

## Combining the Mg/Ca of the ostracod *Cyprideis torosa* with its ontogenic development for reconstructing a 28 kyr temperature record for Lake Banyoles (NE Spain)

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**Abstract:** *Cyprideis torosa* is a ubiquitous ostracod found in fresh to hypersaline waters, and commonly in large numbers across the Mediterranean region. Single valves of 51 adult specimens of *C. torosa* were separated from carapaces that were collected from Lake Banyoles in NE Spain at a depth of 5 m. The Mg/Ca of the valves was compared with known temperatures necessary for successive instar valve calcification, the latter being based on a four-year ecological study of *C. torosa* collected at Dievengat in northern Belgium by Carlo Heip in 1968–72. Hence, we were able to link the Mg/Ca of fossil valves of *C. torosa* recovered for a 28 kyr sequence at La Draga, cored on the fringe of Lake Banyoles, with the ontogenic observations of Heip, and reconstruct mean summer temperatures as well as optimal calcification temperature for *C. torosa*. Principal findings are: (1) the Holocene registered the highest temperatures with also very broad fluctuations; (2) three cold phases are clearly identified at 26.7–23.2, 21.6–20.3 and 16.2–14.3 ka BP; and (3) a prolonged warm phase that lasted about two millennia commenced at 19.5 ka BP and was followed by a progressive temperature decline well over three millennia. Surprisingly the Last Glacial Maximum was not the coldest phase. We finally compare our results with sea-surface temperature (SST) reconstructions from cores from the western Mediterranean Sea. Our record from La Draga clearly matches events recorded in the Alboran Sea that display SST changes obtained from the  $U^{K}_{37}$  index. The Heinrich 1 and 2 events around 16 and 28 ka BP coincide with significant low temperature excursions at Banyoles, and palynological records in the marine cores which define semi-arid conditions on land match the low temperature record in our core.

**Keywords:** ostracod valve chemistry; optimal growth; moulting temperature; Late Quaternary; Last Glacial Maximum; water temperature reconstructions; land–sea correlation

**Supplementary material:** Observational and chemical analysis data for *Cyprideis torosa* valves from the La Draga sequence are available at: <https://doi.org/10.6084/m9.figshare.c.2133543>

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*Cyprideis torosa* (Jones, 1850) is a ubiquitous ostracod found today in fresh to hypersaline waters from the Holarctic in Europe (Elofson 1941) to Africa (Wouters 2002), and is especially abundant, and in large numbers in many lakes in the Mediterranean region. It can tolerate a broad range of salinities (up to <1–60‰ S, De Deckker 1981) and is, therefore, labelled a euryhaline species which usually inhabits waters with a Na<sup>+</sup> and Cl<sup>-</sup> ionic dominance, even in fresh waters (namely <0.5‰ S) and in low alkalinity/Ca proportions (Marco-Barba *et al.* 2012; Reed *et al.* 2012). Consequently, it is commonly found in estuaries which display such ionic dominance. In some estuaries and brackish lakes it can be found in huge numbers (see discussion below on the Dievengat locality in Belgium), with similar densities recorded in several lakes in the Camargue, notably the Etang de Galabert (see De Deckker *et al.* 1988). *Cyprideis torosa*, being usually well calcified, is also found in large numbers (up to 12 000 valves per ml of sediment) in fossil lacustrine sequences, such as the early Pleistocene Baza Basin in southern Spain (Anadon *et al.* 1986, 1987; Anadon & Julià 1990), the Miocene of the Mediterranean Sea and, in particular, the Messinian salinity crisis during which *C. torosa* valves clearly identified a lacustrine system based on ostracod shell chemistry (De Deckker *et al.* 1988; McCulloch & De Deckker 1989). Marco-Barba *et al.*'s (2012) comprehensive study of some 20 water bodies near Valencia in Spain established partition coefficients (for trace metal ratios Mg/Ca and Sr/Ca) and vital effects (for stable isotopes

of carbon ( $\delta^{13}C$ ) and oxygen ( $\delta^{18}O$ )) for *C. torosa* (but see discussion below).

In this paper, we report on chemical analyses of living *Cyprideis torosa* specimens collected from a lake in northern Spain and relate the Mg/Ca of single ostracod valves, combined with knowledge of the life cycle of its species and the lake's seasonal temperature ranges in order to determine the relationship of valve Mg/Ca with ambient water temperature. In the second part of the paper, we apply our findings on the modern material on fossil specimens to reconstruct past lake temperatures. Finally, we will compare our new temperature reconstructions with modern analogues of pollen data determined from the same site and also with sea-surface temperatures (SST) from the western Mediterranean Sea.

### Background

#### *Heip's (1976) ecological investigations on C. torosa*

Critical to our study are the important ecological observations of Heip (1976) who studied the life cycle of *Cyprideis torosa* in the brackish pond called Dievengat in northern Belgium. Heip's (1976) investigations spanned a period of four years during which ostracods were collected fortnightly from August 1968 to December 1972, with a break in collecting from August to November 1969. Several physico-chemical parameters were also



**Fig. 1.** Satellite image of Lake Banyoles and environs taken from Google Earth®. The cross denotes the location of the site of the La Draga core. Note the presence of significant housing near the core site that did not exist when the cores were taken in 1991.

measured and, of relevance here, ambient temperatures were continuously recorded at Dievengat. Individuals of the eight larval stages and adult males and females were counted. Results showed that peak abundance of adults occurred once annually, with the exception of a secondary peak in February 1969. Adult percentages varied between 10 and 40% throughout the year, and the number of instars and adults varied between 20 000 and 40 000 individuals (including adults) per m<sup>2</sup>, with much variation between years. The highest concentration ( $1.8 \times 10^6$  individuals per m<sup>2</sup>) was counted on 4 August 1971. Of interest too was that among those collections were  $328 \times 10^3$  adults found once. Heip (1976) concluded that water temperature had the most pronounced influence on the life cycle of *C. torosa*. He also found that juveniles (from the egg stage to the first three instar stages) were released after internal brooding into the pond at 7.3°C. More importantly, a temperature above 9.3°C was required for reaching adulthood, and moulting from instar stage 4 to stage 5 required the highest temperature (16.3°C) during ontogenic development.

### Material and methods

Three cores were drilled at the La Draga locality some 50 m from the shore of the present Lake Banyoles (Fig. 1). The coring equipment consisted of a steel tube, with a smaller PVC one located inside it,

pushed and linked to a metal derrick. A percussion-type motor was used to push the tubes through the sedimentary pile. These cores were taken 'on land' to facilitate recovery of sediments which would otherwise have been difficult to obtain due to the great depth of the lake. The site was also chosen for its proximity to an archaeological site found in the peat near the surface at the coring site. In any case, the shore area that was cored relates to lacustrine phases. It is accepted that prior to anthropogenic activities (i.e. water extraction and irrigation in the catchment of the lake) the water level was much higher.

The age model for the La Draga sequence relies on two <sup>14</sup>C dates from peat and on nine U/Th dates obtained from bulk sediment material lower in the sequence. Discussion on the veracity of the U/Th dates is presented in Pérez-Obiol & Julià (1994; see table 1).

Each sediment sample was immersed in a 10% H<sub>2</sub>O<sub>2</sub> solution for 6 to a maximum of 24 hours and then washed with water over sieves of 1 mm, 500 µm and 200 µm mesh sizes. Ostracod valves were then picked under a binocular microscope, selected valves were then cleaned individually in tri-distilled water using a fine brush to remove adhering particles and then dried on a paper filter.

Single ostracod valves were analysed by a Spectrometrics Plasma Emission Spectrometer (DCP) at the Université catholique de Louvain-la-Neuve, after dissolution in ultrapure HNO<sub>3</sub> combined with ultrapure LiNO<sub>3</sub>. Additional information on analytical procedures and use of standards etc. is available in Wansard (1995, unpublished thesis, Université catholique de Louvain). All results here are presented in molar ratios.

### Lake Banyoles

Lake Banyoles is located about 25 km west of the Mediterranean Sea and lies at an altitude of 173 m above sea-level. It is a karstic lake, principally fed by groundwater that forms part of a large aquifer (Canals *et al.* 1990). This lacustrine system has been in place since the Pliocene. Bischoff *et al.* (1994) determined that the water chemical composition of the lake directly results from water–rock interactions driven by dedolomitization and, since the residence time of the lake is rather short, water ionic composition and concentration should remain constant over time. Principal ionic composition is as follows: Ca<sup>2+</sup> > Mg<sup>2+</sup> > Na<sup>+</sup> and SO<sub>4</sub><sup>2-</sup> > HCO<sub>3</sub><sup>-</sup> > Cl<sup>-</sup>, resulting from the fact that underlying lithologies that are dissolved by the karstic processes primarily consist of gypsum. The water of Lake Banyoles today is fresh, with total dissolved solids (TDS) ranging between 827 and 1097 mg l<sup>-1</sup> at different depths as measured in March 1991 (Bischoff *et al.* 1994). Annual rainfall in the Lake Banyoles region is c. 750 mm and the warmest months are July and August, with a mean temperature of 23°C.

### *Cyprideis torosa* in Lake Banyoles

Heip's (1976) remarkable work proved applicable to *C. torosa* found in Lake Banyoles. For example, in 1993, 51 adult individuals of *C. torosa* were collected with a grab sampler from a depth of 5 m at various locations in Lake Banyoles. The Mg/Ca of single valves gave a range between 0.00312 and 0.01388 (see Wansard *et al.* 1998). The Mg/Ca of Lake Banyoles water is considered to be constant (see the study of the nature of water–rock interactions that give rise to karstification at Lake Banyoles by Bischoff *et al.* (1994)) because it is part of a flow-through lake system with a residence time of 1 year and 16 days. This fact, combined with previous data for this lake that registered a supply via the aquifer of  $18.4 \times 10^6$  m<sup>3</sup>, with a surface supply of  $6 \times 10^6$  m<sup>3</sup> and an effluent of  $24.4 \times 10^6$  m<sup>3</sup> and estimated evaporation of  $1.1 \times 10^6$  m<sup>3</sup> (Planas 1973; Wansard 1995, unpublished thesis, Université catholique de Louvain), means that the water temperature is considered to have been the principal control on the Mg/Ca of ostracod valves.

There are three significant relationships between water temperature and the Mg/Ca (atomic ratio) of the ostracods already discussed by Wansard (1997).

1. The minimum Mg/Ca value of adult *C. torosa* was 0.00312. In our analyses of 948 fossil valves from in the La Draga core, only four valves had values <0.00312, indicating that Heip's associated minimum adult moult temperature of 9.3°C is robust.
2. The recorded maximum Mg/Ca of *C. torosa* (0.01128) is linked to the maximum water temperature recorded at a depth of 5 m in Lake Banyoles, which today is 25.4°C (see Planas 1973).
3. The mean Mg/Ca relates to the mean water temperature (17.5°C) registered today at Lake Banyoles during spring and autumn (Planas 1973). Such a temperature signal clearly relates to the same seasons recognized at Dievengat by Heip (1976) when *C. torosa* reaches adulthood.

## Results

### *La Draga core*

The three cores sampled at the Draga locality are located about 50 m from the shore of the present lake (Fig. 1). These cores comprise a continuous sequence of up to 33.1 m and sediment analysis confirms that the sequence consists of two main facies. The first one, at the top, is 0.5 m thick and consists of peat; the second one, comprising the rest of the core, consists of carbonate (98% low-Mg calcite of the total weight) with minor clays, feldspars and quartz. The latter (lower) sediments indicate a quiet, littoral facies without transported material. Details of the stratigraphy of the cores are provided in Wansard (1997).

The age model for the sequence relies on two <sup>14</sup>C dates of the surficial peat and on nine U/Th dates obtained from older bulk sediment. Discussion on the veracity of the U/Th dates is presented in Pérez-Obiol & Julià (1994). Overall, the ages confirm that the La Draga sequence is continuous and of high resolution, being *c.* 1 mm per year, with no evidence of subaerial exposure based on examination of the sediment, which thus confirms that the carbonates remained essentially closed to any secondary movement of uranium (Pérez-Obiol & Julià 1994).

### *The Mg/Ca of Cyprideis torosa in Lake Banyoles*

#### *Modern-day data*

Wansard (1996a, b), using 51 living adult valves of *C. torosa* that were collected at various locations in the present-day lake at a depth of 5 m, calculated the following relationship for use in temperature reconstructions (Fig. 2b):

$$T[^\circ\text{C}] = 3.3 + 1971(\text{Mg/Ca})_{C.torosa} \quad (1)$$

Figure 2a exemplifies the three relationships, (1), (2) and (3), that exist between the Mg/Ca of the 51 adult valves and ambient water temperature data obtained by Planas (1973) under which the ostracods calcified. The frequency histograms (Fig. 2a, left) of Mg/Ca point to a mean Mg/Ca value that corresponds to two abundance maxima of calcifying adults of *C. torosa* (seen in the upper shaded plots) following Heip's (1976) data. The 'mean Mg/Ca + 2σ' standard deviation relates to the mean summer temperature during which the ostracods would have calcified. This approach was used to interpret the record obtained for *C. torosa* analyses throughout the core (see discussion below).

### *Temperature reconstructions for the La Draga core samples*

Our study determined the range of Mg/Ca of 948 adult *Cyprideis torosa* valves at 213 levels throughout the core (Fig. 3; these data can be found as Supplementary Material to this paper). It is estimated that, on average, one level represents 20 years of sedimentation, with a mean resolution of a century. Following the relationships established above for the modern system, mean Mg/Ca values represent the mean water temperature for spring and autumn. Under the coldest conditions, only summer temperatures may have been suitable for calcification. Therefore, calculated temperatures using the mean Mg/Ca + 2σ would represent the mean summer temperature (see Fig. 2a).

It should be noted that the mean (Mg/Ca)<sub>*C. torosa*</sub> values for each horizon are displayed by a thin continuous line on the right-hand side of Figure 3. In addition, several horizons were eliminated from the plot due to the paucity of available valves for analysis that would not have provided a suitable/reliable mean Mg/Ca value.

## Discussion

### *The Cyprideis torosa story at La Draga*

The summer temperature reconstruction displays much fluctuation through time, with the highest temperature reconstructions recorded during the Holocene (defined here from 12 to 6.6 ka). However, we do not discuss these in great detail as sampling resolution for that period is too low. Another period of significantly high temperature peaks (but lower than those for the Holocene) spans the interval between 19.2 and 17.7 ka BP. Again, moderately high temperature peaks are seen for the period spanning 23.2–21.5 ka BP. Once more, at 27.5 ka BP, a high summer temperature was recorded.

The most salient coldest periods occurred between 16.2 and 14.4 ka BP with a later brief cold excursion at 13 ka BP. Of note also is that for the period between 21.4 and 20.5 ka BP, colder summer temperatures were encountered, with the lowest temperature drop for that period registered at 21.4 ka BP. Three previous cold excursions were also registered at 27.8, 26.2 and 23.5 ka BP. The exception was the coldest temperature (11.8°C) that was recorded for the entire sequence occurred at 26.2 ka BP, with adjacent levels showing a progressive drop in temperature (only one older level) and a progressive increase (younger levels) after 26.2 ka BP.

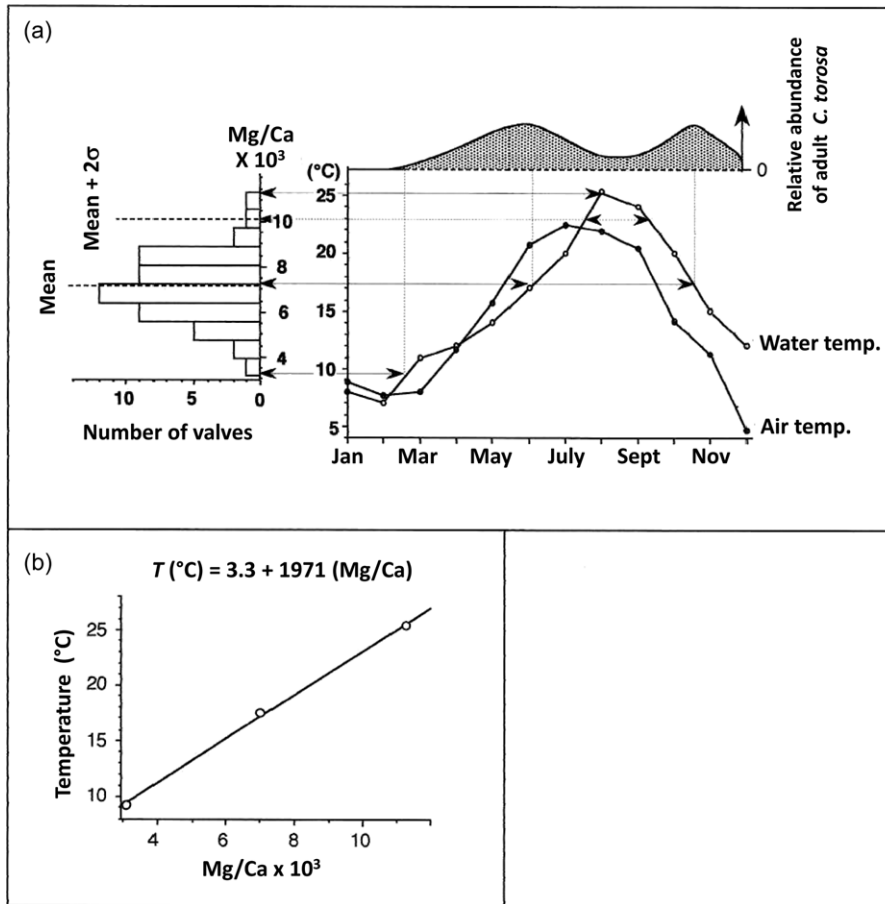
For the period spanning 20.5–16.2 ka BP, broad temperature shifts were witnessed, frequently covering up to 8°C for the summer months.

The lowest summer temperatures recorded for the period between 16.2 and 14.4 ka BP displayed only minor fluctuations, of the order of less than 4°C.

Seven horizons were selected throughout the core to show the various steps in temperature shifts through time. These are presented on the left-hand side of Figure 3 and are discussed below (older to younger in the sequence):

*28.1–26.7 ka BP (31.95–30.35 m)*: this period is the most difficult one to interpret because there were too few valves available for analysis. In addition, the range of Mg/Ca is atypical with a shift towards the lowest Mg/Ca values. Thus, the annual range of lake temperatures for that interval did not go above 17.3°C (having excluded the single valve with the highest Mg/Ca value of 0.00825).

*26.7–23.2 ka BP (30.15–26.15 m)*: for this period, the range of Mg/Ca values is more restrained compared to the present day, with Mg/Ca failing to reach 0.007. The calcification temperatures were, therefore, much lower and the mean optimal calcification temperature was 12.7°C, being close to



**Fig. 2.** (a) Graphic representation that exemplifies the three relationships (1–3) that exist between the Mg/Ca of the 51 adult valves collected at a depth of 5 m in Lake Banyoles and ambient water temperature data obtained by Planas (1973) in the lake under which the ostracods calcified. The frequency histograms (left) of Mg/Ca point to a mean Mg/Ca value that we link to two maxima of abundance of calcifying adults of *C. torosa* (seen in the upper shaded plots) following Heip's (1976) ontogenetic work. For further details, refer to the text. (b) Plot showing the relationship between water temperature and the Mg/Ca of *C. torosa*. The three temperatures represent the minimum, optimal and maximum values for valve calcification. The optimal temperature is linked to the mean value of Mg/Ca for the 51 modern *C. torosa* valves. The mean Mg/Ca + 2σ value corresponds to the mean summer temperature at Banyoles.

the mean summer temperature (15°C). It is during this period that Mg/Ca values were the lowest.

20.3–19.2 ka BP (22.65–21.1 m): this period is very similar to the one discussed above, but the mean optimal calcification temperature and that of the summer temperature were slightly higher (15.7°C and 20.4°C, respectively).

18.4–17.7 ka BP (19.55–18.25 m): we recognize a range of Mg/Ca similar to that for the 26.7–23.2 ka BP period which indicates that summers were warmer than for the period discussed below (but 3.3°C lower than today). Optimal calcification temperature was 15.3°C and occurred during spring and autumn.

16.2–15.8 ka BP (12.45–10.85 m): the range of Mg/Ca values is more limited compared to the present day, with Mg/Ca failing to reach 0.007. The calcification temperatures were, therefore, much lower and the optimal calcification temperature was 12.7°C, being close to the mean annual summer temperature (15°C).

11.6–9.7 ka BP (6.2–5.0 m): this period displays a temperature spectrum that closely mimics present-day conditions (see Fig. 2).

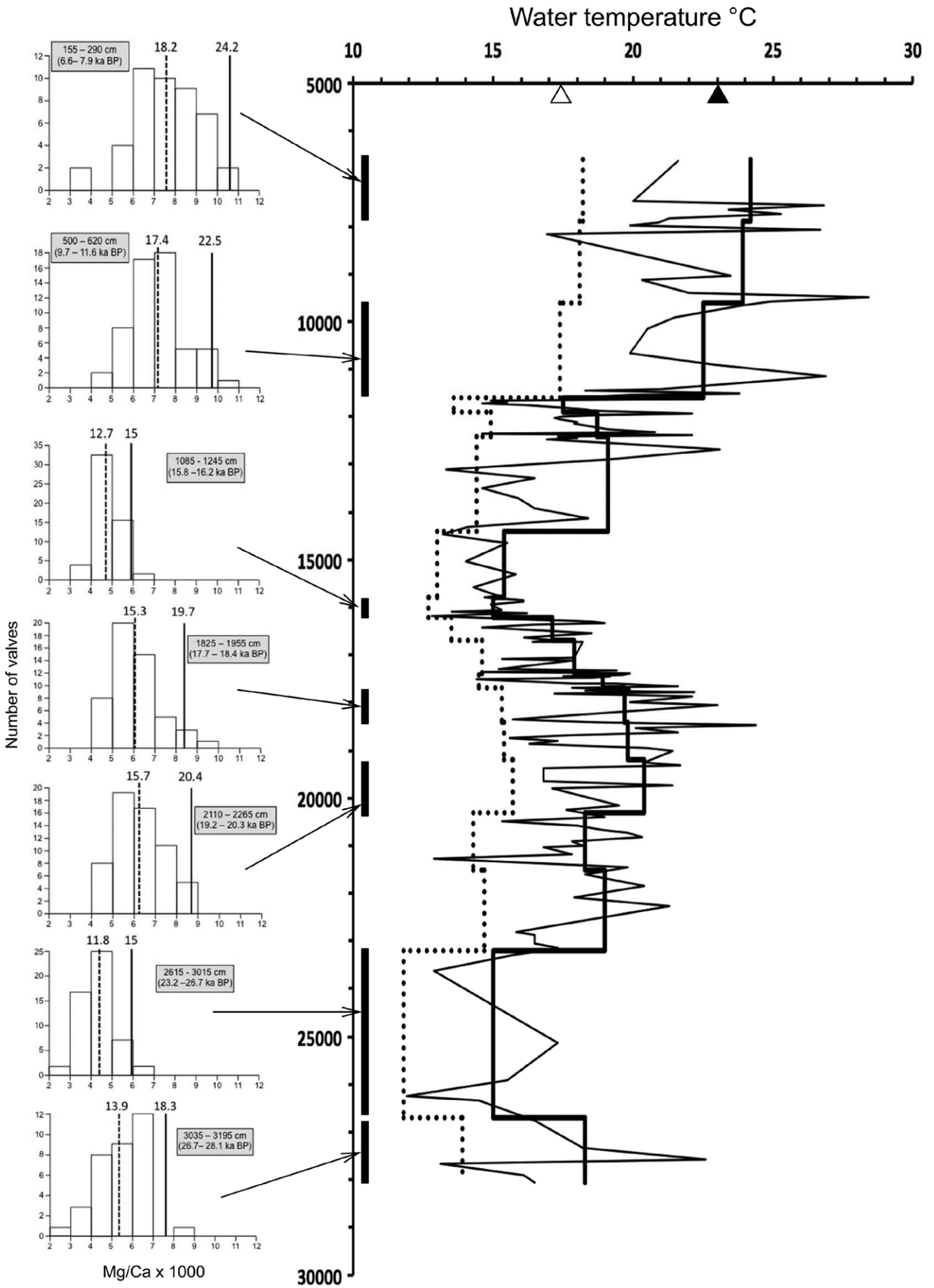
7.9–6.6 ka BP (2.9–1.55 m): the distribution of Mg/Ca values is broad and is comparable with what is found in the lake today (see Fig. 2). The shape of the distribution curve suggests adult moults occurred throughout the spring, summer and autumn, with maximum adult moults occurring at 18.2°C (a value similar to spring today).

### Comparison with the La Draga pollen record

Pérez-Obiol & Julià (1994) examined the pollen spectra from the same horizons from the La Draga core as those examined by Wansard in his thesis (1995) and resulting papers (Wansard 1996a,b, 1997). Pérez-Obiol & Julià (1994) interpreted cold-dry steppe conditions in intervals with low arboreal/non-arboreal ratio (AP/NAP) due chiefly to relatively high concentrations of *Artemisia* and *Chenopodiaceae* pollen centred on four periods peaking around 26, 17, 15 and 13 ka BP. Apart from the 17 ka BP peak, all other periods coincide with the low lake temperatures reconstructed from ostracod Mg/Ca. In addition, one should note the sharp temperature drop around 21.3 ka BP, which nevertheless occurs when steppe conditions are found.

It is important to recognize that the AP/NAP ratio is critical to our understanding of the vegetation changes registered near Lake Banyoles (via the La Draga core site that must have been under water when Lake Banyoles was larger, as was the case for the last 28 kyr, except when the Holocene peat was deposited). However, the presence of *Pinus* pollen that is ubiquitous in the core needs to be discounted as its occurrence is either allochthonous (originating from vegetation at lower altitudes; Pérez-Obiol & Julià 1994) or over-represented due to the high pollen productivity so typical of most *Pinus* trees.

**Fig. 3.** Left: histograms representing seven selected periods of time recognized in the La Draga sequence which not only display the range of Mg/Ca values per number of *C. torosa* valves, but also the reconstructed mean summer temperature (continuous vertical lines) and optimal temperature of calcification for *C. torosa* (dotted vertical lines). Right: temperature record (thin continuous line) for the last 28 kyr based on mean Mg/Ca of valves for the 213 levels using the  $[T (°C) = 3.3 + 1971 (Mg/Ca)_{C. torosa}]$  relationship. In addition, mean summer temperature reconstructions (thick black line) as well as optimal temperature for ostracod calcification (dotted line) are displayed along numerous steps. In total, eighteen steps are portrayed but only seven of these are shown on the left of the diagram; these are the most significant ones. For further details refer to the text. The black triangle at the top points to the actual summer temperature recorded in Lake Banyoles and the open triangle to the optimal temperature of calcification for adult valves.



### **The Mg/Ca in *Cyprideis torosa*: a suitable record of ambient temperature during calcification**

Our record presented above clearly signals that the Mg/Ca values of *C. torosa* valves are linked to past lake temperatures, especially since it is accepted that the Mg/Ca of the lake over time would not have changed, since it is a karstic lake (with water supersaturated in CaCO<sub>3</sub>) and a flow-through system. This may be surprising initially when reading the work of Marco-Barba *et al.* (2012), who analysed live *C. torosa* specimens from 20 different water bodies near Valencia in Spain, and came to the conclusion (p. 160) that ‘no effects of either temperature or water Mg/Ca are observed on the Mg/Ca assimilation in the ostracode *C. torosa* (calcite) in waters with Mg/Ca < 6 (molar ratio)’. This is in contrast with Wansard *et al.* (1998), who analysed 107 individual (live) specimens of *C. torosa* from Lake Banyoles and concluded that the water temperature must be responsible for the large range of Mg/Ca values at Lake Banyoles which has a low Mg/Ca molar ratio (0.652 obtained in 1991 by Bischoff *et al.* (1994)). In addition, De Deckker *et al.* (1999) who cultured *in vitro* a different species of *Cyprideis* (*C. australiensis*) under different water chemical conditions and again returned a positive correlation for the uptake of Mg in ostracod valves in low molar Mg/Ca concentrations. Thus, the discrepancy with Marco-Barba *et al.* (2012)’s conclusion remains unresolved, especially since our lake temperature record matches SST records from cores obtained in the western Mediterranean Sea (see below).

### **Comparison with marine records from the Western Mediterranean**

Two important deep-sea cores obtained from the Mediterranean Sea, MD95-2043 (36° 8.6' N, 2° 37.3' W; Cacho *et al.* 2001, 2002) and ODP site 976 (36°12' N, 4° 18' W; Combourieu Nebout *et al.* 2002), both in the Alboran Sea, have a continuous SST record obtained from the relative abundance of C<sub>37</sub> unsaturated alkenones through the U<sup>K</sup><sub>37</sub> index (Brassel *et al.* 1986). Although both cores are located quite some distance away (c. 1000 km, almost directly south from the La Draga core site), similar events spanning the glaciation and deglaciation periods are evident. In particular, Heinrich 1 and 2 events are clearly registered in the two marine cores around 16 and 24 ka BP, respectively, and these coincide with significant low temperature excursions in the La Draga core. In addition, the low temperature drop around 12 ka BP in the MD95-2043 core, which coincides with the GS-1 GRIP ice core (see Cacho *et al.* 2001, 2002; Martrat *et al.* 2004), parallels the drop in lake temperatures at La Draga (Fig. 3). The palynological investigations of Fletcher & Sánchez Goñi (2008) in core MD95-2043, which define significant peaks of *Artemisia*, in combination with Chenopodiaceae, signifying particular semi-arid conditions on land, coincide with the periods listed above for low SSTs in both marine cores and lake temperature for the La Draga sequence. As a consequence, we confirm that the lake’s low temperature records coincide with drops in SST and semi-arid conditions on the Iberian Peninsula. These correlations thus provide confidence that our local lake temperature reconstructions for the La Draga sequence also reflect major regional phenomena – at least for the eastern side of the Iberian Peninsula and the western Mediterranean Sea.

### **Conclusions**

The combination of Mg/Ca analyses of *C. torosa* recovered from the La Draga sequence and knowledge of optimal conditions for ontogenic development of the ostracods has allowed us to reconstruct lake temperature fluctuations over the last 28 kyr. Comparison of our temperature record with the pollen spectra

obtained from the same levels in the La Draga core sequence confirms that lake temperature drops are synchronous with arid conditions. In addition, for the first time it is possible to provide a lake temperature record for direct comparison with SST conditions in the western Mediterranean Sea. Our record clearly matches most of the marine records. Therefore, this gives us confidence that the use of Mg/Ca analyses of ostracod valves, combined with known ontogenic development of these microcrustaceans that secrete low-Mg calcite valves, is well worth pursuing.

We need to stress that because Lake Banyoles is a karstic lake with a rapid flow-through system with a short residence time, it provides a very suitable record of past environmental changes and, in particular, temperature, at a regional scale. Hence, the search for similar lacustrine systems ought to be recognized for high quality and high resolution palaeoenvironmental reconstructions.

In addition, we believe also that, since there are several other European ostracod species with well-documented life cycles, similar studies such as the one presented here could be applied to reconstruct past lacustrine temperatures. Similarly, many of the Tertiary and Quaternary profiles that yield *C. torosa* valves could be re-examined to provide palaeotemperature reconstructions for comparison with the marine record.

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