Ostracods as ecological and isotopic indicators of lake water salinity changes: The Lake Van example

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Abstract.

Ostracods are common lacustrine calcitic microfossils. Their faunal assemblage and morphological characteristics are important ecological proxies, while their valves are archives of geochemical information related to palaeoclimatic and palaeohydrological changes. In an attempt to assess ostracod ecology (taxonomic diversity and valve morphology) combined with valve geochemistry (δ¹⁸O and δ¹³C) as palaeosalinity indicators, we analysed material from terminal and alkaline Lake Van (Turkey) covering the last 150 kyr. Despite a low species diversity, the ostracod faunal assemblage reacted sensitive to changes in the concentration of total dissolved salts in their aquatic environment. *Limnocythere inopinata* is present throughout the studied interval, while *Limnocythere* sp. A is restricted to the Last Glacial period and related to increased lake water salinity and alkalinity. The presence of species belonging to the genus *Candona* is limited to periods of lower salinity. Valves of limnocytherinæ species (incl. *L. inopinata*) display nodes (hollow protrusions) during intervals of increased salinity. Both the amount of noded valves and the number of nodes per valve appear to increase with rising salinity, suggesting that node formation is related to hydrological changes (salinity and/or alkalinity). In contrast to Lake Van’s inorganic δ¹⁸O record, the δ¹⁸O values of ostracod valves do record relative changes of the lake volume, with lower values during high lake level periods. The δ¹³C values of different species reflect ostracod habitat preferences (i.e., infaunal versus epifaunal) but are less sensitive to hydrological changes. However, combined with other proxies, decreasing Holocene δ¹³C values may indicate a freshening of the lake water compared to the low lake level during the Last Glacial period. The Lake Van example underscores the significance and value of coupling ostracod ecology and valve geochemistry in palaeoenvironmental studies of endorheic lakes basins.

1. Introduction

The water volume of closed lakes (endorheic basins) in arid and semi-arid regions reacts particularly sensitive to climatically induced changes in the ratio of meteoric precipitation to evaporation (P/E). When the lake volume decreases, the concentration of solutes increases (e.g., Dana and Lenz, 1986; Aladin and Potts, 1992) and consequently (pore-) water salinity is a conservative tracer of past climate fluctuations (Tomonaga et al., 2017). Yet, pore water salinity profiles have a relatively low
resolution and record only major changes at millennial time scales. Palaeoecological (e.g., faunal assemblage, phenology/morphologic variation) and geochemical (e.g., biomarker, carbonate trace elemental and isotope geochemistry) salinity proxies offer higher temporal resolution but are, per definition, indirect indicators. In non-marine environments, calcitic valves of ostracods (benthic, bivalve Crustacea) are established biological proxies to infer past environmental conditions from species ecological tolerance, morphometry, and/or valve geochemistry. Numerous previous studies exemplified the application of ostracod valves in tracking past hydrological changes (e.g., Van der Meeren et al., 2010, 2011; Decrouy, 2012; Smith and Palmer, 2012; Horne et al., 2012; Viehberg et al., 2012; Meyer et al., 2016). The composition of an ostracod assemblage is influenced by several factors such as the type of surface sediment, ambient water temperature, dissolved oxygen concentration, and salinity (Holmes et al., 2010; Mesquita et al., 2012; Ruiz et al., 2013). Concerning salinity, not only the concentration of total dissolved ions (De Deckker 1981; Aladin and Potts, 1996) but also the ionic composition of the water control the diversity of ostracod assemblages (Forester and Brouwers, 1985; Smith, 1993). Based on species-specific tolerances and optima towards salinity and water chemistry, ostracod assemblages are valuable palaeosalinity indicators (e.g., Boomer et al., 2003; Keatings et al., 2010). Several authors related a variety of morphological changes of the hard parts (single valves or complete carapaces) of the same ostracod species to changing salinity. Rosenfeld and Vesper (1977) observed an inverse relationship between the roundness of sieve-pores of the species *Cyprideis torosa* (Jones, 1850) and salinity. The valve length or length-height ratio of some species e.g., *Mytilocypris henricae* (Chapman, 1966), *C. torosa* and *Limnocythere inopinata* (Baird, 1843) seem to be salinity dependent (Martens, 1985; Neale, 1988; Van de Meeren et al., 2010). The most easily recognisable morphological change related to salinity is the development of a distinct type of ornamentation on the valves lateral surface expressed as hollow, typically round protrusions termed `nodes´ (Kilenyi, 1972; van Harten, 2000; Keyser, 2005). Among the species developing these nodes, most research focussed on the brackish species *C. torosa* (e.g., Kilenyi, 1972; Vesper, 1975; van Harten, 2000), which is presumed to produce more and prominent nodes with decreasing salinity (Keyser, 2005; Frenzel et al., 2012). In addition, by means of their calcite valves, ostracods have the potential to reinforce palaeoecological and -environmental implications by using a geochemical approach (Smith and Palmer, 2012). The ratios of trace-elements to calcium, primarily Sr/Ca and Mg/Ca often co-vary positively with salinity (Holmes, 1996; Holmes and De Deckker, 2012). However, other factors, not necessarily salinity-related, such as increased inorganic carbonate precipitation and mineralogy, water temperature, Mg concentration and/or alkalinity of the ambient water may also affect Sr/Ca and Mg/Ca ratios of ostracod valves (e.g., Engstrom and Nelson, 1991; De Deckker et al., 1999; Bahr et al., 2009; Zhang et al., 2009; Gouramanis and De Deckker, 2010). The oxygen isotope composition (δ18O) of ostracod valves is a function of the temperature and the isotopic composition of the lake water in which the biominerals were secreted, modified by a vital offset, a systematic, species-specific deviation from the δ18O value of a theoretical calcite precipitated under equilibrium conditions (von Grafenstein et al., 1999, Decrouy, 2012). The carbon isotopic composition (δ13C) of an ostracod valve reflects the δ13C of the dissolved inorganic carbon (δ13CDIC) at the time of moulting (von Grafenstein et al., 1999; Keatings et al., 2002). Three processes control the lake water δ13CDIC: (i) biological activity in the lake, (ii) atmosphere-water CO2 exchange, and (iii) the δ13CDIC of inflowing water (Kelts and Talbot,
1990; Leng and Marshall, 2004). Often and in combination with other proxies, increasing δ13C_ostracod values have been interpreted in terms of a decreasing lake volume, associated with lower freshwater input and enhanced productivity (e.g., von Grafenstein et al., 2000; Frogley et al., 2001; Edwards et al., 2006).

Here we take advantage of Lake Van’s well-constrained palaeoenvironmental conditions and test the versatility of ostracods as salinity indicators in an endorheic lake basin. We juxtapose changes in ostracod taxonomy, valve morphology (nodding) and oxygen (δ18O) and carbon (δ13C) isotopic composition for the last 150 kyr with independent low-resolution salinity proxies including biomarker indicators (Randlett et al., 2017) and directly measured pore water salinity (Tomonaga et al., 2017). Further, we document the variability in the valve isotopic composition of three concurrent ostracod taxa and identify its ecology-related controlling mechanisms. Finally, we compare the isotopic data of ostracod valves and of inorganic carbonates (calcite and aragonite; McCormack et al., 2018b) with proxy records for relative changes in the P/E ratio including arboreal pollen percentage (Litt et al., 2014; Pickarski et al., 2015a, b), XRF-Ca/K ratio (Kwiecien et al., 2014), lithology and total organic carbon content (TOC; Stockhecke et al., 2014a). We expect that, while the mixed nature of the inorganic carbonates (McCormack et al., in review) masks the response of their isotopic composition to salinity changes, the biogenic carbonate mirrors these changes with a higher fidelity.

2. Limnological setting/state of the art of Lake Van

Lake Van is a terminal, alkaline lake in Eastern Anatolia, Turkey, situated on a high plateau with a lake level today at an altitude of 1648 m above sea level (Litt and Anselmetti, 2014). Its alkaline nature, characterised by near equal shares of sodium carbonate and sodium chloride, is a result of the volcanic hinterland and high evaporation rates (Kempe et al., 1991; Reimer et al., 2009). The lakes total alkalinity reaches ca. 151 mmol l–1, salinity ca. 22 g kg–1 and pH 9.7 – 9.8 (Kempe et al., 1991; Reimer et al., 2009; Litt et al., 2012). The Mg2+ concentration in the water is low, whereas Ca2+ is strongly depleted (Kempe et al., 1991; Reimer et al., 2009) and its concentration decreases further below the epilimnion due to the precipitation of carbonate minerals in the surface water (Landmann et al., 1996; Reimer et al., 2009; Stockhecke et al., 2012).

The recovery of a continuous 220 m long sedimentary succession in alkaline Lake Van in 2010 supported by the International Continental Scientific Drilling Program (ICDP) greatly expanded our knowledge about the evolution of the lake itself and the environmental changes in the Near East over the last ~ 600.000 years (Litt and Anselmetti, 2014). Several independent proxy records including palynological, XRF-Ca/K ratios, total organic carbon content (TOC) and lithology show a mostly coherent palaeoclimate signal, involving wetter interglacials with a higher lake level, and more arid glacial periods with a generally lower lake level (Kwiecien et al., 2014; Litt et al., 2014; Stockhecke et al., 2014; Pickarski et al., 2015a, b). A generally lower lake level between ca. 80 to 30 ka BP is also implied from biomarker salinity proxies and direct pore water measurements (Randlett et al., 2017; Tomonaga et al., 2017) with the maximum salinity (ca. 50 to 80 g kg–1) reached during a lowstand between 30 to 14 ka BP and a lake level ca. 200 m lower than present (Stockhecke et al., 2014a; Tomonaga et al., 2017). Seismic profiles reveal palaeo-shorelines/geomorphological features supporting this lowstand (Cukur et al., 2014a, b).
lower lake levels and more arid late glacial conditions are also documented from other lakes in the vicinity such as Lake Xinias (Digerfeldt et al., 2000) and Lake Urmia (Stevens et al., 2012). An array of independent proxy records (e.g., Kwiecien et al., 2014; Stockhecke et al., 2014a; Pickarski et al., 2015b; McCormack et al., 2018a) have demonstrated a high sensitivity of Lake Van and its catchment to Northern Hemisphere temperature oscillations in particular to Greenland Stadials and Interstadials dubbed Dansgaard-Oeschger cycles. Interstadials contrast typical glacial/stadial conditions, and are characterised by higher moisture availability in the Lake Van area (Pickarski et al., 2015b) resulting in a rising lake level and the deposition of finely laminated sediments (Stockhecke et al., 2014a). The bulk carbonate $\delta^{18}O$ record ($\delta^{18}O_{\text{bulk}}$) is at odds with the other proxy records recovered from the 2010 ICDP coring with higher values appearing in both, cold arid periods such as the Younger Dryas and in warm wet periods such as the Last Interglacial (MIS 5e; Kwiecien et al., 2014). McCormack et al. (2018 a, b) have shown that the bulk carbonate fraction consists of variable amounts of different carbonate mineral phases; primary low-Mg calcite and aragonite and early diagenetic calcian dolomite. Further, these authors argue, that surface water carbonates (calcite and aragonite) differ isotopically from each other due to their precipitation in close-to-freshwater and evaporative concentrated lake water, respectively. Consequently the isotopic composition of the bulk carbonate is biased towards the composition of the most abundant inorganic carbonate fraction. Ostracod valves, relatively easy to separate from the inorganic fraction, provide an independent and in the case of Lake Van hitherto unexplored palaeoenvironmental archive/proxy. Although the episodic presence of turbidite layers in the sediment cores implies periodical transport of allochthonous material to the site (Stockhecke et al., 2014a), the presence of ostracod valves in finely laminated undisturbed (varved) sediments and their generally excellent preservation suggest an autochthonous deposition or if any, then a very short transport.

3. Material and Methods

This study was carried out on material recovered in 2010 in the frame of the International Continental Drilling Program PALEOVAN. We resampled 2-cm-thick intervals from the Ahlat Ridge composite profile and off-sections avoiding the sampling of event-deposits. Composite profile depth (and age; Stockhecke et al., 2014b) was assigned to off-section samples by visual correlation based on high resolution core images. The data presented here comprises 256 samples. Sampling range covers the uppermost 68 m (56 m without event deposits) of the composite profile corresponding to 147.8 ka BP with a mean temporal resolution of 54 years per sample. Sediment samples were wet-sieved into three fractions (> 250 µm, 250 – 125 µm, 125 – 63 µm), rinsed with distilled water and air dried. Ostracod valves were picked and counted from the > 250 µm and 250 – 125 µm fractions under a stereomicroscope and stored in microfossil slides. The identification of ostracod valves was based on morphological characteristics and verified with regional and standard identification keys and taxonomic reports (Suzin 1956; Bubikjan 1966; Bubikjan 1984; Meisch 2000; Wilkinson et al. 2005; Karanovic 2012; Külköylüoğlu et al. 2012; Danielopol et al., 2018), using high magnification of stereomicroscope and scanning electron microscope. The diverse
limnocytherid fauna will be subject of an additional paper (McCormack et al. in prep), however, the geochemical studies focus on the dominant species of the fossil record (Fig. 1). For statistical assemblage analyses, only samples with more than 20 ostracod valves were taken into account, similarly cumulative statistics regarding noding are based on samples with at least 20 limnocytherid valves. Only well-preserved valves, i.e. translucent, well calcified and mostly intact were counted. SEM images were taken from gold-sputtered samples using a LEO/Zeiss Gemini 1530 as well as a Gemini 2–Merlin, both operating with an acceleration voltage of 20 kV.

After careful visual inspection with the stereomicroscope, only clean (fully translucent, without any foreign matter) valves were used for isotopic analyses. If necessary valves were manually cleaned using a fine brush and distilled water to remove artefacts. Isotopic analyses were carried out on adult and juvenile *Limnocythere inopinata*, *Limnocythere* sp. A and *Candona* sp. valves. Size range and sex of the valves were noted for each sample to estimate potential influences of ontogeny and sex on valve isotopy. Ostracod valve length was determined using the image software ZEN 2.3 lite based on digital stereomicroscope photographs, taken with a Zeiss AxioCam 105 color camera attached to a Stemi 508 stereomicroscope. Length measurement errors were determined by repeated length measurements (10 times) for five different valves, yielding a maximum standard deviation of 3.2 µm. For isotope measurements of the genus *Candona* sp., large clearly identified fragments, as well as valves from samples with less than 20 valves were also analysed.

Oxygen and carbon isotope ratios (\(\delta^{18}O\) and \(\delta^{13}C\)) were determined on a ThermoScientific Kiel IV carbonate device coupled to a MAT253Plus mass spectrometer at the Ruhr-University Bochum. A total of 140 measurements, including replicate analyses, were performed on samples from the Ahlat Ridge ICDP site, as well as four measurements on samples from a shallow core (Van12-08) at depths between 53 and 31 cm below the lake floor. Between 15 and 60 µg of ostracod carbonate were weighed into Kiel reaction vials and reacted at 70 °C in orthophosphoric acid (105 % H₃PO₄). Depending on valve size and thickness between 2 and 68 valves were measured. Results are reported in ‰ in the common delta notation. Raw data were corrected using the standard ISO-A (Bernasconi et al., 2018) and the international standards NBS-19, IAEA-603, and CO-8. Final isotope ratios are normalised against the Vienna PeeDee Belemnite (V-PDB) standard. The external standard deviation of repeated analyses is <0.05 ‰ for both, \(\delta^{13}C\) and \(\delta^{18}O\).

4. Results

4.1 Ostracod taxonomy and morphology

The three dominant taxa, *Limnocythere inopinata*, *Limnocythere* sp. A and *Candona* sp. were identified (Fig. 1). *L. inopinata*, is present throughout the studied sediment sequence with both valves of females and males, implying the presence of a sexual population (Fig. 1, 2). *Limnocythere* sp. A, also occurs as a sexual population, but clearly differs from *L. inopinata* and other limnocytherinae species from its general outline and morphologic texture (Fig. 1). *Limnocythere* sp. A generally dominates the faunal assemblage contributing up to 98 % to the relative ostracod composition (mean = 63 %) between 36.2 and 5.2 metre
composite below lake floor (mcblf) corresponding to 81.0 to 12.2 ka BP. Valves of the genus *Candona* were not further differentiated herein. *Candona* sp. contributes from up to 43 % to the relative ostracod composition (mean = 5 %), occurring only at depths between 67.6 and 50.9 mcblf, corresponding to an age between 147.9 and 108.9 ka BP.

The valves of polymorphic limnocytherinae species show varying reticulation and valve morphometrics. Here we focus on the most noticeable morphological variation, the appearance of hollow protrusions (nodes) with different intensity (number of nodes and size) and shape (round, spinous). The highest number of noded valves appears between ca. 73-35, 30-12 and 11-3 ka BP with mean percentages of noded valves of 64, 43 and 57 % respectively (Fig. 3). Intervals with very low amounts of noded valves at ca. 148-137, 137-105 and 3-0 ka BP have mean percentages of noded valves of 4, 1 and 3 % respectively. One sample dated at ca. 137 ka BP has 31 % noded valves and the interval between 105-75 ka BP is characterised by valves with highly varying amounts of noding between 0 and 47 % (Fig. 3). Among the noded valves from the Holocene most valves only have one node (Fig. 3). Three noded valves dominate the period of ca. 73-35 ka BP with a mean of 45 % of valves with three or more nodes. Nodes from the Holocene are typically smaller and round and are documented on *Limnocythere inopinata* valves, whereas those from the Last Glacial period are commonly larger and often spinous (Fig. 4).

4.2 Ostracod valve oxygen and carbon isotopy

The isotopic composition of valves varies for both $\delta^{18}$O and $\delta^{13}$C between different species (Tab. 1). Geochemical data from valves belonging to the same species, sex, reticulation intensity and size range, within one sample, generally show a mean isotopic variability in the order of up to 0.6 ‰ only (Fig. 5 a; Tab. 1). Geochemical data from *L. inopinata* valves of different reticulation intensity, size range and sex showed no consistent differences in $\delta^{18}$O and $\delta^{13}$C that could be related to either of these factors (Fig. 5 a, b, c). Co-occurring smooth and reticulated valves of *L. inopinata* dated between 137 to 117 ka BP have a $\delta^{18}$O difference of up to 0.4 ‰, while only one sample shows smooth valves with 1.9 ‰ higher values compared to the more reticulated valves (Tab. 1). The valves of *Limnocythere* sp. A are with one exception continuously higher in both $\delta^{18}$O and $\delta^{13}$C compared to *L. inopinata*, from the same stratigraphic horizon, by 0.4 to 2.9 ‰ and 0.4 to 1.3 ‰ respectively (Fig. 5 d, e). *Candona* sp. valves from the same sample have constantly 0.4 to 0.9 ‰ higher $\delta^{18}$O values and 2 to 6 ‰ lower $\delta^{13}$C values than those of *L. inopinata* (Fig. 5 d, e).
5. Discussion

5.1 Ostracod taxonomy and morphology as palaeosalinity proxies

5.1.1 Variations in relative species abundance

In the sample material studied, the taxonomic diversity is relatively low, as expected from a saline lake with low Ca\(^{2+}\) concentrations (De Deckker and Forester, 1988; McCormack et al., in prep.). Only *L. inopinata* is found throughout the profile. *L. inopinata* tolerates high alkalinity (Meisch, 2000) and a high salinity range (ca. 0 - 50 g kg\(^{-1}\)), favouring a Na\(^{+}\)-HCO\(_3^{-}\)-CO\(_3^{2-}\)-rich and Ca\(^{2+}\)-depleted water composition (Forester, 1983; 1986; Neale et al., 1988; Smith, 1993; Holmes et al., 1999; Li et al., 2010). The presence of *L. inopinata* throughout the profile suggests a close to constant Na\(^{+}\)-HCO\(_3^{-}\)-CO\(_3^{2-}\)-rich water composition and is in agreement with a close to steady-state relative proportion of most ions indicated by pore water analyses (Tomonaga et al., 2017).

Species belonging to the genus *Candona* sp. are typically associated with lower salinities (ca. 0 - 15 g kg\(^{-1}\); e.g., De Deckker, 1981; Anadón et al., 1986; Neale, 1988; Forester, 1991; Li et al., 2010). *Candona (Fabaeformiscandona) rawsoni* (Tressler, 1957), for example, is mainly documented in alkaline lakes with low water salinity, but can also be found in lakes with higher salinity and less alkaline conditions (Forester, 1986). In Lake Van, *Candona* sp. valves occur in sediments for which pore water and biomarkers indicate deposition under lower salinity conditions (Fig. 2; Randlett et al., 2017; Tomonaga et al., 2017) and lithology and TOC suggest well ventilated water column (Stockhecke et al., 2014a). The presence of *Candona* sp., an infaunal genus (Decrouy et al., 2012), appears to be controlled here by a lower concentration of total dissolved salts, alkalinity and higher dissolved oxygen concentrations in the bottom water, rather than changes in the ionic composition of the lake water. *Limnocythere* sp. A is near-constantly present between ca. 81 and 12 ka BP and generally dominates the assemblage. Based on its occurrence restricted to the Last Glacial period (Fig. 2), coinciding with high pore water salinity and alkalinity (Tomonaga et al., 2017) and generally higher values for biomarker salinity proxies (Randlett et al., 2017), *Limnocythere* sp. A had likely a high salinity and/or high alkalinity preference. Between 26 and 18 ka BP, *Limnocythere* sp. A reached its highest relative taxonomic abundance of 86 to 98 % (Fig. 2). At the same time, Lake Van’s lake level was at its lowest and the salinity concentrations at its highest (ca. 50 to 80 g kg\(^{-1}\); Tomonaga et al., 2017). At the Pleistocene/Holocene transition, characterised by more humid conditions, an increasing lake level and lower salinity (Litt et al., 2014; Tomonaga et al., 2017), *Limnocythere* sp. A disappeared from the sedimentary record.

5.1.2 Noding in limnocytherinae species (morphological variation)

For some species (e.g., *Cyprideis* species and *Leucocytherella sinensis*, Huang 1982) noding is a phenotypic reaction to a decrease in salinity (Keyser and Aladin, 2004; Keyser, 2005; Frenzel et al., 2012; Fürstenberg et al., 2015; Meyer et al., 2016). However, whether nodes in limnocytherinae species, especially *L. inopinata*, are morphological traits that are genetically controlled (genotypic; Yin et al., 1999; Fuhrmann, 2012) or environmentally influenced (phenotypic; Benson, 1969) is at
present open to debate. As far as we know, the occurrence of noded *L. inopinata* within a geological record has not been directly compared in detail to other proxies of past water hydrochemistry including parameters such as salinity and alkalinity. While the physiological process of noding has been studied for *C. torosa* (Keyser, 2005), there are no such studies for limnocytherinae species. In Lake Van, the highest concentration of noded *L. inopinata* and other limnocytherinae species, in terms of the highest number of nodes per valve, and most pronounced nodes occurred during the Last Glacial period (Fig. 3, 4) strongly suggesting a relation with salinity.

The number of noded individuals and the number of nodes per valve starts to increase at the end of MIS 5 and reaches maximum values during MIS 4 and 3. Concurrently, Lake Van data indicate generally increased lake water salinity, due to increased aridity and a decreasing lake level (Fig. 3; Litt et al., 2014; Stockhecke et al., 2014a; Pickarski et al., 2015; Tomonaga et al., 2017; Randlett et al., 2017). This observation is in disagreement with the interpretation of node formation as a genotypic trade suggested by Yin et al. (1999) referring to culture experiments exposing ostracods to variable aquarium water salinities. Based on the increase of noded individuals and the number of nodes under intensified aridity and increasing Lake Van salinity and alkalinity (Fig. 3), we propose that the node formation on limnocytherinae species (incl. *L. inopinata*) is primarily a phenotypic phenomenon.

Further we suggest that nodes on *L. inopinata* represent a malfunction during or shortly after molting, before the newly formed valves calcified, analogue to studies on *C. torosa* (Keyser and Aladin, 2004). During the hormone-induced molting process, the ostracod increases the volume of its body fluid by an intake of ambient water (Aladin and Potts, 1996; Keyser and Aladin, 2004). This leads to an inflation of the valve producing tissue, which under too high pressure may rupture during this process, leading to the formation of nodes during the subsequent biomineralisation (Keyser and Aladin, 2004; Keyser, 2005).

According to Keyser (2005), the formation of nodes in *C. torosa* results from the lower osmotic pressure of the ambient water (low salinity) and the inability of the ostracod to regulate its internal osmotic pressure accordingly. A higher-than-normal pressure takes effect in the caverns between the inner and outer epidermal layers, when the ostracod presses its bodily fluid (haemolymph) into the valve. This is caused by the higher osmotic concentration within the haemolymph relative to the external aquatic medium. The higher pressure causes cell-to-cell connections between the inner and outer epidermal layer to tear allowing the flexible valves to bulge out in these areas and form protrusions that are stabilised as nodes during the subsequent calcification. However, limnocytherinae species (i.e., *L. inopinata*) are hyperosmotic regulators at salinities below 8 g kg\(^{-1}\) and isosmotic regulators between salinities of 8 and 14 to 20 g kg\(^{-1}\) (Aladin and Potts, 1996). Hence, we presume that the haemolymph of limnocytherinae species will be hypo-osmotic relative to the lake water, and the mechanism of node formation is also related to the difficulty of achieving an osmotic balance during molting.

Similar to the observation of van Harten (2000) for *C. torosa*, noded and unnoded valves of *L. inopinata* and other limnocytherinae species typically co-occur and while some stratigraphic horizons are free of noded valves, unnoded valves can be found throughout the profile. Keyser (2005) explains this by the ability of some individuals to better adjust to the environment. Not all individuals will have the same specific genetic predisposition (i.e., vulnerable cell-to-cell connections between the inner and outer epidermal layer) triggered by less favourable environmental conditions (i.e., salinity or alkalinity).
This may explain why there is no linear relationship in relative abundance of noded valves and salinity (Fig. 3). However, it is evident that the occurrence of noded individuals and the number of nodes per valve is higher at periods of inferred high salinity from MIS 4 to 2. Moreover, it is also noteworthy, that the relative number of noded individuals increased again in the Holocene, but contrary to the Last Glacial period, the absolute size and number of nodes is smaller (Fig. 3 f; Fig. 4). Keyser (2005) associated the size, shape, and extent of the protrusion (largest extent as spine) in *C. torosa* to the amount of pressure applied to the caverns between the epidermal layers, with larger nodes at higher pressure. In analogy, we interpret the higher number of nodes and the larger size of nodes for *L. inopinata*, as an expression of enhanced environmental stress reflected in increased and more excessive malfunctions during moulting. The Ca\(^{2+}\) deficiency in the water was suggested, next to salinity changes, as another driver of node formation in *C. torosa* (Keyser, 2005). Low Ca\(^{2+}\) concentrations within the bodily fluid during the moulting increase the risk of disrupting stabilising structural elements within the epidermal cavities by causing spasm-like reactions (Keyser, 2005; Frenzel et al., 2012). Modern Lake Van water is strongly Ca-depleted (0.105 to 0.087 mmol L\(^{-1}\), Reimer et al., 2009). We assume that lake water Ca\(^{2+}\)-concentrations have not varied significantly within the last 150 kyr, as Ca\(^{2+}\) transported into the lake is quantitatively precipitated in the epilimnion as inorganic calcite and aragonite (McCormack et al., in review). The Ca\(^{2+}\) limitation in Lake Van may increase the likelihood of node formation in limnocytherinae species but is apparently not the ultimate controlling mechanism.

In the literature the relation between noding and alkalinity is yet unresolved (Van Harten, 2000; De Deckker and Lord, 2017). In Lake Van salinity and alkalinity of the pore water correlate exceptionally well and both increased during the documented generally lower lake level of the Last Glacial (Tomonaga et al., 2017). Due to this correlation, we cannot evaluate the effect of either of these parameters on node formation independent of the other. Still, our results suggest that noding of *L. inopinata* and other limnocytherinae species is controlled by the ambient water salinity and perhaps alkalinity. Noding of limnocytherinae species is therefore a valid indicator for relative palaeohydrological changes.

### 5.2 Ostracod valve oxygen and carbon isotopy

#### 5.2.1 Isotopic composition of ostracod valves and the “vital effect”

Similar to other studies (e.g., Heaton et al., 1995; Li et al., 2007; Marco-Barba et al., 2012), we observe no systematic variation between sex, valve size, reticulation and the isotopic composition of ostracod valves of the same species in Lake Van (Fig. 5 a, b, c; Tab. 1). The isotopic composition, however, varies systematically between different species from the same stratigraphic horizons (Fig. 5 d, e). This observation may be related to different microhabitats, or different vital effects. Ostracod calcite is typically enriched in \(^{18}\)O (Xia et al., 1997; von Grafenstein et al., 1999) relative to inorganic calcite precipitated in isotopic equilibrium with the lake water (Kim and O’Neil, 1997) under the same geochemical conditions. While the exact controls of this vital offset remain ambiguous, its amplitude is species-specific (von Grafenstein et al., 1999) and perhaps related to the
salinity and/or the ionic composition of the bottom water (Decrouy, 2011; Decrouy and Vennemann, 2013), water temperature, lake water pH conditions (Chivas et al., 2002) or the ambient water \([\text{CO}_3^-]/[\text{DIC}]\) molar ratios (Devriendt et al., 2017). In the same stratigraphic horizon, *Limnocythere* sp. A has, with one exception, constantly higher \(\delta^{18}O\) values relative to *L. inopinata* by a mean of 1.4 ‰ (n = 13; Fig. 5 d). The positive correlation between the \(\delta^{18}O\) values of both species (r = 0.57, Fig. 6 a) and the persistent \(^{18}O\) enrichment in *Limnocythere* sp. A suggests a different vital offset from *L. inopinata*. Similarly, generally higher \(\delta^{18}O\) of *Candona* sp., relative to *L. inopinata* (mean 0.6 ‰ for n=9), indicates a different vital offset (Fig. 5 d). The mean offset between Candoninae species and *L. inopinata* is lower than expected from studies in freshwater environments, where the vital offset of Candoninae is ca. 2 to 3 ‰ and for *L. inopinata* ca. 0.8 ‰ (von Grafenstein 1999; Keatings et al. 2002, Decrouy et al. 2011; Decrouy and Vennemann, 2013). The positive correlation between \(\delta^{18}O\) of *L. inopinata* and *Candona* sp. from the same stratigraphic horizon (r = 0.93, Fig. 5 d; Fig. 6 b), however, not only supports a relatively constant vital offset between both taxa, but also suggests that both respond to changes in the \(\delta^{18}O\) of the lake water. Determining the vital offset for ostracod valve \(\delta^{13}C\) is more complex due to the species-specific microhabitat preferences of ostracods (von Grafenstein et al., 1999). Within the ostracods microhabitat, the carbon isotope composition of the dissolved inorganic carbon \(\left(\delta^{13}C_{\text{DIC}}\right)\) may vary significantly from that of the open water column (Decrouy et al., 2011). For most ostracod taxa (including Candoninae) the carbon isotopic composition presumably represents a value expected for equilibrium calcite formation (von Grafenstein et al., 1999; Keatings et al., 2002). The carbon isotope values of *L. inopinata*, however, are suggested to be 1 to 3 ‰ lower than what is expected for equilibrium precipitation, a feature that may be attributed to the biomineralisation pathway of the species (von Grafenstein et al., 1999; Decrouy et al., 2011). The \(\delta^{13}C\) values of *Limnocythere* sp. A are generally higher by ca. 0.6 ‰ relative to *L. inopinata*. The statistically relevant correlation between \(\delta^{13}C\) values of *Limnocythere* sp. A and *L. inopinata* (r = 0.72; Fig. 5 e; 6 a) suggests a constant vital offset. Alternatively, both species may moult within different microhabitats. The second scenario explains the large offset between *Candona* sp. and *L. inopinata* \(\delta^{13}C\) values (Fig. 5 e). While *L. inopinata* is a preferentially epifaunal species, the genus *Candona* sp. is considered to be infaunal (Decrouy et al., 2012b). The \(\delta^{13}C\) values of *Candona* sp. will in contrast to *L. inopinata* reflect not the \(\delta^{13}C_{\text{DIC}}\) of the bottom water, but that of the pore water. The oxidation of \(^{13}C\)-depleted organic matter shifts the \(\delta^{13}C_{\text{DIC}}\) of the pore water towards lower values (von Grafenstein et al., 1999). The pronounced carbon isotope difference between both species implies a strong gradient between pore water and lake water \(\delta^{13}C_{\text{DIC}}\) (Fig. 5 e, 6 b).

We cannot exclude that larger variations in the past water chemistry affected the magnitude of the biologically-induced disequilibrium. However, the relatively constant offsets among the isotopic compositions of different species (Fig. 5 d, e), implies only minor variations in the magnitude of the vital offsets. The offset between *Candona* sp. and *L. inopinata* \(\delta^{13}C\) values is an exception, and is primarily a function of varying microhabitats. Variations in the isotopic composition of species-specific ostracod valves over glacial/interglacial timescales are larger than the potential amplitude of disequilibrium effects related to the biomineral secretion. Moreover, these patterns are synchronous with variations in other proxy records (Fig. 7, 8), indicating a sensitivity of the ostracod valve \(\delta^{18}O\) and \(\delta^{13}C\) records towards relative changes in Lake Van’s palaeohydrology.
5.2.2 Ostracod $\delta^{18}O$: Palaeoenvironmental implications and comparison to inorganic carbonate isotope signatures

The $\delta^{18}O$ value of ostracod valves is not directly affected by salinity, but rather by the isotopic composition and the temperature of the ambient water. In some cases ostracod valve $\delta^{18}O$ is used to estimate relative changes in the lake volume (e.g., Lister, 1988; Gouramanis et al., 2010; Wrozyna et al., 2012; Marco-Barba et al., 2013), which also affect lake water salinity. Changes in the $\delta^{18}O$ of the lake water ($\delta^{18}O_{\text{Lake}}$) in large closed lakes are predominantly controlled by the precipitation/evaporation (P/E) ratio, with higher $\delta^{18}O_{\text{Lake}}$ values indicating lower P/E ratios (decreasing lake level) due to the preferential loss of $^{16}O$ during evaporation (Leng and Marshall, 2004). A comparison of the isotopy $L. \text{inopinata}$ valves with the depositional lithostratigraphy indicates generally lower $\delta^{18}O$ values for valves deposited in finely laminated compared to such sedimented in banded or mottled deposits (Fig. 7). The generally lower $\delta^{18}O$ values within laminated sediments deposited during high lake levels (Fig. 7) emphasises the sensitivity of ostracod valve chemistry in Lake Van to environmentally-driven lake level fluctuations.

Despite its low resolution, $L. \text{inopinata}$ $\delta^{18}O$ data seem to reach lower values at the transition from the penultimate glacial period (MIS 6) to the Last Interglacial (MIS 5e; Fig. 8 h). Ostracod valves are almost absent in the Ahlat Ridge sediments deposited during the early MIS 5e (124 – 133 ka BP; Fig. 2 j), a period in which the lake level probably rose sufficiently to establish a short-lived outflow (Stockhecke et al., 2014a; Tomonaga et al., 2017; North et al., 2017). Apparently, this has led to a larger and/or more oxygen-depleted suboxic/anoxic water body compared to other highstand periods, preventing or hindering a colonisation of the profundal zone by ostracods. Subsequent periods representing lake level highstands (ca. 86-77 ka BP and 106-99 ka BP; Stockhecke et al., 2014; Tomonaga et al., 2017) document decreasing $L. \text{inopinata}$ $\delta^{18}O$ values (Fig. 8 h) and thereby increasing P/E ratios and decreasing salinity.

Within the sediments of MIS 3 and 4, high amplitude fluctuations (> 3 ‰) in the $L. \text{inopinata}$ sp. A and $L. \text{inopinata}$ $\delta^{18}O$ values likely indicate frequently changing P/E ratios and a subsequent rising (interstadials) and falling (stadials) lake level. $L. \text{inopinata}$ sp. A shows less variable, $^{18}O$-enriched values (4 – 5 ‰) between ca. 33-17 ka BP (Fig. 8 h, j). This supports relatively stable but arid conditions (Pickarski et al., 2015b; Kwiecien et al., 2014; Stockhecke et al., 2014a) and a low lake level (Cukur et al., 2014; Tomonaga et al., 2014). Following the uniformly high values during MIS 2, $L. \text{inopinata}$ sp. A $\delta^{18}O$ values show a slight decrease (to ca. 2.8 ‰) at ca. 15 ka BP, while higher values (ca. 4.4 ‰) are reached during the arid Younger Dryas. A significant rise in lake level at the onset of the Holocene (Landmann et al., 1996; Stockhecke et al., 2014a; Cukur et al., 2014; Çağatay et al., 2014; Tomonaga et al., 2017), led to lower Holocene $L. \text{inopinata}$ $\delta^{18}O$ values (Fig. 8 h).

The Lake Van bulk carbonate is composed of varying concentrations of the inorganic carbonate minerals aragonite, low-Mg calcite, and calcian dolomite and, volumetrically less important, biogenic carbonates (ostracods). The significantly different isotopic composition of each component results from their precipitation in isotopically distinct host waters (McCormack et al., 2018a, in review). McCormack et al. (in review) has shown that both calcite and aragonite precipitate within isotopically contrasting surface water: Calcite under close-to-freshwater-conditions within river plumes and aragonite within evapoconcentrated lake water. Therefore, the bulk $\delta^{18}O$ values, but also the isotopic composition of surface water precipitates calcite and aragonite ($\delta^{18}O_{\text{Ar+Cc}}$, $\delta^{13}C_{\text{Ar+Cc}}$), represent isotopically mixed signals shifted towards the dominant polymorph. An
estimation of the aragonite $\delta^{18}O$ ($\delta^{18}O_{Ar}$) (assuming a range for the $\delta^{18}O$ of calcite between -4 and -10 ‰, and a constant surface water temperature at the time of calcite precipitation at 10 °C) represents the closest approximation for changes in Lake Van’s surface water isotopic composition over glacial/interglacial time scales (McCormack et al., in review; Fig. 8 i). The estimates of $\delta^{18}O_{Ar}$ values may be compromised by the uncertainty in the relative concentrations of aragonite and calcite and the adequacy of our assumptions. Nevertheless, the estimated $\delta^{18}O_{Ar}$ record shares more similarities with the $\delta^{18}O$ pattern of ostracod valves than with the bulk $\delta^{18}O$ record (Fig. 8). While the bulk $\delta^{18}O$ record shows no systematic variations, both the estimated $\delta^{18}O_{Ar}$ and the $\delta^{18}O_{Ar+Cc}$ records document decreasing values coinciding with the lake level highstands at ca. 106 – 99 ka BP and 86 – 77 ka BP synchronous with the ostracod $\delta^{18}O$ data. The shift towards lower $\delta^{18}O_{lake}$ values from the late glacial into the Holocene, however, is evidenced by the estimated $\delta^{18}O_{Ar}$ and ostracod $\delta^{18}O$ records but not in the $\delta^{18}O_{Ar+Cc}$ or bulk record (Fig. 8 f, g, h, i). The ostracod $\delta^{18}O$ record shows a higher sensitivity to relative lake level changes than the inorganic isotope records in Lake Van. Concluding, in lakes with a mixed inorganic carbonate composition, ostracod $\delta^{18}O$ signatures may be a more accurate recorder of palaeohydrological changes than the $\delta^{18}O$ values of inorganic carbonate.

5.2.3 Ostracod $\delta^{13}C$: Palaeoenvironmental implications and comparison to inorganic carbonate isotope signatures

The species-specific $\delta^{13}C$ variability is much lower than the respective $\delta^{18}O$ variability (Fig. 8 e, h). This pattern is particularly well pronounced within the Last Glacial period, when the amplitude of $\delta^{13}C$ change is low for both $L. inopinata$ and Linmocythere sp. A, while the amplitude of $\delta^{18}O$ change is large. The lower variability in ostracod $\delta^{13}C$ is probably related to the large dissolved inorganic carbon (DIC) pool of Lake Van (ca. 100 mmol kg$^{-1}$, Reimer et al., 2009). In general, the $\delta^{13}C$ of large DIC pools is less variable with changes in the lakes hydrology compared to that of $\delta^{18}O_{lake}$ (Li and Ku, 1997).

Importantly, the $\delta^{13}C$ of the infaunal Candonia sp. valves do not reflect bottom water $\delta^{13}C_{DIC}$ but the $\delta^{13}C_{DIC}$ of the pore water of the uppermost sediment column.

In contrast to the ostracod taxonomy, morphological variability, and valve $\delta^{18}O$, the ostracod $\delta^{13}C$ appears to be a less sensitive recorder of lake volume (salinity) or other hydrological changes in Lake Van. Still, markedly lower $\delta^{13}C$ values of the epifaunal $L. inopinata$ during two periods, the Holocene and the late MIS 5e (ca. 120 to 115 ka BP) document lower $\delta^{13}C_{DIC}$ of the bottom water. Interestingly, for both periods, other proxy records (TOC, lithology and ostracod $\delta^{18}O$; Fig. 8 b, h, j) show contrasting signals. One interpretation of this feature is that the shift towards lower $\delta^{13}C$ values was possibly triggered by different processes for each period. The decrease in $L. inopinata$ $\delta^{13}C$ values at the Pleistocene/Holocene transition is here tentatively explained by the significant rise in the lake level (ca. 200 m) and more humid conditions. This may have resulted in a dilution of the lake water by the influx of $^{13}C$-depleted freshwater. However, two previous lake level highstands at ca. 106 – 99 ka BP and 86 – 77 ka BP documenting decreasing $L. inopinata$ $\delta^{18}O$ values similar to the Holocene are not associated with decreasing $\delta^{13}C$ values (Fig. 8 e, h, j). Further, the low $\delta^{13}C$ values in $L. inopinata$ valves that calcified within the well-ventilated bottom water during the late MIS 5e (Stockhecke et al., 2014a) cannot be interpreted by increasing $^{13}C$-depleted runoff due to the very different depositional setting. Another potential explanation for lower ostracod valve $\delta^{13}C$ values may
be varying degrees of bottom water DIC exchange with upward diffusing $^{13}$C-depleted pore water at the lake floor. The lack of correlation between ostracod $\delta^{13}$C values and other proxy records and the differences in the depositional setting between both periods with lower $L. \text{inopinata}$ $\delta^{13}$C values does not allow for a conclusive interpretation of our data. While any palaeoenvironmental interpretation based on changes in ostracod $\delta^{13}$C remains at this point speculative, the shift towards lower values within Holocene sediments likely document changes in the lakes bottom water DIC composition. An opposite trend towards higher values is clearly visible in the inorganic $\delta^{13}$C$_{\text{Ar+Cc}}$ record (Fig. 8 d, e). The complementary evolution in Holocene inorganic versus ostracod $\delta^{13}$C values may be related to a highly stratified water column. Given that $\delta^{13}$C$_{\text{Ar+Cc}}$ is a mixture of $^{13}$C-enriched aragonite and comparably $^{13}$C-depleted calcite, the Holocene increase in aragonite content (Fig. 8 c, McCormack et al., in review) may have masked a trend towards lower water column $\delta^{13}$C$_{\text{DIC}}$.

6. Conclusions

Taking advantage of the legacy of the ICDP PALEOVAN project – the well-documented hydrological evolution of Lake Van – this study examined the applicability of ostracods as multi-proxy archives for relative changes of the past lake water chemistry, with the emphasis is on salinity reconstructions. We focussed on the ostracod faunal assemblage, valve morphology (nodding) of limnocytherinae species (incl. $L. \text{inopinata}$) and the valve geochemistry ($\delta^{18}$O and $\delta^{13}$C) of three different ostracod taxa from ICDP cores covering the last 150 kyr. We conclude:

1) The composition of the ostracod assemblage of Lake Van is primarily controlled by the salinity and/or alkalinity of the lake water. While $L. \text{inopinata}$ is present only during high salinity and alkalinity intervals, $C. \text{sp.}$ valves are limited to periods of less saline lake water. $L. \text{inopinata}$ a cosmopolitan species with high tolerance to changing water chemistry is present throughout the record.

2) The presence and amount of nodes (hollow protrusions) is compared here to independent palaeohydrological proxies. Our results indicate, that node formation on valves of limnocytherinae species is primarily a phenotypic response to higher salinity and/or alkalinity and as such represents a novel promising proxy in semiquantitative lacustrine palaeohydrology.

3) The $\delta^{18}$O records from ostracods in Lake Van are sensitive towards relative changes in the lake volume related to varying precipitation/evaporation ratios. Ostracod valves have generally lower $\delta^{18}$O values when embedded in sediments deposited during lake level highstands and higher values when embedded in sediments deposited during a low lake level.

4) Ostracod $\delta^{13}$C values while less sensitive to hydrological changes due to the large dissolved inorganic carbon pool of Lake Van, still reflect the microhabitat of the respective species.

5) The isotopic composition of ostracod valves, particularly their $\delta^{18}$O values, document hydrological changes that are not recorded by the inorganic (bulk) isotope records due to their mineralogically-mixed composition. The isotopic analyses of ostracod valves is therefore particularly useful for estimating changes in the isotopic composition of the water in lakes in which more than one inorganic carbonate phase accumulates in the bulk sediment.
Acknowledgements

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References


Table 1. Isotopic variability (minimum, maximum and mean) between different species, sex, valve size and reticulation intensity from the ICDP Ahlat Ridge cores. For six samples, replicate analyses were performed with valves showing no differentiating characteristics. Calculated variance is represented by the difference of these replicate analyses. Analyses comparing sex, valve size and reticulation intensity were measured from the same stratigraphic horizon. n represents the number of measurements.

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Figure 1: SEM photographs of the external lateral views of key species used in this study. 

a) female right valve *Limnocythere inopinata*, b) male right valve *Limnocythere inopinata*, c) female right valve *Limnocythere* sp. A, d) male right valve *Limnocythere* sp. A, e) female left valve *Candona* sp..
Figure 2. Relative distribution of ostracod taxa in Lake Van in comparison to various palaeoenvironmental proxy records. a) Isotopic composition of the NGRIP ice core (NGRIP, 2004; Steffensen et al., 2008; Svensson et al., 2008; Wolff et al., 2010) and a synthetic Greenland record (GL_T_syn) (Barker et al., 2011). Sedimentary proxies from Lake Van include (b) XRF-Ca/K ratio (Kwiecien et al., 2014), (c) arboreal pollen and *Quercus* pollen percentage (Litt et al., 2014; Pickarski et al., 2015a, b; Pickarski and Litt, 2017), d) pore water salinity plotted against depth in metre composite below lake floor (mcblf; Tomonaga et al., 2017), e) biomarker Archaeol and Caldarachaeol Ecometric (ACE) index (Randlett et al., 2017), and k) lithologies with genetic interpretations related to lake-level variability as coloured bar (simplified after Stockhecke et al., 2014a) and major lake-level variations (Stockhecke et al., 2014a; Tomonaga et al., 2017) in metre above/below present lake level (mapll/mbpll). f-h) relative abundance of ostracod taxa. f) *Candona* sp., g) *Limnocythere* sp. A, h) *Limnocythere inopinata*. I) Percentage of noded limnocytherinae species. j) Position of samples containing less than 20 valves, these samples were not included in the statistical assemblage analyses. The grey shaded areas represent interglacials.
Figure 3. Amount and number of noded limnocytherinae species valves relative to Lake Van palaeoenvironmental proxy records. Sedimentary proxies from Lake Van include a) arboreal pollen and *Quercus* pollen percentage (Litt et al., 2014; Pickarski et al., 2015a, b; Pickarski and Litt, 2017), b) pore water salinity plotted against depth in metre composite below lake floor (mcblf; Tomonaga et al., 2017), c) biomarker Archaeol and Caldarchaeol Ecometric (ACE) index (Randlett et al., 2017) and h) lithologies with genetic interpretations related to lake-level variability as coloured bar (simplified after Stockhecke et al., 2014a) and major...
lake-level variations (Stockhecke et al., 2014a; Tomonaga et al., 2017). d-f) Number of nodes in percent. g) Total percentage of noded limnocytherinae species. The grey shaded areas represent interglacials.
Figure 4. Illustration of amount and intensity of noded limnocytherinae species valves (as SEM images) within the studied interval. Roman numerals indicate the depth and age of individual valves. The valves displayed here are both from adult and juvenile ostracods.

Figure 5. Isotopic variability between ostracod measurements from the same stratigraphic horizon against age. a) Variability between valves of the same taxa and sex. b) Variability between L. inopinata and Limnocythere sp. A female and male valves. c)
Variability between *L. inopinata* of different valve size. d) $\delta^{18}O$ variability between *L. inopinata* and *Limnocythere* sp. A and *L. inopinata* and *Candona* sp.. e) $\delta^{13}C$ variability between *L. inopinata* and *Limnocythere* sp. A and *L. inopinata* and *Candona* sp.. *Limnocythere* sp. A and *Candona* sp. could not be compared, as they never occur in the same stratigraphic horizon.

Figure 6. Isotopic composition of *L. inopinata* valves versus *Limnocythere* sp. A (a) and *Candona* sp. (b).
Figure 7. Ahlat Ridge *L. inopinata* δ¹⁸O versus δ¹³C values, colour coded after the lithology of their respective sampling horizon. Lithologies are colour coded after their genetic interpretations related to lake-level variability following Stockhecke et al. (2014a).
Figure 8. Ostracod isotopy compared with pore water salinity and inorganic carbonate isotopy and mineralogical composition. a) Pore water salinity plotted against depth in metre composite below lake floor (mcblf; Tomonaga et al., 2017). b) Total organic carbon content (Stockhecke et al., 2014a). c, d, g, i) Inorganic mineralogy and isotopy from McCormack et al. (in review). c) Relative aragonite content of dolomite poor samples (< 15 % dolomite) expressed by an aragonite/non-dolomite ratio Ar/(Ar+Cc) in weight % and d, g) isotopic composition of dolomite poor samples ($\delta^{13}$C$_{Ar+Cc}$ and $\delta^{18}$O$_{Ar+Cc}$). f) Bulk carbonate oxygen isotope composition from Kwiecien et al. (2014). i) Estimated $\delta^{18}$O$_{Ar}$ values for $\delta^{18}$O$_{Cc}$ values between -4 and -10 ‰. j) Lithology-based relative lake-level changes (simplified after Stockhecke et al., 2014a) and major lake-level variations (Stockhecke et al., 2014a; Tomonaga et al., 2017) in metre above/below present lake level (mapll/mbpll). e, h) Valve $\delta^{18}$O values and $\delta^{13}$C values.