern species. It occurred in both Stratum F and Stratum C.

5. Mollusc assemblages

Molluscan data for Stratum F were derived from the quantified faunal list provided by Sparks (1956), recovered from a bulk sample taken from section no. 100 of the 1953 season of the R.G. West excavations. This has been included in Fig. 6 to give an impression of the complete Hoxne molluscan succession, but it should be noted that it was obtained from a more marginal part of the lake than the material from overlying strata. A series of nine samples (9–16, 18) from Stratum E was recovered during the 2000 season (AHOB excavations) from an exposure in Area I. Only two samples (91, 89) from Stratum D yielded limited molluscan assemblages, both collected in 2001 from Area III. Mollusc shells from Stratum C were recovered from the same series of 19 samples (301–319) processed for vertebrate remains (Fig. 2). Stratum B2 was excavated in 2001 in Area III, yielding a sequence of 17 samples (68, 69, 71, 74–79, 81–88) with a further 8 samples from Stratum B1 excavated in 2002 from a section in Area IV, exposed in a narrow trench previously excavated in 1978.

6. Stratum C small vertebrate assemblages

The presence of *Dicrostonyx* is particularly noteworthy since this genus is a valuable environmental indicator. In broad terms it is taken to indicate regionally cold and open conditions, similar to the modern tundra and Pleistocene mammoth steppe (Guthrie, 1968). Today *Dicrostonyx* has a circumpolar distribution confined to the tundra and forest-tundra with a chain of closely related species distributed from the Kanin Peninsula in western Russia, across northern Siberia to Alaska, northern Canada and Greenland. Ecologically, the North American and Eurasian species are alike and they exhibit similar adaptations for life in extreme northern climates (Stenseth and Ims, 1993). These specializations include the ability to grow white pelage in winter and greatly enlarged claws of the forefoot, enabling them to claw through compacted snow. The various species of *Dicrostonyx* also occupy a similar range of high-arctic habitats, with preference for dry slopes and river valleys with patchy vegetation; marshy areas and woodland are avoided. As winter approaches they congregate in places with early snow cover, such as hill slopes and dry river banks, where they overwinter in burrows under the snow. In summer their runways extend through grass tussocks and thickets of birch and willow; they also dig underground burrows above the permafrost. Winter food consists of twigs and bark of birch and willow; in summer, grasses, sedges, berries and leaves of dwarf trees are the main food sources.

In Europe, several Pleistocene *Dicrostonyx* species have been described. A succession of chronospecies – Middle Pleistocene *D. simplicior*, Late Pleistocene *D. gulielmi* and the modern *D. torquatus* – has been established using morphological characters of the teeth, notably an increase in the complexity of the molar occlusal pattern (Nadachowski, 1982). The relatively simple form of the M² from Stratum C falls within the range of morphotypes that characterize '*D. simplicior*'. Although the specific identity of Middle and Late Pleistocene *Dicrostonyx* is debated (Ponomarev and Andreicheva, 2019), it appears that the specialized ecology and habitat requirements of *Dicrostonyx* can be traced at least as far back as the early Middle Pleistocene. For the Late Pleistocene, this is illustrated by ancient DNA analyses of AMS-dated collared lemmings from Belgium and South West England (Brace et al. 2012). This study shows that collared lemmings in western Europe were acutely sensitive to climatic instability, particularly short-term climatic warming events, which resulted in population declines and local extinctions. During ecologically challenging periods, lemming ranges contracted to refugial areas, from which they recolonized areas of their former range when favourable conditions returned (Palkopoulou et al., 2016).

A particularly informative ecological record associated with Middle Pleistocene *Dicrostonyx* comes from the early Anglian (MIS 12) 'Arctic Fresh-water Bed' at Ostend, Norfolk (Parfitt et al., 2010). Here, the biota suggests a distinctly high boreal/arctic environment and an open landscape with occasional dwarf shrubs and conifers. The associated beetle fauna includes at least two species that currently have their closest occurrences on either the Kola or Kanin peninsulas in arctic Russia. Palaeotemperature reconstructions (MCR) on the Ostend beetle fauna suggest that the mean July air temperature lay somewhere between +9 °C and +11 °C, and mean January air temperature between –36 °C and –10 °C. The associated ostracod assemblage yielded consistent MOTR results with mean July and January air temperatures between +10 °C and +13 °C and between –21 °C and –20 °C, respectively, a possible modern climate analogue region being the Bolshezemelskaya Tundra in the northeastern European Russian Arctic (Horne et al., 2012). Elsewhere in the British Pleistocene, arctic lemmings are invariably associated with faunal or palaeobotanical evidence for tundra or steppe-tundra conditions (Sutcliffe and Kowalski, 1976).

7. Full taxonomic names of species found at Hoxne and mentioned in the text, tables, figures and Supplementary Material

Chironomidae

Chironomus anthracinus Zetterstedt 1860-type

Chironomus 1st instar larva

Chironomus plumosus (Linnaeus 1758)-type

Cladatanytarsus mancus (Walker 1856)-type

Cladopelma lateralis (Goetghebuer 1934)-type

Corynocera ambigua Zetterstedt 1838

Cricotopus bicinctus (Meigen, 1818)-type

Cricotopus laricomalis Edwards 1932-type

Cricotopus oliveri Soptonis 1977-type

Eukiefferiella claripennis (Lundbeck 1898)-type

Dicrotendipes notatus (Meigen, 1818)-type

Endochironomus impar (Walker, 1856)-type

Endochironomus albipennis (Meigen, 1830)-type

Glyptotendipes pallens (Meigen 1804)-type

Glyptotendipes severini Goetghebuer, 1923-type

Limnophyes

Metriocnemus eurynotus (Holmgren, 1883)-type

Metriocnemus hygropetricus (Kieffer, 1911)-type

Microtendipes pedellus (De Geer, 1776)-type

Monodiamesa

Nanocladius branchicolus Saether, 1977-type
Parachironomus varus (Goetghebuer, 1921)-type
Paracladius conversus (Walker, 1856)-type
Paracladopelma nais (Townes, 1945)-type
Parakiefferiella bathophila (Kieffer, 1912)-type
Paratanytarsus penicillatus (Goetghebuer, 1928)-type
Paratendipes albimanus (Meigen, 1919)-type
Phaenopsectra flavipes (Meigen, 1818)-type
Polypedilum nubeculosum (Meigen, 1804)-type
Polypedilum pedestre (Meigen, 1830)-type
Procladius
Prosilocerus jacuticus (Zvereva, 1950)-type
Psectrocladius (Allopsectrocladius) flavus (Johannsen, 1905)-type
Psectrocladius (Mesopsectrocladius) barbatipes Kieffer 1923-type
Psectrocladius (Monopsectrocladius) septentrionalis Chernovskij, 1949-type
Psectrocladius (Psectrocladius) sordidellus (Zetterstedt, 1838)-type
Pseudochironomus prasinus Meigen, 1818-type
Pseudodiamesa
Pseudosmittia
Sergentia coracina (Zetterstedt, 1850)-type
Smittia
Stempellina bausei (Kieffer, 1911)-type
Stempelinella - Zavrelia
Stictochironomus rosenschoeldi (Zetterstedt, 1838)-type
Tanytarsus lugens (Kieffer in Thienemann & Kieffer, 1916)-type
Tanytarsus mendax Kieffer, 1925-type
Tanytarsus pallidicornis (Stephens in Walker, 1856)-type

Coleoptera

Agonum chalconatum Faldermann, 1836
Bembidion guttula (Fabricius, 1792)
Bembidion hasti Sahlberg, 1827
Bembidion mckinleyi Fall, 1926
Boreaphilus hennigianus Sahlberg, 1832
Colymbetes dolabratus (Paykull, 1798)
Colymbetes fuscus (Linnaeus, 1758)
Diacheila polita (Faldermann, 1835)
Donacia aquatica (Linnaeus, 1758)
Donacia cinerea Herbst, 1784
Donacia semicuprea Panzer, 1796
Donacia thalassina Germar, 1811
Helophorus obscurellus Poppius, 1907
Hippodamia arctica Schneider, 1792
Holoboreaphilus nordenskiöldi (Mäklin, 1878)
Notaris aethiops (Fabricius, 1792)
Olophrum boreale (Paykull, 1792)
Oreodytes alpinus (Paykull, 1798)
Plateumaris affinis (Kunze, 1818)
Pycnoglypta lurida (Gyllenhal, 1813)
Simplocaria metallica (Sturm, 1807)
Stenoscelis submuricatus (Schönherr, 1832)
Tachinus caelatus Ullrich, 1975
Xestobium rufovillosum (De Geer, 1774)

Ostracoda

Candona candida (O.F. Müller, 1776)
Candona neglecta Sars, 1887
Cyclocypris sp.
Cyclocypris obunca Fuhrmann, 1991
Cyclocypris ovum (Jurine, 1820)
Cypridopsis vidua (O.F. Müller, 1776)
Cytherissa lacustris (Sars, 1863)
Darwinula stevensoni (Brady & Robertson, 1870)
Fabaeformiscandona levanderi (Hirschmann, 1912)
Fabaeformiscandona protzi (Hartwig, 1898)
Herpetocypris reptans (Baird, 1835)
Ilyocypros spp.
Ilyocypris bradyi Sars, 1890
Ilyocypris decipiens Masi, 1905
Ilyocypris gibba (Ramdohr, 1808)
**Ilyocypris quinculminata* Sylvester-Bradley, 1973
Leucocythere batesi Whittaker & Horne, 2009
Limnocythere falcata Diebel, 1968
Limnocythere suessenbornensis Diebel, 1968
syn. *Limnocythere friabilis* Benson & McDonald, 1963
Limnocytherina sanctipatricii (Brady & Robertson, 1869)
Metacypris cordata Brady & Robertson, 1870
Paralimnocythere compressa (Brady & Norman, 1889)
Pseudocandona sp.
Scottia browniana (Jones, 1850)

Mollusca

Ancylus fluviatilis Müller, 1774
Anisus leucostoma (Millet, 1813)
Bathyomphalus contortus (Linnaeus, 1758)
Bithynia tentaculata (Linnaeus, 1758)
Galba truncatula (Müller, 1774)
Gyraulus crista (Linnaeus, 1758)
Gyraulus laevis (Alder, 1838)
Hippeutis complanatus (Linnaeus, 1758)
Lymnaea stagnalis (Linnaeus, 1758)
Myxas glutinosa (Müller, 1774)
Pisidium spp
Pisidium amnicum (Müller, 1774)
Pisidium casertanum (Poli, 1791)
Pisidium clessini Neumayr, 1875
Pisidium henslowanum (Sheppard, 1825)
Pisidium milium Held, 1836
Pisidium moitessierianum Jenyns, 1832
Pisidium nitidum Jenyns, 1832
Pisidium obtusale (Lamarck, 1818)
Pisidium subtruncatum Malm, 1855
Pisidium tenuilineatum Stelfox, 1918
Planorbis planorbis (Linnaeus, 1758)
Radix balthica (Linnaeus, 1758)
Sphaerium corneum (Linnaeus, 1758)
Stagnicola palustris agg. (Müller, 1774)
Valvata cristata Müller, 1774
Valvata piscinalis (Müller, 1774)

Pisces

Alburnus alburnus (Linnaeus, 1758)
Esox lucius Linnaeus, 1758
Phoxinus phoxinus (Linnaeus, 1758)
Pungitius pungitius (Linnaeus, 1758)
Perca fluviatilis Linnaeus, 1758
Gymnocephalus cerna (Linnaeus, 1758)

Mammalia

Dicrostonyx sp.

Plantae

Azolla filiculoides Lamarck, 1783
Betula nana Linnaeus & Klase, 1743
Ceratophyllum demersum Linnaeus, 1753
Hedera helix Linnaeus, 1753
Ilex aquifolium (Linnaeus, 1753)
Miriophyllum spicatum Linnaeus, 1753
Sanguisorba officinalis Linnaeus, 1753
Typha latifolia Linnaeus, 1753

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