THE USE OF OSTRACODS TO RECONSTRUCT CONTINENTAL PALAEOENVIRONMENTAL RECORDS

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ABSTRACT

Ostracods are environmentally sensitive organisms which readily preserve as fossils because of their calcitic shells. Ostracod occurrence appears to be controlled by hydrochemical parameters such as water composition and salinity, and also by the seasonal variability of water temperature.

Ostracod shells serve as a principal source of biogenic carbonate and, as for many geochemical studies of marine shells, can inform on δ^{18} O, δ^{13} C, and Mg/Ca and Sr/Ca ratios of their host water, thus providing a variety of data on past aquatic environments such as temperature, salinity, seasonal variation, water composition and solute pathways.

The close links between lacustrine environments and climatic parameters are discussed at length to demonstrate how necessary it is to understand them before attempting to unravel palaeoclimates. Emphasis is given on temperature in lakes and also on the relationship between hydrochemistry, solute evolution and the evaporation precipitation ratio over the lakes. A broad classification of lakes is also presented with a discussion on the type of palaeoclimatic information they can offer.

The coupling between climates and lakes is seen through aquatic parameters which appear to control ostracod occurrence and productivity. In this sense, ostracods from climatically sensitive lakes may supply very detailed information on past climates affecting the lakes.

INTRODUCTION

Ostracods living in continental aquatic environments are quite selective with respect to the environments in which they live. In fact, particular species are very much environment-specific, and therefore ostracods can be used to characterize nearly every possible type of water found on the earth surface, provided it is oxygenated and not highly ephemeral. Some ostracods are also living interstitially in groundwater aquifers.

The remarkable environmental diversity of ostracods has been known in a general way for quite some time especially when their latitudinal and salinity distributions were documented (for reviews see Löffler and Danielopol,1978 and De Deckker, 1981). Indeed, the importance of parameters such as water temperature for their life cycle was known quite early on through the work of Alm(1916). Unfortunately, most ostracod specialists focussed their attention on taxonomic problems rather than intergrating ostracod species and environmental data for the characterization of (palaeo-)environments. Delorme(1969) drew attention to the palaeoenvironmental potential of ostracods based on a very extensive data base for Canadian inland waters, and thus suggested that life cycles of ostracods appear to be related to all aspects of their hydrological environment, and through that to climate.

The concept of continental palaeoenvironment used herein includes two major environments of the atmosphere as reflected by climate, and 2) surface waters of the hydrosphere, referred as the limnological component. The climate parameters of interest typically involve air temper ture, moisture balance, precipitation, and the seasonality of these parameters. The limnological parameters of interest largely involve water temperature, salinity, pH, dissolved ion compositions as well as their seasonal distributions. The discussion of limnological properties will for principally on limnic (standing) rather than lotic (flowing) waters and will include all aspect of groundwater discharge, but especially the spring and seep environment. Frequently climate properties and limnological properties are closely related or coupled to each other. For example, daily water temperature variability especially of many shallow water bodies may express a direct but usually buffered relationship to daily air temperature variability. The dissolves ion composition of many waterbodies may be expressed in terms of evaporation or the season variability of humidity of the air over the waterbody. Thus relationships exist between climate and limnological parameters that permit one to study a purely aquatic record and make bot limnological and climatic interpretations.

Knowledge about palaeoclimate and palaeolimnology is of great importance to both basi and practical problems. Basic problems include acquiring knowledge about past environment in order to better understand the processes that have led to earth surface history, such as specie evolution, tectonics, and climate. Practical problems include discovering economic mineral de posits or a safe site for storage of various forms of toxic wastes. Environmental knowledge usually involves interpretation of proxy records that too often entail terrestrial components such as pollen. Terrestrial components may provide direct information about climate, but they offer little information about limnology. In contrast, aquatic records are often believed to be less desirable for climate studies, because they are derived from processes that at best are imperfectly coupled to the atmosphere. Paradoxically, aquatic data may contain a more sensitive record than terrestrial data for not only water, but also climate. In order to describe the merits and problems with aquatic proxy data a general discussion that illustrates the links between climate, limnology, and in this example ostracods are warranted. The focus of this discussion will treat only the coupling of air and water temperature and the coupling of moisture balance and major dissolved ion composition in water rather than the full spectrum of climate limnologic interactions. These parameters seem to have the strongest signal within aquatic proxy records and are the most commonly sought values.

We propose to discuss the nature of information various types of lakes can offer with respect to palaeoenvironmental reconstructions. Emphasis is also given on the relationships that exist between ostracods, as well as ostracod shell chemistry, and the host environment, once again for the scope of a better definition of past conditions of aquatic environments.

Temperature and Lakes

Air and water temperature are complex but very important climatic and hydrologic variables that may be described in terms of various time scales ranging from the geologic time scale to daily or even finer time scales. Interpretations of seasonal or annual temperature variability of water and in particular air temperature are important aspects of palaeoenvironment reconstruction and thus contribute significantly to our understanding of climatic change. Interpretation of water temperature from aquatic data is relatively straight forward, with the accurracy of that interpretation being a function of both the sensitivity of the proxy data and sediment accumulation rate. Interpretation of a water temperature record in terms of air temperature, however, demands that the relationship between air and water temperature be generally understood as well as the particulars of the record under investigation.

Thermally stratified lakes

Many permanent lakes, either very large or small, have a basin morphometry that induces thermal stratification within the water column on a regular (seasonal) or irregular basis. The epilimnion (surface water mass) (see Figure 1) of a large lake gains and/or loses heat on daily and seasonal cycles (Ragotzkie, 1978). Wind-induced turbulence may move heat downward, especially when the densities of surface and subsurface waters are similar. Lakes in the temperate belts usually mix twice a year (Dean, 1981). During the winter the temperature of the hypolimnion of such dimictic lakes is usually 4°C whereas the epilimnion is less than 4°C. During spring and fall after the ice thaws and before ice forms, any wind-induced turbulence readily mixes the entire water column, thereby bringing nutrients to the epilimnion and oxygen to the hypolimnion (bottom water mass). Warming of the epilimnion in summer produces warmer, less dense water that becomes thermally isolated from the hypolimnion. The temperature of the epilimnion increases to some maximum value and then cools to 4°C in the autumn, when the lake mixes again.

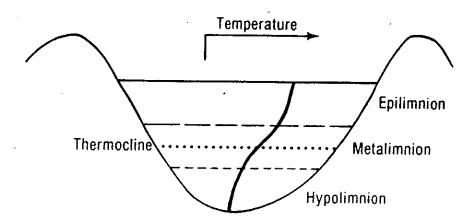


Figure 1. Typical temperature profile in a thermally stratified lake, and terminology associated with the different portions of the lake affected by temperature changes.

In polar lakes, the epilimnion may never become warmer than 4°C so that mixing may occur throughout the warm season, whereas coastal temperate lakes may never become colder than 4°C and thus may mix throughout the winter but stratify in summer. These lakes are known as cold and warm monomictic lakes respectively (Wetzel, 1975).

In tropical lakes, at low elevation, the epilimnion usually remains warm, above 20°C throughout the year, whereas deeper water may only be slightly colder so that the lake may be mixed by any passing storm. The lakes mixing on an irregular basis are known as polymictic lakes and those remaining warm are called warm polymictic lakes, and those remaining cold, usually located at high elevations in the tropics, being cold polymictic lakes. Every style of lake mixing has a latitudinal distribution on the globe, and thus knowledge about a lake's mixing schedule provides at least general climatic information (Hutchinson and Löffler, 1956).

The temperature of the epilimnion, including the littoral zone, may respond to daily or seasonal changes in atmospheric temperature depending on its size. A large volume of water may take longer to warm up or cool down in response to a change in air temperature and thus would exhibit less thermal variability than the air over the lakes whereas an epilimnion with a small volume may exhibit thermal variability that more closely tracts the air over the lake.

The volume of an epilimnion is usually a function of numerous local factors with basin morphometry, availability of wind, and seasonal ranges of air temperature being especially important. These factors may change over time with changing lake level and climate, and thus the response of water temperature to air temperature may also change over time. Therefore knowledge about a lake's epilimnion heat budget often provides information about air temperature, but the character of that record must be evaluated on the nature of the local system. A very large lake such as the Lake Bonneville, which existed in western North America during the Late Pleistocene, is likely to have had an epilimnion thermally buffered from seasonal air temperature, whereas much smaller lakes that exited near Lake Bonneville may have had a thermal record closely related with local temperature.

The epilimnion of lakes with a water mass dominated by river water or groundwater input may exhibit a complex heat budget that is some integration of the river-water heat budget and the atmospheric heat budget. Carmack et al (1986) treat this phenomenon in more detail.

The hypolimnion usually remains relatively isothermal or may vary gradually throughout the year depending on the morphometry of the basin and the depth of the epilimnion. In temperate areas the water in the hypolimnion is derived from mixing events when the epilimnion is cold, during fall, winter, and spring. In some polar lakes, on the other hand, mixing occurs in summer. The bottom water temperature therefore is related to the mixing season and, even if the hypolimnion warms or cools slightly during the non mixing-seasons, the temperature is not directly coupled to seasonal variation in air temperature. In contrast, tropical lakes mix frequently on an irregular basis and thus the hypolimnion temperature is, or can be closely tied to the epilimnion temperature, which in turn is related to air temperature.

Shallow lakes, ponds, marshes, seeps, and springs

Many lakes are not deep enough to stratify thermally, and therefore the entire waterbody loses or gains heat on a daily or other short term cycle. Maximum and minimum air- and watertemperature data collected weekly from late winter through summer 1986 from a small suburban pond in Lakewood, Colorado, U.S.A, illustrate the relationship between these parameters (Fig.2). Air temperature varied over a wider range than water temperature, and water temperature usually lagged behind air temperature. Variations in air temperature, lasting only a day or so, often are not recorded by water temperature. In general, however, when a pond is icefree, water temperature varies with air temperature. Small lakes may also indirectly record the average winter air temperature through the length of their ice-free season. Small arctic lakes, for example, are only ice-free for 2 to 3 months of the year (Winter and Woo, in press), and although they may reach temperatures above 20°C in summer, they only do so for short periods of time. In contrast, small lakes in the Denver area, Colorado, are ice-free for at least 9 to 10 months and may remain at temperatures above 20°C for 2 to 3 months. Note also that many shallow lakes only fill up with water for certain periods of the year (e.g. in Australia, the wet season occurs in summer in the north, and in winter in the south of the continent), so it becomes necessary to identify those periods of fill to interpret temperature records.

The temperature of shallow groundwater discharge, e.g., springs or seeps, may approximate mean annual air temperature, but groundwater discharging from very deep aquifers may be warmer than mean annual air temperature. Discharging groundwater is relatively isothermal throughout the year, but the water-temperature of pools or ponds supported by groundwater may vary with air temperature. Thus, the temperature of groundwater discharge and the aquatic environments it supports can provide information about mean annual air temperature and seasonal air-temperature variability.

Precipitation, evapotranspiration, and hydrochemistry

The annual balance and seasonal distribution of precipitation (P) and evapotranspiration (E) are important climate parameters (Winter and Woo, in press). Moisture balance, or the balance between precipitation and evaporation, is often evaporatively coupled to water chemistry. As evaporation from a waterbody increases its salinity, salt minerals precipite. Mineral precipitation may alter the relative proportion of solutes in the waterbody, resulting therefore in a loss or enrichment of particular dissolved ions in the water column. The loss or enrichment of solutes from the water column is known as solute evolution (Eugster and Hardie, 1978, Eugster and Jones, 1979). Lakes that are chemically coupled to climate through evaporation can provide information about moisture balance through their hydrochemical records. This relationship is complex because the major dissolved ion composition (solutes) and concentration (salinity) of surface water is a product of both climate and non-climate processes (Gorham, 1961; Jones, 1965; Hardie, 1968; Garrels and McKenzie, 1967; Jones and Bowser, 1978; Eugster and Hardie, 1978; Eugster and Jones, 1979; Jones and Weir, 1983; Bodine and Jones, 1986). Inflow from rock-water reactions (weathering), selective solution of precipitated minerals, atmospheric precipitation, CO2 solution, and solution of atmospheric dust are primary solute sources. Selective mineral precipitation due to evaporative concentration or mixing of waters with different salinities or compositions are the primary solute sinks, along with biologic processes, CO2 outgassing, exchange reactions, and outflow.

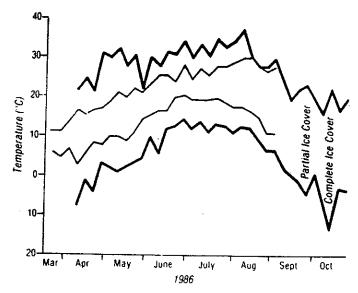


Figure 2. Maximum and minimum air temperature (thick lines) and water temperature (thin lines) measured for a small pond in Lakewood, Colorado, U.S.A.

The sum total of all solutes that reside in surface waterbody whether derived from water-rock reactions within a basin or from atmospheric input from outside the basin provides the principal chemical components that are available as a response to changes in climate. Forester (1987) provided a discussion of this process using several simplified examples of lakes that were evaporatively coupled to the atmosphere for different moisture balance situations. This process can also be discussed from the perspective of very wet climates where the water table is at or above-ground surface, versus climates dry enough to only have surface water supported seasonally by groundwater discharge (wet playas).

Fundamentally, we may consider a range of climates from a very wet place to a very dry one. In very wet places, where precipitation greatly exceeds evaporation, all solutes entering the surface waterbody are generally lost to outflow. The water column therefore has a low salinity and a solute composition that in temperate or polar areas is typically dominated by Ca²⁺ + HCO₃. In tropical regions low salinity waters may also be dominated by solutes other than $Ca^{2+} + HCO_{5}^{-}$, commonly $Na^{+} + (Mg^{2+}) - Cl^{-}$. Under wet climates, whether warm or cold, the processes that couple limnic environments to the atmosphere involve dilution of dissolved ions, solution of salts or other minerals and discharge of most solutes via surface or groundwater routes. Because salinity is very low, inorganic mineral precipitation will be minimal, but biogenic mineral production (calcite as in ostracods and charophytes (algae); opaline silica as in diatoms (algae)) will occur. Biogenic carbonate may not be stored in the sediment owing to the water column being undersaturated with respect to both Ca2+ and HCO3. Sorption of solutes on clay or other reactive surfaces, however, may be an important solute evolution mechanism and because of the flow-through nature of the system solute residence is low. The result of this series of processes (dilution, solution, and discharge) typifies low salinity water whose solute composition will be derived from atmospheric and hydrologic sources.

In tropical areas where bedrock is deeply weathered, the input composition is essentially that of rain water, which is often very similar to marine water (Gibbs, 1970). In wet temperate and polar areas the input sources are both hydrologic and atmospheric and these are often dominated by $Ca^{2+} + HCO_3^-$. The differences in solute inputs in tropical versus temperate and polar regions may be further accentuated by the much higher evaporation in the tropics.

In dry areas where evaporation exceeds precipitation, the principal output of water is to the atmosphere. Water output via evaporation results in processes that couple limnic environments to the atmosphere involving concentration, mineral precipitation, and salt storage. These are in contrast to the processes typical of a wet climate. Concentration raises salinity and mineral precipitation may occur (Eugster and Jones, 1979; Bodine and Jones, 1986). Carbonate precipitation also results from bioinduced mineral production (Dean, 1981) and direct biogenic production. Such mineralization is often preserved in the sediments, thus providing an abiotic or biotic record of the environment in which it was produced.

Even though the salinity of many lakes may never reach brine levels, the capillary fringe surrounding the lake often helps form an efflorescent salt crust that is composed of highly soluble salt minerals. Rain may dissolve these soluble minerals while leaving the less soluble ones (e.g. alkaline carbonates, gypsum) behind enriching the adjoining lake water in the soluble ions. The precipitation and solution of efflorescent salt crusts form an important process of solute evolution (Eugster and Jones, 1979) which may link climate with limnology.

The process of concentration, mineral precipitation, and salt storage are all parts of solute evolution (Bodine and Jones, 1986). As a result of this the water column becomes enriched in a particular cation or anion resulting in the depletion of the complimentary anion or cation. The loss or enrichment of a cation (anion) to mineral precipitation is due largely to input ratios of cations and anions being greater or less than 1.0. Thus, as precipitation continues, cations and anions are lost in equal proportions, but due to their presence in unequal proportions in solution depletion of one will eventually occur while the other will become enriched. The depletion (enrichment) of a cation (anion) describes a solute branchpoint for which the carbonate branchpoint is the only solute branchpoint at low salinity, about 2 to 3% TDS. Other mineral branchpoints, e.g. halite or gypsum, occur at very high salinities. Although, the climatic significance of the calcite branchpoint has not yet been established, Forester (1987) suggested that in the upper mid-western part of the United States this branchpoint approximately coincided with the forest prairie boundary and hence with a region where annual precipitation is about equal

to or less than annual evaporation. Thus this process may represent the aquatic expression of the climatic transition from a precipitation-to evaporation-dominated form of moisture balance, and therefore it is an aquatic ecotone.

The carbonate branchpoint also roughly coincides with a commonly accepted salinity boundary between fresh and saline water and as will be discussed below, it separates waters containing largely "freshwater" from saline water ostracods. In these terms the calcite branchpoint is of major climatic, limnologic, and biologic importance. Continued concentration of water that has evolved beyond the calcite branchpoint only results in an increase in the concentration of the dissolved ions until highly soluble salt minerals begin to precipitate and reach their respective branchpoints. Passing the carbonate branchpoint may result in waters that are enriched or depleted in Ca^{2+} or HCO_3^- and therefore the evolution of water beyond this branchpoint can result in two compositionally different types of saline water. As a consequence, three major types of water exist: (1) those that are dominated by both Ca^{2+} and HCO_3^- , (2) those that are enriched in Ca^{2+} but may be dominated by Ca^{2+} and any anion except CCO_3^- , and (3) those that are enriched in CCO_3^- , but may be dominated by any cation other than Ca^{2+} and any anion.

The abovementioned wet versus dry climate situations do not include the impact of temperature on the climate-hydrochemical processes. Evaporation from a water surface is lower when both air and water temperatures are cold and higher if water is warm and the air is both warm and dry. Because the processes that reflect moisture balance are driven by evaporation, not precipitation, changing temperature and humidity with latitude and longitude will have an important impact upon the hydrochemistry. In a cold dry place we may expect the water composition to behave more like that of a warmer wetter place. In addition, a very wet cold place may be expected to have a different composition from a very wet, hot locality.

Lake types

It is necessary to become aware that most lakes are the "above-ground" components of groundwater aquifers. Phenomena that control broad lake-level changes, the water chemistry and whether or not a lake retains permanent water directly affect the aquifer below the lakes: any modification in the aquifer will be registered by a change in the "above-ground" (=surface) water, that is the waterbody itself.

Saline lakes will infer the presence of a saline groundwater, at least for parts of the hydrological basin in which they occur. Naturally, changes in the saline-lake water will operate at a much faster rate than below the lake floor, simply resulting from a variety of processes, such as direct evaporation and precipitation, physicochemical phenomena (authigenic mineral precipitation, anoxia associated to meromixis) and terrigenous input (clastics as well as organic matter). Nevertheless, an overall change in the evapotranspiration to precipitation ratio (E/P) in a region will naturally affect the groundwater and thus change the status of the lake (see above). Water may change from saline to fresh, change solute composition, or change from a perennial status or an ephemeral one.

Basin morphometry is another important factor that must be considered when evaluating the relationship between surface water and climate. Obviously water in a completely lotic setting will always lose solutes to the surface or subsurface flow. Flow minimizes the effect of evaporation and hence high flow can reduce the evaporative effects of high temperature and low humidity or, conversely, can accentuate the effects of low temperature and high humidity. Therefore flow may operate against the effects of temperature and humidity or add to these processes. The rate of flow through a basin is not only the product of the elevation of a surface outlet, but also the configuration and transmissivity of the groundwater relative to the basin. Similarly, a basin in a semiarid area receiving surface flow from highlands will have a different response

than one receiving only local water. Ideally, when seeking for palaeoenvironmental or climatic records one might seek a limnic setting that has zero flow unless conditions are very wet and combined with low evaporation. However, in actual situations most lakes exhibit some degree of non climatic lotic behaviour. The surface area of a limnic waterbody will also be important in determining evaporation rate in addition to the temperature and humidity of the air over the water. A basin shaped like a shallow pan should have a much higher evaporation rate than one shaped like a deep dish and so forth.

There is a great diversity of lake types and a thorough documentation of all types is already available in Hutchinson (1957). Only the major lake types of interest to palaeoenvironmental reconstructions are discussed here. Before going further, it is necessary to know that different types of lakes will change differently through time, even if they are affected by similar climatic conditions and this for a variety of reasons. These will be discussed below. Caution therefore has to prevail when attempting to correlate lake level changes from within one region as recorded during the last 100 years for example. Noticeably, some lakes may dry up in contrast with other that register a rise in water level. As a consequence, and as mentioned above, it is necessary therefore to have a full understanding of the phenomena that regulate physicochemical conditions affecting lakes. Already De Deckker (1981) has discussed the kind of information lakes in Australia can offer with respect to their typology and the biota which inhabit them. Only those significantly different lake types of application worldwide are discussed below:

- 1) Large, permanent and geologically-long-lived lakes such as Lake Tanganyika in Africa. These lakes have large basins, may or may not be hydrologically open, and have a sufficient mass and supply of water to buffer them from most types of climate change. Because their limnology is highly buffered from climate their aquatic biological and geochemical records may only register major changes in climate, and these may be hard to distinguish from other types of changes such as tectonic ones. Such lakes may have complex internal systems such as large endemic ecosystems of circulation patterns that further isolate them from the "external" world. These lakes may have very long geological records, and therefore be an excellent source for detailed pollen or other terrestrial records.
- 2) Large playa lakes including those in tectonic basins that may form deep lakes during wet climate or high runoff periods (e.g. pluvial lakes in the Great Basin in the United States). These lakes are usually part of very large drainage basins, and therefore may only register major hydrological changes occurring within their basin. These changes are registered through variations in sedimentation rates, sediment types, and physicochemical (limnological) factors. Minor (decadal or perhaps centennial) climatic fluctuations may only affect these lakes in small ways, and thus are unlikely to be recorded but, if so, the significance of the record may be hard to decipher. Nonetheless, these lakes and their records are usually coupled to their external (climatic) environment, but owing to their size and complexity may only provide records of low frequency climate events. Large playa lakes often have long geologic records that contain long climatic records.
- 3) Small lakes, with a well defined drainage, like crater lakes or kettle lakes, largely respond to local changes, especially climatic ones. Slight modifications in the E/P ratio above the lakes, for example, will be registered by and within the lakes. Those lakes that are in little contact with the groundwater, especially if they are sealed by an indurated layer (e.g. soil horizon), are important to study because they can be considered to function like gigantic "rain gauges". The sedimentary and biological record of these lakes should therefore relate to the climatic conditions operating above the lakes. As a consequence, the location of one of those "rain gauges" for the study of palaeoclimates is very important. For example, it would be possible to illustrate shifts of climatic belts in a region if a crater lake or series of them, all situated at a boundary between

2 climatic zones were selected for study.

- 4) Glacial lakes register a very different kind of information. Obviously, changes in glacial activity of nearby glaciers are recorded by a variety of physicochemical modifications seen through sediments, their chemical composition and the biota (see Teller (1987) for more information). Glacial lake sediments are often dominated by clastics and may not contain chemical sediments or preserve fossils owing to their very dilute nature and thus their sediment records must often be interpreted in terms of allogenic input rather than endogenic dynamics. Glacial lake records often contain a high frequency limnological, but a low frequency climatic signal. These records are important however because they provide direct evidence for glacial activity, which is of profound climatic significance.
- 5) Lakes associated with streams including oxbows and those behind alluvial dams. Lakes associated with streams may respond more to stream flow, which would include both surface and groundwater seasonal discharge than directly to climate. A record of runoff, however, may be interpreted climatically and may contain a valuable regional climatic record (e.g. Atwater et al, 1986). Unfortunately, the high energy and often erosive nature of streams may leave these lakes with short and very patchy records.
- 6) Lakes supported by groundwater discharge by which we imply environments such as marshes, ponds, spring pools or other waterbodies that are all dominated by groundwater discharge. Water near the discharge area will exhibit properties common to the aquifer, which may include a water temperature that is approximately equal to mean annual air temperature (shallow aquifers) and a solute chemistry that is related to rock-water reactions within the aquifer. When groundwater discharge resides in pools or ponds the physicochemical properties of that water may be controlled by climate over the water just as in small lakes. Thus knowledge about springs and their nearby pools may provide important hydrologic and often climatic information.

THE RESOLUTION OF LACUSTRINE RECORDS USING OSTRACODS

Seasonal changes in air temperature, precipitation, and evapotranspiration may be recorded with varying resolution by the water temperature and chemistry of the water column in a lake. Unfortunately, sediment-accumulation rates in most lakes are too low to record the events of a single year, let alone seasons. Small lakes or ponds that are potentially the most climatically sensitive usually have the lowest sediment accumulation rates. The best sediment-time resolution comes from rhythmic sediments in some dimictic lakes, where each layer integrates about six months (Anderson et al, 1985; De Deckker et al, 1979). Otherwise, a lake's sediment resolution scale reduces the daily to yearly sensitivity of its water column to decadal or coarser temporal scales.

Aquatic organisms, through their ecologic response to the environment, provide an important palaeohydroenvironmental record, which is especially sensitive to dilute saline or freshwater environments (Forester, 1986; De Deckker, 1988). Endogenic minerals also provide a primary record of the lake's physical and chemical properties, but they usually provide the most information for highly saline waters, where numerous solute- and temperature-sensitive evaporite minerals can precipitate (Bodine and Jones, 1986). It is also difficult to assess if mineral precipitates have undergone diagenesis or not. Although, lakes also contain numerous aquatic organisms, few of these organisms can be commonly recovered as fossils in statistically useful numbers. A typical aquatic-microfossil sample will contain abundant ostracods and diatoms along with aquatic palynomorphs, cladocerans, reproductive organs of charophyte algae (e.g. gyrogonites), chrysomonad cysts, thecamoebans, and remains of several aquatic insect groups as well as other taxa, such as the calcareous algae Phacotus. Ostracod valves, which are composed of low-magnesium calcite, are readily preserved in all alkaline environments and occasionally in some

acidic environments. Ostracod species are environmentally and geographically diverse and are known from aquatic environments in the arctic to the tropics, from deserts to high-mountains, and from very dilute to highly saline waters. They are also common in groundwater.

General ecology and palaeoenvironmental utility of ostracods

Ostracods, although common in virtually all non-marine aquatic environments, have not been studied extensively, and their palaeoenvironmental interpretive utility is not widely appreciated. The poor reputation of ostracods for various Quaternary studies apparently lies in part with the belief that the carapace is difficult to identify to species, that most species are environmentally insensitive, and that ostracods are rare in nonmarine environments. These views are unfounded: ostracods are no more or less taxonomically complex than any other group of organisms, they are very sensitive environmental indicators, and they are found in most alkaline sediments that are usually deposited under oxic conditions. Depending on the nature of the environment a 20 gram sample of raw sediment may contain from 1 to 25 or more species whose abundance ranges from a few to over 1,000 adult valves. Delorme (1969) was the first to recognize that ecology and biogeography of nonmarine ostracods were so habitat-specific that they could be used to make quantitative palaeoenvironmental interpretations. He established a modern quantitative data base for Canadian ostracods and has used this information to interpret past hydroenvironments and climate (e.g. Delorme et al, 1977; Delorme, 1987).

Relative to most microorganisms ostracod species are long-lived animals. An ostracod life cycle may be as short as 3 to 5 weeks or as long as a year or more (Delorme, 1978). Modern ostracod species are often latitudinally limited in their distribution, suggesting that not only water temperature per se, but its seasonal variation are both important limiting factors (Delorme, 1971, references therein; Forester, 1985). Delorme and Zoltai (1984) have shown that the distribution of certain shallow-water species may be defined in terms of both water- and airtemperature ranges. Studies of the living ostracods in Scandinavia by Alm (1916) suggest that hatching and growth to reproductive maturity is temperature-dependent. Martens et al (1985) show that Mytilocypris henricae (Chapman) populations take longer (4 to 5 months) to reach maturity in winter than in summer (2 to 2.5 months) and they also noted that eggs will not hatch below certain temperatures. Laboratory experiments by Chivas et al (1985) on the same ostracod species also demonstrated that rate of calcification of ostracod shells is temperature-dependent. McLay (1978 a,b) shows how water temperature plays a vital role in the life cycles including egg hatching of several North American ostracod species. Most ostracod species therefore must have lower and upper survival temperatures and life-cycle temperatures, as well as particular egg hatching temperatures. Knowledge of a species' temperature requirements should provide at least seasonal temperature ranges for a waterbody, whereas such knowledge applied to many species may provide detailed temperature information. Moreover, if ostracods have survival and life cycle temperature limitations, they must also have optimal temperature ranges within which productivity is maximized, so that abundance of taxa within a sample should provide additional temperature information. These biological scale responses to water temperature are integrated over a species' biogeographic range on a geologic time scale, because species are known to expand and contract their biogeographic ranges with climate change (Delorme and Zoltai, 1984; Forester, 1985). Thus an ostracod species living in waters that are thermally coupled with the atmosphere will provide general information about air temperature, whereas an assemblage of species in the same situation may provide detailed air-temperature information. Ostracods from the bottom waters of deep lakes provide little or no information about seasonal air-temperature variability.

Since ostracod species occupy well defined habitats in the majority of aquatic environments, ranging from shallow water nearshore in association with particular types of aquatic

vegetation down to deep water where temperature and oxygen levels are low, it is possible to directly reconstruct the various facies to which ostracods are usually associated. The recovery of free swimming ostracod species are of course necessary to permit correlation across facies boundaries. Illustration of this application is presented in Colin and Lethiers (this volume) using Palaeozoic marine ostracods but this principle has been used to allow correlation between wells, in Chinese Tertiary lacustrine basins (Yao Yimin, pers. comm.) and Mesozoic Graben Brazilian Basin (Moura, 1985). Benthic ostracods may also be transported by turbidity flows and shore currents. For example, the benthic ostracods living in the profundal area of Lake Bonneville are represented not only in open lacustrine sediments, but also in the shore-zone deposits. Thus the generalized Bonneville biostratigraphy identified by Spencer et al (1984) may be used successfully as a correlation tool for the entire basin.

Additional information on energy levels associated to particular environments can be obtained from the study of the adult to juvenile ratio of ostracod valves recovered in samples. By studing all the size of ostracod valves belonging to individual species, thus inferring recovery of an entire or incomplete life assemblage, it is possible to indicate whether or not a sample has undergone some sorting or reworking. For more details on this refer to the articles by Brouwers and Whatley (this volume). Recognition of a shoreline facies should be obvious after examination of the composition and preservation of a fossil ostracod fauna.

Shoreline environments are characterized by high energy and disturbance. Thus ostracod shells will often become sorted, broken, abraided and finally mixed with a variety of organic debris other fossil remains and terrigenous material.

Some organisms are also known to bore and leave gnawing trails that are visible on ostracod shells especially when viewed under the scanning electron microscope (see Danielopol et al, 1986). This phenomena, which usually occurs after death of the organisms affects the preservation of their shells. As a result of this, many bored shells become brittle, and, for some specimens even, damage may be such that fossilization is impeded. So once again, it is necessary to be aware that the absence of fossil ostracods or of some species may be the result of post mortem phenomena. Recovery of heavily chitinized parts of the anatomy of ostracods without their shell, as already done by Löffler (1978) can confirm the original presence of ostracods and thus inform on palaecenvironmental conditions, especially for sites which became acidified and therefore caused the dissolution of ostracod shells.

Elsewhere, knowledge of the levels of tolerance to salinity for a number of ostracod species in Australia, for example, has allowed De Deckker (1982) and De Deckker et al (1982) to reconstruct past salinity levels in lakes. In one particular case, De Deckker (1982) studied a series of crater lakes considered to be nearly closed systems and he was able to reconstruct past salinity levels in those lakes for the Holocene from examination of the fossil ostracod fauna recovered from a series of cores (for more information on salinity, see Neale, this volume). Additional information and examples on the topics discussed above dealing with the use of ostracods to reconstruct lake facies are available in Carbonel et al (1988) and De Deckker (1988).

Response to the chemical environment

Hydrochemistry also plays a vital role in ostracod ecology. Delorme (1969) showed that ostracod hydrochemical sensitivity is great enough to describe particular environments in terms of salinity and solute composition. Forester (1983) and Forester and Brouwers (1985) suggested that solute composition is more important than salinity for some marine and nonmarine ostracod species. Forester (1986) suggested that ostracod species delineate species-specific areas on anion trilinear diagrams and that an ostracod's upper salinity tolerance might be anion-specific (see below). In general, freshwater ostracods are usually restricted to waters dominated by $Ca^{2+} + (Mg^{2+}) + HCO_3^-$, whereas saline-water ostracods are usually restricted to or prefer Ca^{2+} or

carbonate-enriched waters although in those waters other ions like Na and Cl usually are the dominant ones. Even when the salinity of a waterbody is low $(<3\%_{oo})$, it will contain "saline" water ostracods if it is not dominated by $Ca^{2+} + (Mg^{2+}) + HCO^{3-}$. Preliminary observations by Forester (1987) suggest that the various chemical properties of surface water described above directly relate to the occurrence and/or abundance of particular ostracod species (unpublished data). Ostracods are therefore sensitive to the moisture balance aspect of climate when climate and hydrochemistry are coupled.

Hydrochemistry - solute evolution through time as show by ostracods

Water composition as well as salinity are often controlled by climate (Fig. 3). The relationship between hydrochemistry and climate, as well as non-climatic factors, was discussed above whereas here we treat the relationship between ostracods and hydrochemistry. In a review of ostracod occurrences at various salinities De Deckker (1981) clearly demonstrated that different species have different salinity tolerances. The dissolved ion composition of the water also appears to be important as indicated in the discussion above and in the treatment of trilinear diagrams below. Moreover, composition also appears to play an important role in determining ostracod species diversity. Figure 4 shows that numerous ostracod species occur in waters that are saturated or supersaturated with respect to Ca-carbonates whereas waters that are undersaturated or depleted with respect to Ca-carbonates have fewer species. The data to support this generalizations is qualitative and based largely on collections made in North America. Nonetheless, when lakes are sampled along evaporation gradients, those that are dominated by Ca2+ and HCO₅ but undersaturated with respect to carbonate precipitation, have a low species diversity (1 to 5 species). Species diversity rises and then reaches a plateau as waters become saturated and consequently undergo depletion (20 to 30 or more species). Once water has become saline and is depleted in either Ca2+ or HCO3, species diversity is low (1 to 5 species). Perhaps high species diversity is related to the ease with which ostracods can build a shell and thus diversity is maximized in waters that are saturated with respect to Ca2+ carbonates. However, this is probably an over simplification because, for example, Australian lakes that are generally depleted in carbonates and enriched in Ca2+ may sometimes have a relatively high species diversity.

Ostracod occurrences may be used to distinguish species-specific areas on anion trilinear diagrams (Forester 1986). Within each species area salinity tolerance appears to vary with respect to anion composition. In general, the upper salinity tolerance of most species may depend on anion type rather than just the concentration of dissolved ions. This relationship may be applied to all taxa but, for freshwater species (in a compositional sense), the relationship is not that informative because they are defined as occurring in waters dominated by HCO_3^- . Halobiont taxa, which are those restricted to saline water (again in a compositional sense), however, may reveal important hydrochemical information about waters.

Forester (1987) described the ostracod stratigraphy from a core taken in the Great Salt Lake, Utah, U.S.A. The ostracod Limnocythere staplini, which was abundant in the lower part of the ostracodal sediments, was replaced stratigraphically upwards by the ostracod Limnocythere ceriotuberosa. Limnocythere ceriotuberosa in turn was replaced stratigraphically upwards by L. staplini. Because these two species describe different, but adjoining areas, on an anion trilinear diagram (Forester 1986), their stratigraphic distribution in this core can be used to show the compositional changes which occurred during this interval (Fig. 5). Spencer et al (1986) who studied the composition of pore fluids from another core covering the same ostracod stratigraphic interval described the same type of compositional changes as implied by the ostracods. Because climatic and hydrological changes operate on both the composition and salinity of a waterbody, ostracod hydrochemical sensitivity thus becomes especially valuable for understanding palaeoenvironmental changes.

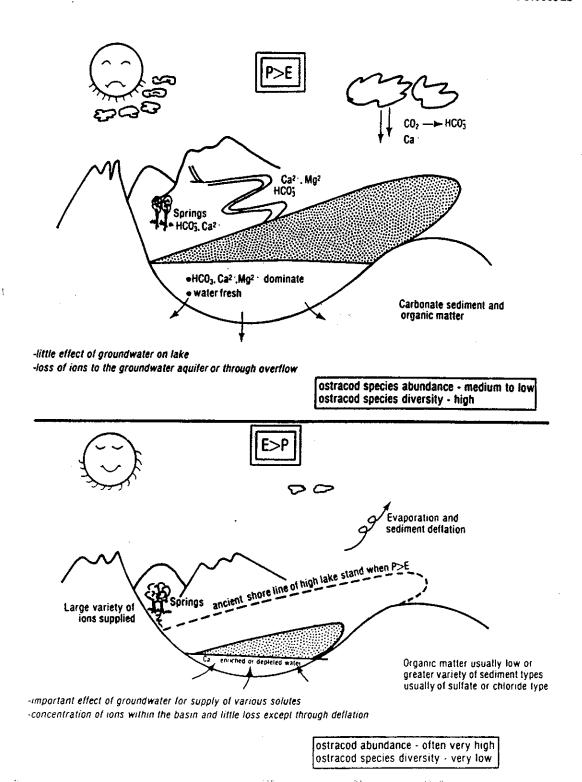


Figure 3. Schematic diagram showing the difference between lakes under two different climatic regimes. At the top, precipitation is greater than evaporation (P > E), and this controls the type of water chemistry, sediment type and the ostracod fauna. At the bottom, evaporation is greater than precipitation, and this in turn has a different effect on the lake water, its sediment and ostracod fauna.

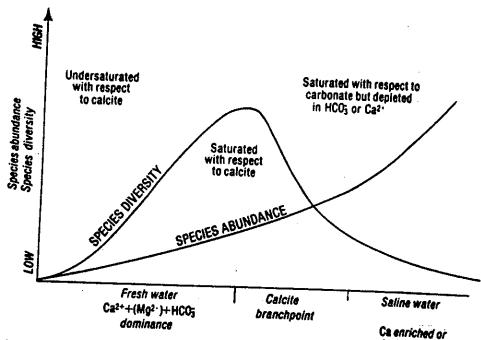


Figure 4. Diagram showing the broad relationship between ostracod species abundance and diversity with respect to the calcite saturation levels of waters in which they live, and for waters which have passed the calcite branchpoint.

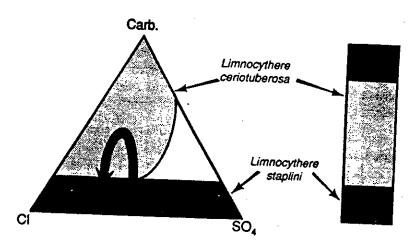


Figure 5. Diagram showing the areas of an anion trilinear plot where Limnocythere ceriotuberosa and L. staplini occur, and a stratigraphic column (on the right) showing the ostracod stratigraphy for these species from a core taken in Great Salt Lake, Utah, U.S.A. (for more details see Spencer et al, 1984). The arrow on the trilinear diagram shows in a relative way how the anion composition of Great Salt Lake changed over time as ancient Lake Bonneville rose and fell during the Late Pleistocene.

Relationship between the chemical composition of ostracod shells and the aquatic environment

As mentioned earlier, all ostracod shells are composed of low Mg calcite. To reach maturity they need to shed their valves several times (usually up to 8 times), and soon after shedding valves, new ones are formed by using components taken from within the host water at that time.

Turpen and Angell (1971) have demonstrated by using Ca-45 as a tracer in in-vitro experiments that there is no uptake of calcium by ostracods before moulting or once the shell is fully calcified. This phenomenon is significant when trying to relate the features of the ostracod valves with the environment in which they were formed: apart from mechanical processes which could affect the preservation of the ostracod valves (caused during life of the organisms (e.g. damage) or after their death (e.g. reworking)), all the features of ostracod shells (size, thickness of shell, ornamentation, chemical composition) should relate to those conditions of the environments which affect formation of the valves at the time of their calcification only. Relationship between the external environment and the ornamentation of ostracod shells is being discussed at length by Carbonel (this volume). These will not be referred to here.

Trace elements in ostracod shells

The chemical composition of estracod shells has been investigated by several authors (Sohn, 1958; Bodergat, 1983; Cadot and Kaesler, 1977; Chivas et al, 1985). To summarize, up to 25 trace elements have been found in estracod shells (Bodergat and Andreani, 1981), with the most common ones being Mg, Sr, K, Ba. Mg is the element in highest concentration in the trigonal calcite lattice. Hence the thermodynamic properties which guide the uptake of trace elements in such a crystallographic structure will prevail and thus Mg uptake in the estracod shell lattice is affected (controlled) by the temperature and the Mg/Ca of the water in which the estracod lived at the time of shell formation. On the other hand, the uptake of Sr by estracods in their shells is only affected by the Sr/Ca of the host water. There is apparently no obvious temperature effect controlling this uptake. These abovementioned characteristics have already been checked with in vitro experiments by Chivas et al (1985, 1986a, in prep.). These authors especially focused their attention on the uptake of Mg and Sr in estracods, and quantified the relationships existing between the composition of the estracod shell and the host water with respect to Mg and Sr. Thus, they defined the molar distribution coefficient KD for either Mg and Sr for estracods as being

$$K_D(Me) = \frac{(Me/Ca)_{shell}}{(Me/Ca)_{water}}$$

Me being either Mg or Sr

Chivas et al (1986a) discovered that ostracod species belonging to the same genus or to a group of genera closely related phylogenetically do share the same coefficient of partitioning for Mg and Sr. Species which belong to obviously very different ostracod families, and especially to families which emerged in the fossil record at very different periods of time, have significantly different K_D . In fact, it appears that the ostracods with the eldest ancestry have a K_D approaching that of inorganic calcite, also like for the unicellular (hence more primitive than the metazoan ostracods) organisms such as foraminifers. More evolved ostracods have K_D values approaching those of high Mg calcite. A series of K_D values calculated by Chivas et al (1986) are presented in Table 1.

Current work by De Deckker, Chivas and Shelley (in prep.) has permitted the calculation of the temperature effect on the uptake of Mg in the ubiquitous ostracod Cyprideis. Results indicate that the temperature effect can be quite substantial when the temperature range is of the order of 10°C or more. However, the extent by which the Mg uptake is controlled also depends on the Mg/Ca of the water in which the ostracod lived. For example, if the range of water temperature is of the order of 5-10°C during the moulting period of several ostracod specimens, the difference between the Mg/Ca measured in the various ostracod shells should be very broad.

TABLE 1

Distribution coefficients K_D [Sr] and K_D [Mg] for several genera of non-marine ostracods from both natural waters and laboratory cultures (from Chivas et al, 1986a)

Ostracod genus	Strontium Magnesium K _D [Sr] K _D [Mg]		
Cyprideis	0.474 ± 0.061 F, n=37 0.475 ± 0.057 L, n=32 (25°C)	0.0046 ± 0.0007 L, n=15 (25°C)	
Australocypris Mytilocypris (several species combined)	0.208 ± 0.048 F, n=89		
Limnocythere	0.350 ± 0.058 L, n=16 (20°C)		
Limnocythere mowbrayensis	0.350 ± 0.050 F, n=10		
Diacypris (3 species combined)	0.212 ± 0.020 F, n=10		
Reticypris	0.237 ± 0.027 F, n=7		
Cyprinotus edwardi	0.176 ± 0.014 F, n=10		

F = field collection, L = laboratory culture, n = number of analyses of individual ostracod valves. Errors in Kp are 10 σ values

Note that Diacypris and Reticypris are genera related phylogenetically.

Nonetheless, through a combination of analyses of Mg and Sr of single ostracod valves for any one sample representing a life assemblage, or for a series of samples which occur above one another stratigraphically, it is possible to detect changes in water properties. A summary of these possibilities is listed below:

- (1) if the Sr/Ca and Mg/Ca of ostracod shells within one sample remain unchanged, the water temperature and the Sr/Ca and Mg/Ca of the water must have remained unchanged, suggesting therefore that no substantial amount of carbonate precipitated in the water [otherwise the water's Mg/Ca or Sr/Ca, or both, should have registered a modification in ratio].
- (2) if Mg/Ca values vary, but Sr/Ca values remain relatively constant, then most probably a water temperature varied, but salinity remained unchanged.
- (3) if Sr/Ca values change and Mg/Ca remain the same, it is likely that the Sr/Ca change in the host water is caused by precipitation of aragonite or a Sr mineral (e.g. celestite or strontionite), this without a temperature.

A summary diagram (Fig. 6) also gives the various possible interpretations for analyses of individual ostracod shells for single horizons within a stratigraphic sequence.

	ANALYSES OF INDIVIDUAL OSTRACODS		Interpretation of the aquatic environment	
EVENTS (Mg/Ca) Shell		(Sr/Ca) Shell		
Top of care	• • • •	• • •	Broad fluctuations in the chemistry and temperature of the water, hence very shallow water body	
4			Progressive decrease of temperature accompanied by salinity increase during the precipitation of aragonite	
3	• • • •		Broad temperature variations, and perhaps precipitation of calcite; water body probably shallow	
2			Loss of CaCO ₃ at first, and then re-establishment of previous composition meaning increase and then decrease of salinity- no temperature change	
Sottom of			No chemical changes and no temperature change, so apparently deep water body	

Figure 6. Summary diagram showing the types of aquatic environments reconstructed from Sr/Ca and Mg/Ca analyses of individual ostracod shells obtained from various horizons sampled from a core. Dots represent analyses of individual shells and lines connect points of mean values for each horizon.

One other possible application of trace elements in ostracod shells would be to compare the shell chemistry of benthic and planktic species from the same lake. This could help detect temperature and chemical gradients in the water column. In addition, analyses of valves belonging to the various juvenile growth stages and of adults from within a single sample might reveal seasonal temperature as well as chemical changes. Species with different life cycles together might reveal very detailed information. Further possible applications of trace element analyses of ostracods living under different conditions in lakes are schematized in Figure 3.

Through the judicious choice of a crater lake, known not to be affected much by a groundwater aquifer, a potential palaeo-rain gauge can therefore be selected for study. As a consequence, a change in the evaporation/precipitation ratio (E/P) over the lake should be registered by a

change of water level in the lake, and a change in water salinity. Under normal conditions, especially when there is no substantial mineral precipitation within the water column, an increase in water level in the lake should be paralleled with a decrease in salinity, and vice versa.

The value of both ostracod ecology and ostracod shell chemistry to understand the palaeoen-vironmental history is nicely illustrated by studies conducted on a 4m core from Lake Keilambete in western Victoria in Australia. This lake occurs in a volcanic maar and is very saline today $(70\%_{00})$. The core taken in the centre of the lake at a depth of 10 m, was analysed for its ostracod fauna (De Deckker, 1982) and for the trace elements composition of the fossil ostracods (Chivas et al 1985, 1986a). With knowledge of the K_D of the ostracod genera recovered in the core, it has been possible to trace the history of salinity¹, and therefore lake level changes in the lake for the Holocene. The reconstruction is in good agreement with other water level reconstructions obtained using other techniques (e.g. grain size analyses of Bowler (1981), faunal and floral occurrences (De Deckker, 1982, and Dodson 1974, respectively). For more details, refer to Figure 7.

Trace elements analyses of ostracods from a variety of sequences have already been used successfully (De Deckker et al, in press a; Gasse et al, 1987) to reconstruct past salinity changes for a variety of aquatic environments. Analysis of trace elements of Late Miocene ostracods from the Lago Mare during the Messinian salinity crisis in the Mediterranean, for example, implied that nearly fresh water existed in various parts of the Mediterranean, and that it was occasionally deep (when Mg/Ca and Sr/Ca values for individual ostracods from within a single sample formed tight clusters), and also that the Lago Mare consisted in a series of separate lakes (when Sr/Ca ratios for ostracods from different locations gave different values) (De Deckker et al, in press b). The analysis of these Miocene ostracods already demonstrates that it is possible to apply this technique of trace elements to fossil material of even a substantial geological age, provided it is well preserved and has not undergone diagenesis. (A rapid examination under a binocular microscope or by using a scanning electron microscope can already inform on the state of preservation of ostracod valves). Thus the trace element composition of ostracod shells from controversial sites still being argued for possible marine connections should help define the origin of the water in which ostracods lived. For example, analyses of Sr in ostracod shells should rapidly confirm whether the water was of oceanic origin or not (see De Deckker et al, in press a).

Stable isotopes combined with trace element analyses

Stable isotope analyses of ostracod shells yet provide another source of environmental information. Knowing that δ^{18} O values increase with an increase in water salinity, and that δ^{18} O values decrease with a temperature rise, it becomes possible to detect temperature and salinity changes from the analyses of ostracod shells. A combination of δ^{18} O analyses with those of Mg/Ca and Sr/Ca on shells from the same ostracod sample/horizon should further define whether a Mg/Ca change in ostracods is caused by the water's Mg/Ca change or a temperature effect. A summary diagram detailing the possible interpretations combining results of Mg/Ca and δ^{18} O analyses is already available in Chivas et al (1986b). Additional information for the interpretation of past conditions operating in aquatic environments can be obtained with the use of δ^{13} C analyses of ostracods. Although δ^{13} C results are more difficult to interpret because

Although chemical changes recorded by the ostracod shell composition and which have been related to salinity changes also relate to changes in mineral precipitation within the water column. For example, a change in ostracod shell Sr/Ca directly related to the precipitation of aragonite since, when the latter precipitates, the Sr/Ca of the lake water also changes accordingly.

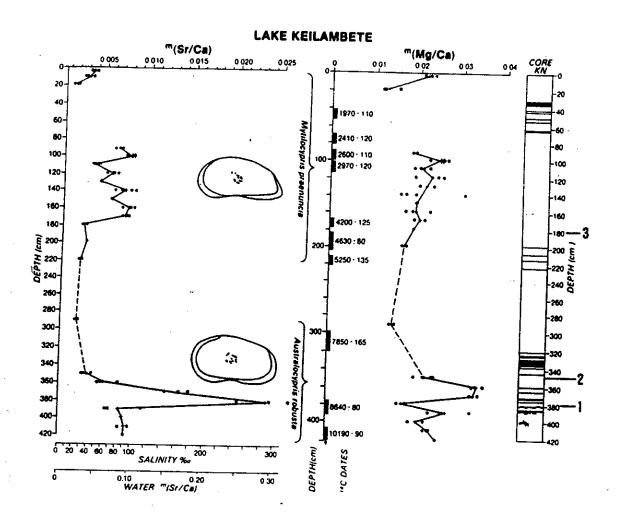


Figure 7. Plots of Sr/Ca and Mg/Ca molar ratios of individual ostracod shells from Lake Keilambete (core KN) in Victoria, Australia. Samples above 220 cm are Mytilocypris praenuncia and those below 220 cm, and one sample (x) at 100 cm are Australocypris robusta. The mean Sr/Ca and Mg/Ca at each horison is marked by a cross (+). The palaeosalinity and palaeo-Sr/Ca ratios of the lake (lower abscissae) are constructed using a K_D [Sr] of ~ 0.082 measured on modern Australocypris robusta living in Lake Keilambete [Note that this value is different to the one given in Table 1 — the reason for this exception will be explained elsewhere in De Deckker, Chivas and Shelley, in prep.]. Additional information for the following horizons labelled on the right hand side is worthy of attention: (1) Salinity is at the highest ever recorded in the lake which is extremely shallow at this stage (for further discussion on extrapolated water salinities, refer to Chivas et al, 1986a); the low Mg/Ca values probably indicate a temperature drop compared to horizons above and below it. (2) The progressive drop in Mg/Ca and Sr/Ca registered up to this horizon indicate an increase in Ca values compared to Sr in the lake water probably originating from the weathering of the crater rim. From then on, the lake became quite deep and Mg/Ca values form tight clusters up to level (3) thus indicating small temperature fluctuations. (3) At this stage a chemical change is about to occur in the lake as documented by Bowler (1981); there is a change in the composition of the sediment from aragonite to dolomite, and this explains the change of Sr/Ca registered by the ostracods in the next sampled horizon. [Figure reproduced with permission from Junk Publishers.

they can be related to a variety of conditions which alter this ratio, like fermentation or algal bloom (both causing an increase in δ^{13} C), and carbonate precipitation resulting from algal bloom (recorded as δ^{13} C increase in the ostracod shells). For more information see Lister (this volume). Nevertheless, by examining trace elements (Mg, Sr) and stable isotopes δ^{18} O, δ^{13} C) data together, a better understanding of the environmental conditions can be obtained.

Climatic information obtained from ostracods

The previous discussion describing both the relationship between climate and limnology and ostracods provides the basis for using ostracods for climatic interpretations. Ostracods are not direct indicators of climate, but rather provide detailed information about the chemical and physical aquatic environment through both their sensitive environmental ecology and through the multitude of geochemical parameters that can be obtained from their shells.

Aquatic environments that are coupled to climate are extremely sensitive climatic recorders because the seasonal variability in moisture balance and air temperature are expressed in different ways in the aquatic environment. Water chemistry responds in a predictable way to moisture balance, being directly linked to evaporation. Water temperature variability is usually directly proportional to, although buffered from, air temperature variability.

Most lakes operate on an annual cycle that is a direct result of the annual weather cycle. Changes in weather or high frequency climatic changes produce changes in lakes, which in turn affect the occurrence and abundance of ostracod species in them, because ostracod life cycles and productivity typically operate on seasonal to annual cycles. Thus a climatic change should be registered immediately by ostracods and the resulting palaeoclimatic interpretation may be tested with the various geochemical measurements on the ostracod shells. The potential resolution of the environmental interpretation is limited by the rate of sediment accumulation and by the physiological tolerance of the ostracod species found in a sample. Although many taxa have rather broad physiological tolerances, this is aimed at survival and reproduction during a particular season rather than for coping with environmental variability during the following year(s).

Climate variability which, for example, causes a three year drought with a proportional change in physicochemical properties of a lake may force one ostracod species to remain dormant as eggs (zero productivity) whereas another species might start hatching and breeding successfully (high productivity). A climatic change forcing a complete shift of limnological conditions may cause local species extinctions and also engender appearances of taxa as the new conditions favour expansion and contraction of the geographic ranges of various species. Studies by Delorme and Zoltai (1984), Forester (1985, 1987), and Forester et al (1987) document examples of how ostracods responded to low frequency climatic changes such as glacial advances as well as to high frequency changes operating on scales of centuries or decades.

CONCLUSIONS

Ostracods are one of the only groups of lacustrine microorganisms which are both environmentally sensitive and found as fossils in statistically significant numbers. Important environmental parameters controlling ostracod occurrence and productivity include the composition and salinity of water and the temperature of water. Other parameters such as substrate texture, turbidity, or predators must also be important, but probably affect productivity more than occurrence. Ostracods have the advantage over other common and environmentally sensitive lacustrine taxa, such as the diatoms, in that they have a shell made of calcite. The ostracod shell is a source of four geochemical parameters (δ^{18} O, δ^{13} C, Mg/Ca, Sr/Ca) with the potential to

provide environmental information. It is also one of the common source of biogenic carbonate in lacustrine environments. Ostracod shell geochemistry offers a means of testing ostracod environmental interpretations and in many cases a means of refining those interpretations.

Knowledge about ostracod environmental tolerances to assure their value for interpreting past environments is far from complete. The correlations between most taxa and water salinity and composition of their environment require further documentation as does the relationship between taxa and temperature. Perhaps of even greater significance is to find out how the life cycle and productivity of ostracods are related to chemical or thermal parameters. But, so far, too little is known about these factors. Moreover, variability in ostracod ornamentation or valve outline are known to occur possibly as ecophenotypic responses of valve calcification to particular environmental parameters (see Carbonel, this volume), but their causation needs further investigation.

Additional chemical analyses are certainly necessary to obtain additional coefficients of partitioning (K_D) for Sr and Mg for ubiquitous genera. The temperature dependance on Mg uptake for numerous species needs to be established in order to be able to reconstruct palaeotemperature curves from lacustrine records. Stable isotope records would certainly provide additional information on lake palaeo-temperature and -productivity. It is only then that we will be able to provide adequate information for comparison between the continental and oceanic records. Such a possibility is definitely not too far away.

Studies examining the relationship between limnology and climate are just in their infancy (La Baugh et al 1987), but they are required if ostracods and other aquatic organisms are to be successfully used for palaeoclimatic as well as palaeolimnological investigations. Such studies should ideally pay attention to the biological component of lakes, such as on ostracod life cycles, so that the links between ostracods, limnology and climate can be utilised at the same sites.

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