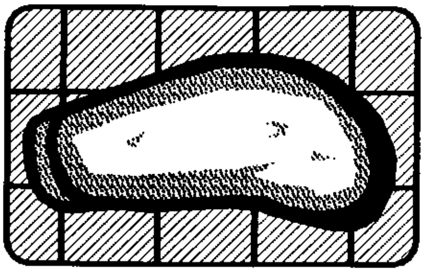

Methods in Quaternary Ecology #7. Freshwater Ostracodes

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Summary

Ostracodes that have lived in lakes, ponds, and streams are recovered as fossil shells from lacustrine and some fluvial sediments. Knowing some details of the physical and chemical habitat in which ostracode species live (autecology) allows one to decipher past habitats from fossil bearing sediments. Based on changes in ostracode faunal associations, changes in the physical and chemical habitats, can be interpreted. Climate, the driving force behind most changes in lakes and ponds, can also be delineated. The history of ostracode paleoenvironmental research as it pertains to Canada and to some extent North America is the subject of this review paper.

Introduction

The word ostracode is derived from the Greek *οστρακωδηζ* (ostracodes) which means testaceous, from *ostracon* — shell of a testacean (Moore, 1961). Most British and some American writers use the spelling "ostracod", while the *Treatise on Invertebrate Paleontology* (Q)Arthropoda 3 (Moore, 1961) prepared by a group of international scientists have adopted the spelling "ostracode".

Ostracodes have two calcitic valves, hinged dorsally to form a carapace. The shells are readily preserved as fossils in well-buffered sediments of oceans, lakes, ponds, and streams. The age range is from upper Cambrian to Recent. In terms of systematics, ostracodes belong to phylum Arthropoda, class Crustacea, and subclass Ostracoda (Moore, 1961). Most of the freshwater ostracodes of North America can be found in the suborder Podocopina (Table 1).

Historical Development

Ostracodes were first formally identified by the Danish naturalist O.F. Müller (1776). These were freshwater forms. The first freshwater ostracodes identified from Canada were reported on by Sars (1915) from samples collected from Georgian Bay by E.M. Walker; and samples from Ottawa, Medicine Hat (Alberta), Old Man River (Alberta), Port au Port (Dolphin and Union straight NWT) collected by J.B. Tyrrell, F. Johansen, and A.G. Huntsman (Sars, 1926). The first checklist of Quaternary fossil and modern ostracodes for Canada was given by Delorme (1964). The only detailed systematic work on Canadian freshwater ostracodes was carried out by Delorme (1967, 1970a,b,c,d, 1971a).

In the United States, workers of note are Hoff (1942), Kesling (1951a,b, 1952, 1954), Furtos (1933), Staplin (1963a,b), and others. Compilation of ostracodes in text books have been given by Pennak (1953) and Tressler (1959). Zoologists dealing with benthic invertebrates frequently encounter ostracodes. Most are simply reported in the literature as Crustacea or Ostracoda or both.

Quaternary freshwater species are not used in biostratigraphy. The length of time needed for the evolutionary process to take place has not been long enough to define chronostratigraphic units. In lake basins, zones may be defined by changes in the ostracode fauna brought about by changes in the habitat. Interglacial ostracodes and a paleoenvironmental interpretation were reported on by Klassen *et al.* (1967). Pleistocene ostracodes were described by Delorme (1968) from the Old Crow Basin, Yukon Territories.

Table 1 Classification scheme for freshwater and brackish water ostracodes (Moore, 1961; the treatise is in revision, other classifications are available).

- Subclass OSTRACODA
- Order PODOCOPIDA
- Suborder PODOCOPINA
  - Superfamily CYPRIDACEA
    - Family CYPRIDIDAE
      - Subfamily CYPRIDINAE
      - Subfamily CYPRIDOPSINAE
      - Subfamily HERPETOCYPRIDINAE
    - Family CYCLOCYPRIDIDAE
    - Family CANDONIDAE
    - Family ILYOCYPRIDIDAE
      - Subfamily ILYOCYPRIDINAE
    - Family NOTODROMADIDAE
  - Superfamily DARWINULACEA
    - Family DARWINULIDAE
  - Superfamily CYTHERACEA
    - Family CYTHERIDEIDAE
      - Subfamily NEOCYTHERIDEIDINAE
    - Family ENTOCYTHERIDAE
      - Subfamily ENTOCYTHERINAE
    - Family LIMNOCYTHERIDAE
    - Family LOXOCONCHIDAE

An important step in the use of freshwater ostracodes as indicators of past environmental conditions was the collection of autecological data starting in 1962 (Delorme, 1965) and continuing until 1976. This included the collection of modern ostracodes and related physical, chemical, and climatic data, from over 6700 sites. The sites were located in the accessible areas of Alberta, Saskatchewan, Manitoba, Ontario, and along the McKenzie Valley transportation corridor of the Northwest and Yukon Territories. The sites, other than those in the Territories and British Columbia, were collected from within an eight mile by eight mile grid. Each site was sampled once except for some large lakes where a number of samples were taken at various depths along a transect. It was not the intent to study the indigenous ostracode fauna of a given lake, but rather to study as many different types of physical and chemical ostracode habitats as possible. The chemical parameters, for which data were collected, were Ca, Mg, Na, K, SO_4, Cl, HCO_3, CO_3, OH^-, pH, CO_2, O_2. Physical parameters recorded were depth of water, bottom and surface water temperature, air temperature one metre above the water surface, and distance to the nearest point of the shoreline. As well, the presence and/or absence of aquatic vegetation was noted, as was the terrestrial vegetational association. Climatic data from the three closest meteorological stations to the site were obtained from the Monthly Records published by the Canadian Atmospheric Service. The modern climatic values, used in the paleo-interpretive model, are based on five-year averaged data, which included the year the sample was collected plus the two preceding and two following years. These data form the basis for ostracode paleoenvironmental interpretations for Canada and the north central part of the United States. A preliminary interpretive model was developed for use with fossil assemblages from Holocene exposures and cores (Cvancara *et al.*, 1971; Delorme, 1971b,c) culminating in Delorme *et al.* (1977). Since then, efforts have concentrated on improving the model so the predictive capabilities of interpreted climatic parameters are acceptable.

Preservation and Morphology of Ostracode Shells

Preservation of the calcareous shell dictates the enclosing sediments must be well buffered. Some ostracode species can live in water with a pH of less than 8.3. Above this level, the carbonate shell is stable, but below this value the carbonate will dissolve as the epidermal lining of the shell disintegrates after the animal dies. Calcareous shells are only rarely preserved in sediments, such as bogs and marshes, where the pH is below 8.3. Ostracodes are best preserved in marl deposits.

North American ostracode shells range in size from 0.4 to 5.0 mm (Figure 1) but most fall in the range of 0.6 to 2.0 mm (Delorme, 1969). A microscope is required to study the shape, size, and ornamentation of ostracode shells. The shells are commonly rectangular to sub-elliptical in outline and may be compressed to inflated in the dorsal view. Many of the shells are smooth (Figures 1a-g) on the exterior surface with some pore canals interrupting the surface. Other shells may have a reticulate surface to the more extreme scabrous surface (Figure 1h). These forms may also have protuberances on the surface, variously called alae or pustules, As well, there may be depressions called sulci. In many species, the interior of the valve is rimmed by a shelf of calcite called the inner lamella. Muscle scar patterns are distinctive at the generic and higher taxonomic levels. The shells, generally referred to as the hard parts, are what is preserved and are taxonomically significant to the species level. If the two valves remain intact after the organism dies, the interior void may contain the more resistant chitinous appendages such as claws and Zenker's organs. This preservation of appendages is very rare.

With reference to shell morphology, dimorphism is fairly common. In most species, male shells are generally larger and more robust than the female shells. Some species have no males. Further problems arise with some species where the left valve is not a mirror image of the right valve. Therefore, the ostracode taxonomist must be able to recognise four distinct valve types as belonging to one species. Juveniles are not identified to species level and might not show dimorphism.

Ecology

In order to collect fossil ostracodes, it is helpful to know in what environments their modern counterparts live. Ostracodes are benthic or bottom-dwelling organisms of lakes, ponds, and streams. Some species have limited swimming power which allows them to swim between plants. The true benthic forms crawl over the substrate with their shells slightly agape. Other groups, in particular the limnocytherids, crawl between the interstices just below and at the sediment-water interface. Ostracodes generally do not live in high energy environments except where there may be fine sand to coarse silt sediments. As detritus feeders, this group of animals prefers an organic rich, well defined, clay to fine silt textured sediment at the sediment-water interface.

The presence and/or absence of ostracodes in a habitat may be controlled by salinity (total dissolved solids), solute composition, dissolved oxygen, pH, depth of water, and availability of food. In general species diversity (the number of species in an assemblage) decreases with an increase in the thickness of the water column and/or the salinity. It also decreases with a reduction of food supply, or when the pH falls below 7 or increases above 10. Figure 2 shows the range of salinity that can be tolerated by a few species and Figure 3 shows the range of pH for the same species. Figure 4 illustrates the range of physical habitat as a percent probability. As all of the habitats (lakes, ponds, streams) were not sampled equally, the number of each habitat was taken to a common base. If $A_{i\text{-}n}$ is the sum of sites for each habitat collected and $B_{i\text{-}n}$ is the count of the number of samples species *X* occurs in for each of the habitats, then $B_i/A_i = C$. Using the sum of these values $(C_1 + C_2 + C_3 = D)$ to arrive at a common base, the percentage of species *X* for a particular habitat would be $(C_1/D) \times 100$.

Field and Laboratory Techniques

Ostracode shells are difficult to recognize with the naked eye in exposures or cores. When wet, the shells are translucent and about the same size as the sediment particles. There are, however, some rules of

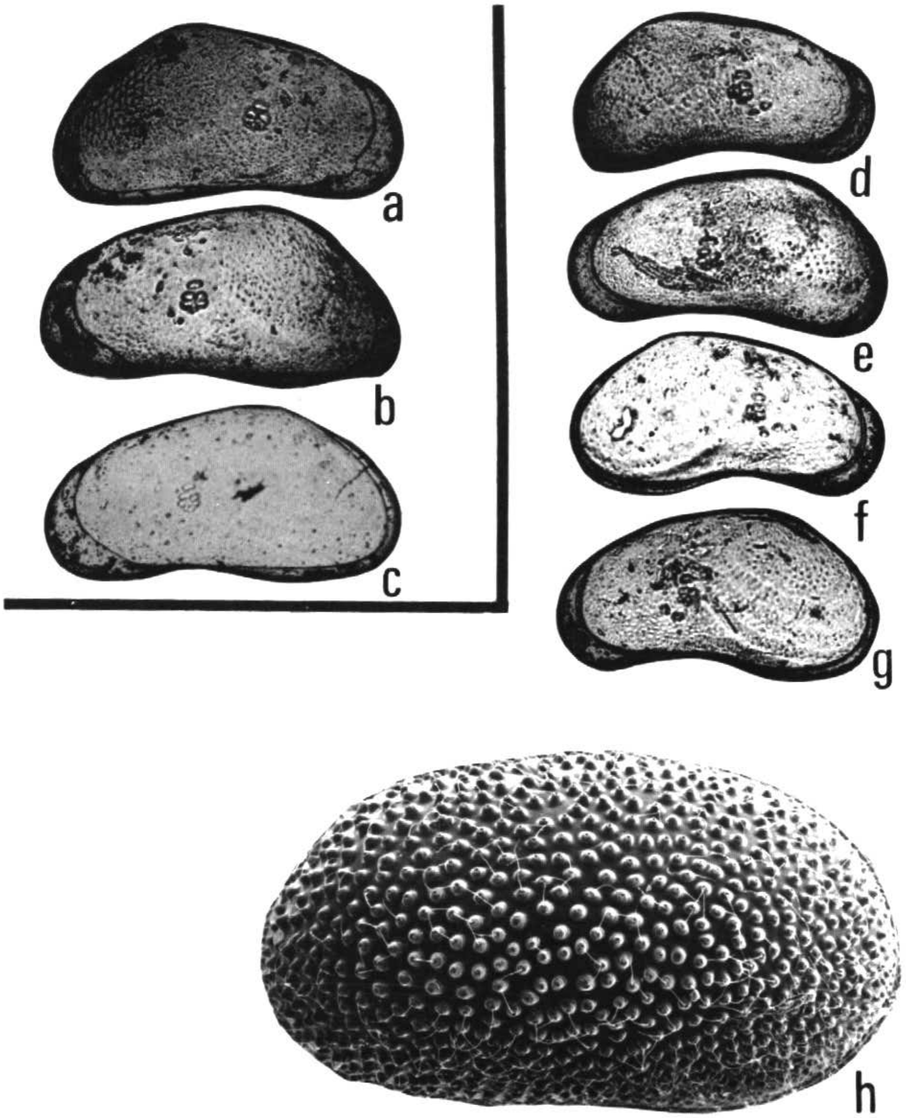

Figure 1 *Exterior views of freshwater ostracodes.*

a-c. Candona acuminata *(Fischer), 1854;* 40 ×
- **(a)** *female right valve*
- **(b)** *female left valve*
- **(c)** *male left valve*

d-g. Candona acuta *Hoff, 1942;* 40 ×
- **(d)** *female right valve*
- **(e)** *female left valve*
- **(f)** *male right valve*
- **(g)** *male left valve*

h. Cypricercus horridus *Sars, 1926;* 100 × *SEM photograph of the left valve.*

thumb that can be used to recognize lacustrine sediments which may contain ostracode shells. Sediments containing molluscan gastropods and pelecyopods (*i.e.*, *Pisidium* or *Sphaerium*) will normally contain ostracode shells. Calcareous gyttja or marl will always be rich in ostracode remains. They will be present in most carbonate-buffered pond or littoral lake deposits. Organic laminae may have abundant shells (Cvancara *et al.*, 1971). Coarse-grained sediments should be avoided. Varves are generally devoid of ostracode shells. Diamicton may occasionally contain ostracode shells (Westgate *et al.*, 1987).

Standard procedures should be followed when collecting lacustrine samples with coring devices (Delorme, in prep.-b). When extruding cores, the sample interval will be a function of the purpose of the study. One centimetre intervals are standard in ostracode work. It may well be that not all the samples will be used, however, the samples are then available if more stratigraphic or paleoenvironmental detail is required from a segment of the core. Sample volume should not be less than 50 mL.

Ostracode shells may be separated from the sediment matrix in two ways. First, one may gently wash the sediments through a bank of sieves (#20 mesh, and #60 mesh). The #60 mesh will retain the majority of ostracode shells although the larger cyprids will be retained on the #20 mesh. The residue should then be oven or freeze-dried. The major disadvantage of this method is the loss of sediment and other microfossils. The second method, which is preferred, is by freeze-drying the sediment. In this procedure, the slice of the core is placed in a vial, frozen, and then placed into an evacuation chamber under a vacuum. After about 48 hours, depending on the size of the freeze dryer, the ice will have been sublimated and disaggregated sediment is left. With all of the sediment retained, analyses for fossil pollen and diatoms (Delorme *et al.*, 1986), size analyses (Duncan and LaHaie, 1979), specific gravity (Holloway and Delorme, 1987), some geochemical work (Wong *et al.*, 1984), ^{210}Pb (Turner and Delorme, 1988) and ^{14}C dating can be carried out on the same sample.

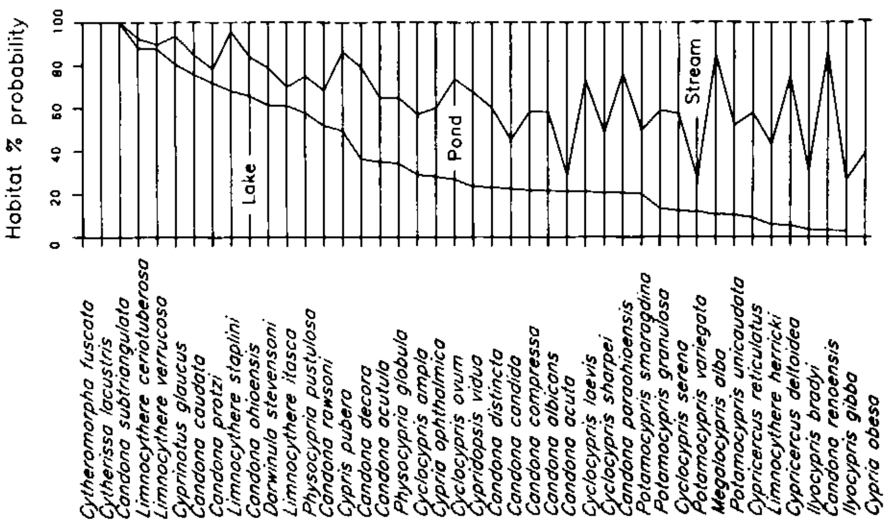

Figure 4 The % probability of finding freshwater ostracodes in a lake, pond, or stream.

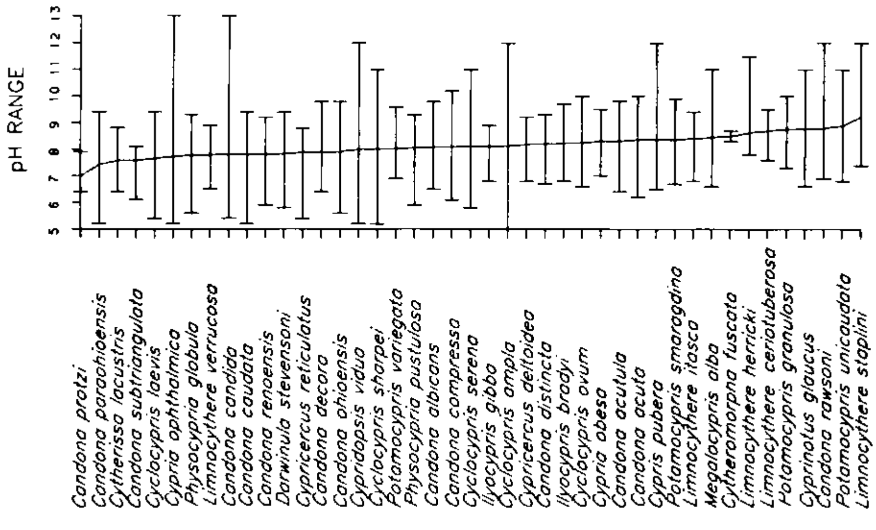

Figure 3 The pH range for some freshwater ostracodes. The solid line represents the mean, while the bars represent the minimum and maximum values.

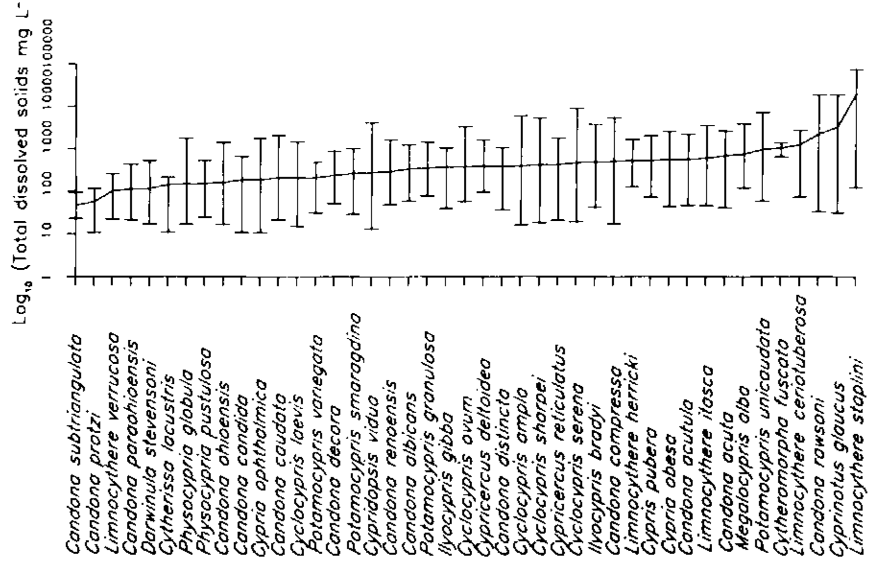

Figure 2 The total dissolved solids range for some freshwater ostracodes. The solid line represents the mean, while the bars represent the minimum and maximum values.

The adult shells are identified and counted using a stereoscopic microscope. Because of the large number of adult shells usually encountered in a sediment sample, only five to ten valves of each species are picked and mounted onto micropaleontological slides. Juvenile shells are not counted. One of the oculars should be equipped with a micrometer so that measurements of length and height of shells can be readily made to aid in species identification. Magnifications up to 750 × are adequate for general taxonomic work. No special preparation of shells is needed. Scanning electron microscopy is useful for detailed work on sculpturing, muscle scar patterns, and internal structures of the valves. As well, soft part morphology for modern specimens may be studied through SEM work.

Quaternary Paleoenvironmental Models

Lacustrine sediment cores have been used for many years to tell us something about lakes and ponds. Paleo-interpretive models are constantly being improved in order to enhance their predictive capabilities and hence paleoenvironmental reconstruction. The major task is to identify significant changes that have occurred in the associated habitats of organisms and hence in the lake.

It is necessary that fossils be recovered from the sediments and that autecological data be available for each species. There then remains the task of taking the qualitative and quantitative autecological information on the species and making some sense out of it.

The modern geographical range of a species in many instances is very restrictive. Species distribution crosses temperature and precipitation boundaries as well as land vegetation zones. The water chemistry of the species habitat will also vary from place to place within its range. In a slice of a sediment core from a pond or lake, there are generally several fossil species represented. When the modern physical and chemical characteristics of the habitats and the geographic distributions of each species are combined into one data set, then an interpretation of what the conditions were like when the sediments were deposited and the fossil organisms lived is possible. Paleoenvironmental parameters have been interpreted based on a specified interpretive model from fossil freshwater ostracodes and their associated autecological data by Delorme (1965, 1971b,c, 1972, 1982), Delorme *et al.* (1977), and Delorme and Zoltai (1984).

If one accepts the assumption that correlations do exist between climatic parameters and chemical and biological species, then the next step is to interpret paleoclimate from autecological data referenced by fossil ostracodes. A review of the model used to interpret past climatic and chemical data will be given.

First, one must take the theoretical faunal assemblage (TFA, Delorme *et al.*, 1977) from a core slice and determine the corresponding net geographical distribution for the modern species counterpart (Delorme, in prep.-a). The gross geographic distribution contains all those modern ostracode sample sites where the species, identified by the TFA, occur; while the net geographical distribution is restricted to the common area where members of the TFA occur. This model includes the autecological data base for those modern samples of the TFA species within the net geographical distribution. These normalized ($\log_{10}$) modern physical, chemical, and climatic data define the attributes for the habitats of the fossil ostracodes. The modern species tolerance limit for each parameter is represented by mean, minimum, and maximum values (Delorme *et al.*, 1977). The *preliminary-interpreted* mean value, *e.g.*, temperature, is the mean value of the parameter weighted using the reciprocal of the variance and the number of the shells in the core sample. Simply, this says if the variance of annual temperature is small for a given species of an assemblage, it will greatly influence the interpreted annual temperature for the sample. Similarly, if the species is represented by a large number of shells in the sample, then the interpreted value will likewise be influenced. For chemical and physical parameters, other than climatic ones, the preliminary-interpreted values are the *final-interpreted* parameters.

The number of years taken to deposit the sediment thickness of the sample may be longer or shorter than a year. The preliminary-interpreted value of the parameter is then an integrated value of maybe a year's duration or more. To compare the interpreted climatic parameter to the observed parameter it may be necessary to integrate several years of observed data, represented in a slice of a core, into one year to produce *revised-observed* data.

The next step in the analysis is to determine a relationship between the theoretical faunal assemblage (TFA) and the twelve monthly climatic values. *Species dependent files* are produced from preliminary-interpreted data from several cores and revised-observed data from nearby meteorological stations. The upper parts of the cores used correspond to the length of time represented by the climatic record of the closest meteorological station. The uncompacted mid-depth of the core corresponding to the first year that climatic data is available, at the nearest meteorological station, dictates the number of samples or lines of data available per core. Data for those ostracodes not represented in the upper portion of the core being analyzed may be obtained from the upper portion of cores in other geographic areas were the fossil species are present.

The relationship between preliminary-interpreted and revised-observed climatic data is expressed as an equation. Transfer functions are established by applying stepwise multiple regression analyses to both revised-observed (independent variable) and preliminary-interpreted derived climatic data (dependent variable) in the species dependant file. The regression analyses produce 12 monthly equations for every species combination found in the TFA for both temperature and precipitation. Preliminary examples of final-interpreted mean annual temperatures (Figure 5) and total annual precipitation (Figure 6) have been provided by Delorme (in prep.-a) for the Clearwater Lake core. Wherever that species composition is encountered in a core slice, the linear equation uses the preliminary-interpreted data to produce a *final interpreted* value of the climatic parameter. The selection of the appropriate equation is based on the climatic parameter selected, correlation coefficient, and the species composition. The selection is based on the highest correlation coefficient derived from the stepwise multiple regression of the species dependant files.

The predictive capability of the final-interpreted value (y) when compared to the revised-observed value (x) is given by the linear expression $y = a + bx$. When the y-intercept $a = 0$ and the slope $b = 1$ then $y = x$ and the relationship is perfect. As the values for the y-intercept approach zero and b approaches one, in the preliminary examples used by Delorme (in prep.-a), 100% of the final-interpreted 12 monthly temperature and precipitation values are acceptable when a is within the range of ± one standard error of a. One hundred (100) percent of the final-interpreted 12 monthly temperature values and 83% of the precipitation values are acceptable when b is within the range of ± one standard error of b.

Paleoenvironmental Reconstruction

The sedimentary record may read like a book, providing the researcher with an insight of what has happened throughout the pond or lake basin's history. In the glaciated regions of Canada, this record started when the glaciers melted from over or near the pond or lake exposing the landscape as we know it today. Ostracodes can tell us a great deal about this record by providing an interpretation of the physical and chemical habitat in which they lived. Several parameters which characterize the habitats will be discussed and examples given where possible.

Habitat. Some ostracode species have a high probability (Figure 4) of being found only in a lake (*Candona subtriangulata, Cytherissa lacustris*; Delorme, 1978, 1982). Other species are found predominantly in ponds (*Candona renoensis, Cypricerus deltoidea*) while others are mainly confined to moving waters, such as streams and springs (*P. variegata, Ilyocypris gibba, Cypria obesa, Ilyocypris bradyi*). This means when these indicator species in combination with other ostracode species are recovered, the physical habitat can be interpreted for that core slice. Based on the fossil ostracodes from the sequence of sediment slices the physical habitat is reconstructed for the total length of the core. In addition, the depth of water above the sediment-water interface at the collection site can be interpreted as can the distance to the nearest point of the shore. As successional development progresses, one should be able to see the physical habitat getting smaller by virtue of sediment infilling which reduces the water volume and depth of water (Delorme, 1971a). An increase in the volume of water would indicate a change in climate, sill level or erosion (Delorme, 1982).

Salinity. The optimal salinity or total dissolved solids for the habitat of Canadian freshwater ostracodes is between 100 and 1000 $mg \cdot L^{-1}$, although the maximum can go up to 18800 $mg \cdot L^{-1}$ (*Limnocythere staplini*, Figure 3). In closed basins, salinity values can get very high, while flow-through systems have a more constant flushing rate and a lower salinity (Delorme, 1971a,b). Implicit in the interpretation of the habitat's salinity is the ability of the model to interpret average concentrations of the major ions for each core slice.

Oxygen/anoxia. A number of ostracode species have become notably absent from the central basin of Lake Erie (Benson and MacDonald, 1963; Delorme, 1978). It has been shown that both the life cycle and the requirement for dissolved oxygen have played a role in the survival of *Candona subtriangulata* and *C. caudata* (Delorme, 1982) in Lake Erie. *C. subtriangulata* has a life cycle of over one year and also has a minimum requirement for dissolved oxygen of 5.6 $mg \cdot L^{-1}$. When the central basin of Lake Erie becomes anoxic during the summer, oxygen levels go below 5.6 $mg \cdot L^{-1}$ and the species does not reach sexual maturity. Over a few years, this species' egg pool becomes depleted and the species becomes locally extinct. Another species, *C. caudata*, has a life cycle of three to four weeks and a minimum dissolved oxygen requirement of 2.3 $mg \cdot L^{-1}$. Although the oxygen levels go below 2.3 $mg \cdot L^{-1}$ in the central basin and the species does not survive during the anoxic period, it persists in Lake Erie because the species reaches sexual maturity and lays eggs during other times of the year.

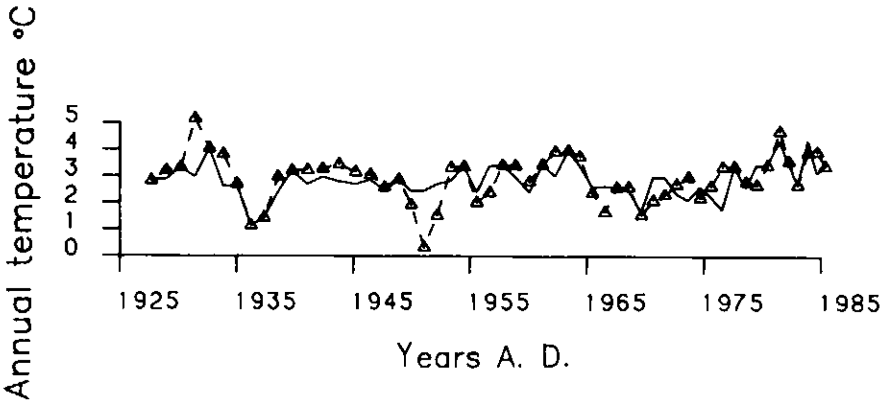

Figure 5 *Mean annual temperature profile based on revised-observed (dashed line with triangle) and final-interpreted (solid line) values for the last 60 years of sediment deposition from Clearwater Lake core. (After Delorme, in prep. - a).*

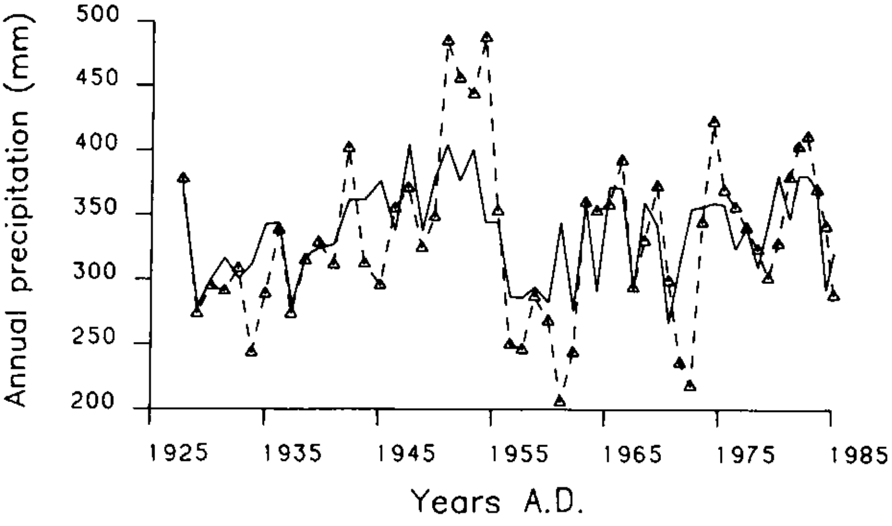

Figure 6 *Total annual precipitation profile based on revised-observed (dashed line with triangle) and final-interpreted (solid line) values for the last 60 years of sediment deposition from Clearwater Lake core. (After Delorme, in prep. - a).*

Temperature/precipitation. Freshwater ostracodes may show an indirect relationship to climatic parameters (Forester, 1983; Delorme, in prep.-a) through salinity and probably more specifically through solute composition. There are several species which are restricted to a geographical area, apparently controlled by climate. Delorme and Zoltai (1984) and Delorme (1971c) indicate that such species as *Candona protzi* and *Cyclocypris globosa* are found only north of latitude 65°, and *Candona rectangulata* is restricted to north of latitude 62°. However, these species have been found as fossils in basal lacustrine sediments of southwestern Manitoba (49°23'N lat, 98°35'W long) indicating a cold-climate, cold-water type of environment adjacent to a retreating ice-margin. Conversely, species found in sediments (7100 to 8610 years B.P.) at the Jiggle Lake site (67°41'N lat, 132°07'W long) reflect a warmer climate like that found on the Canadian prairie today (Delorme and Zoltai, 1984).

Conclusions

The use of Quaternary freshwater ostracodes is a recent advance in paleoenvironmental research. The reasons for this relatively new interest has been a confused systematics of the group and a lack of autecological data. The systematics are not as unaccommodating as they may appear with many good references now available. For Canada and the northern United States, autecological data are now available.

A carefully designed model is used to interpret Holocene paleolimnologic and paleoclimatic conditions. These results are acceptable within certain statistical limits. The most important aspect of these studies and their results is that they provide trends in water chemistry, changes in the physical habitat, and paleoclimate. These trends and changes may be equivalent to temporal or regional variation. Some workers are still hesitant to accept objective paleoenvironmental results, but more and more there is the acceptance that the fossils did exist at the time the lacustrine deposits were being deposited and that their distribution may have been controlled, in their environments, by physical and chemical factors. We are attempting to understand these relationships in the modern fauna. As pointed out by Smol (1987) and many other paleolimnologists, the best approach is the multi-disciplinary approach, each approach complimenting the other.

Current concerns regarding climatic change in Canada are centered in two regions: the prairies (Arthur, 1988) and coastal areas including the Great Lakes. The agricultural economy of the prairie region fluctuates with climate. Long-term climatic records are not available for this region, therefore, those wishing objective data going back farther in time for research on drought scenarios must rely on climatic proxy data. We are now at the point in this research where we can begin to produce such data from the Holocene lacustrine record. Changes in climate may affect water levels in coastal regions (Sanderson, 1987; Martec Limited, 1987; P. Lane and Associates Limited, 1988). Despite control structures on the Great Lakes system, fluctuations in water levels related to climate do occur. Extensive water level fluctuation data for the Great Lakes are not available. Therefore, lacustrine sediments, with their inherent fossils, should be able to provide objective water level and paleoclimatic data.

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