Cladocera in space and time: Analysis of lake sediments

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Abstract

Shells of Bosminidae and Chydoridae are quantitatively preserved in lake sediments. The chronological deposition of these remains provides the means for longterm observation of these Cladocera, both in terms of species and communities.

Chydorid analysis, as based on subfossil assemblages, is an analysis of community and provides direct observation of community dynamics over extended periods of time. It has proved to be a valuable method to obtain information on the influence of environmental factors and time on community characteristics.

Morphological variation in *Bosmina* (*Eubosmina*) has been followed for some thousand years. This is of special interest for the evaluation of taxonomic rank (species, forms) if closely related taxa have co-existed.

Bosmina successions, as well as shifts in the chydorid fauna, are related to environmental change. Thus, cladoceran analysis of lake sediments provides information on the developmental history of lakes and allows observation of the effects of longterm environmental changes, such as climatic changes and eutrophication.

Introduction

In deep, stratified lakes sediments are deposited in chronological order. Analysis of such sediment records has become the most significant method of reconstructing the developmental history of lakes.

Remains of plants and animals document the flora and fauna of past lake stages. They have been used successfully (1) to follow the development in certain taxa and (2) to indicate former environmental conditions.

However, not only is this method particularly interesting for the description and elucidation of the developmental history of lakes, but it is also of more general interest in providing an opportunity for long term observation of populations and communities. This is of particular significance in some areas of general biology and ecology where processes that continue over extended periods of time, such as evolution and community succession, cannot be analysed by direct observation or experi-

ment. This is also true for environmental changes, such as climatic changes, eutrophication/oligotrophication, and the aging of ecosystems. Analysis of animal remains in lake sediments is a method of direct observation over such very long periods of time and a source of information on these longterm processes.

An important methodological limitation lies in the fact that only a very small fraction of the lake fauna is represented by remains in the sediment, while, furthermore, an even smaller portion is available in sufficient quantity in small sediment volumes, as usually obtained by coring methods. In general, only three groups of animals comply with the methodological requirements: Chironomidae, Ostracoda, and Cladocera (Frey, 1964). Among the latter, only those taxa represented by remains that allow species determination and morphological analysis can be considered, i.e. the planktonic Bosminidae and the littoral Chydoridae (Frey, 1976).

The Chydoridae

Due to the work by Frey (1958, 1959) identification of subfossil head shields and shells of Chydoridae has become relatively easy. This has stimulated cladoceran analysis in paleolimnological research.

Frey (1960, 1976, 1986) also provided comprehensive summaries of cladoceran analysis of lake sediments and a report on methods for conducting such analyses. Hence, this paper concentrates on particular points which need further discussion and which are related to presentation and interpretation of results of chydorid analysis.

Extensive information on the ecology of chydorid species is available in the literature, for example Poulsen (1928), Flössner (1964, 1972), Whiteside (1970), Hollwedel (1975/76), Frenzel (1982). The data clearly show that the relationships between the occurrence of individual species and particular ecological conditions or particular water bodies are generally rather poor. With respect to the analysis of chydorid remains from lake sediments, the indicator value of individual species is therefore low. Hence, Frey (1976, 1986) emphasized the use of community analysis methods.

Initially one must establish what was happening in the chydorid assemblage. Conventional plots of abundance or relative abundance of the individual species against sediment depth very often show no clear trends in community development. However, a plot of percentage-classes of species by symbols facilitates assessment of the whole assemblage and reveals shifts in the predominating species discernible (Hofmann, 1978a, 1984a). Thus, the pattern of time-space distribution of relative abundances is based on classes of percentages and not on percentages alone, for which confidence limits are almost always unknown. This method, therefore, produces a general pattern of development and avoids statistical analysis.

One disadvantage in the use of percentages lies in the fact that the values are interdependent: a decrease in the abundance of one species produces an increase in the percentages of the other taxa. Furthermore, the percentage of a species may decrease, even though its absolute abundance, calculated from accumulation rates, increases. However, in long-core studies there is generally a lack or an insufficient number of dated horizons. Dates only at the pollen zone boundaries are inadequate, as they neglect variation in sedimentation rates within pollen zones. Thereby, an error of unknown magnitude is introduced in the calculation of accumulation rates where mean sedimentation rates are used for long periods of time.

Further treatment of the data in terms of community analysis has been summarized and discussed by Frey (1986). This may include similarity indices, cluster analysis, calculation of species diversity and evenness, correlation, regression, discriminant analysis. These methods lead to data reduction and facilitate the recognition of general trends. Because manipulation of the original data is involved, a critical evaluation of the methods and the results is strongly recommended (cf. Frenzel, 1982).

With respect to the interpretation of data, it must be remembered that the assemblages of chydorid remains found in the sediment are secondarily composed assemblages that are not identical with the communities from which they originated. Chydorid species are not distributed randomly over the littoral zone but instead prefer particular habitats, such as macrophytes, sand, or mud. So, the percentage composition of the chydorid fauna in the total littoral zone, and consequently the assemblage of remains in the sediment, are determined by the diversity of the habitats in the lake (Table 1). This means that subfossil assemblages do not represent communities as such but originate from a variety of different communities.

Interpretation of such subfossil assemblages is used to reconstruct former communities and their environments, i.e. a reconstruction of the characteristics of the former littoral zone. It cannot be overstressed that this is a very difficult and often ambiguous work. Whiteside & Swindoll (ms.) have shown impressively how many varied biotic and abiotic factors are involved. The chydorids are exposed to these and may respond to even small changes in them.

Most chydorid species occur preferentially in certain littoral habitats, but their distribution is in general not restricted to a particular type of habitat (Flössner, 1964; Whiteside, 1970), thus of course reducing their indicator value.

With such limitations, it seems more profitable to outline a scenario of the conditions over a certain period of time on the basis of all the data available, rather than a priori to favour certain factors,

Table 1. Hypothetical chydorid assemblages of different littoral habitats and the resulting assemblage of remains in the sediment.

Littoral habitats	Macrophytes	Sand	Mud
Chydorid species	*Acroperus harpae* *Graptoleberis testudinaria* *Alonella exigua*	*Chydorus piger* *Monospilus dispar* *Rhynchotalona falcata*	*Leydigia quadrangularis* *Pleuroxus uncinatus* *Disparalona rostrata*
Assemblage of chydorid remains in the profundal sediment		*Acroperus harpae* *Pleuroxus uncinatus* *Graptoleberis testudinaria* *Chydorus piger* *Monospilus dispar* *Alonella exigua* *Leydigia quadrangularis* *Rhynchotalona falcata* *Disparalona rostrata*	

such as climate, eutrophication, or predation.

Case studies of various lakes have shown that chydorid assemblages may indeed respond distinctively to climatic changes and to eutrophication. These responses can be read from changes in the community structure.

In different areas (Denmark, England, Germany, Switzerland) (Harmsworth, 1968; Goulden, 1964; Whiteside, 1970; Hofmann, 1978a, 1983, 1984a; Lotter & Boucherle, 1984) the same developmental trend in the chydorid fauna occurred: a poor fauna in the late-glacial period, with increasing diversity in the following postglacial, leading to an almost constant maximum. As a whole this development obviously does not represent a maturing of the original chydorid community (Goulden, 1969), but indicates the existence of two different communities.

The late glacial assemblage cannot be considered an immature phase of a postglacial mature stage, but is itself equivalent to a specific community that is controlled by the extreme climatic conditions of that period:

1. The species composition was almost identical in the areas under discussion (*Acroperus harpae, Alona affinis, Alonella nana, Chydorus sphaericus*).

2. These species were classified by Harmsworth (1968) as arctic and subarctic according to their latitudinal affinities.

3. Such assemblages do not change if the climatic conditions remain extreme, as shown by Boucherle (pers. comm.) fo the Hobschensee (Swit-

zerland), an alpine lake (2017 m a.s.l.) with 5–7 months of snow cover per year. In this lake a similar poor assemblage remained constant for 8000 years. A rather stable chydorid assemblage consisting of almost the same species has been reported by Einarsson (1982) for the 2300 year-history of the Iceland water Lake Myvatn.

An immature stage of the chydorid fauna occurred at the beginning of the postglacial period, when the climate ameliorated. The community response shows a rapidly increasing diversity (Harmsworth, 1968; Goulden, 1964; Whiteside, 1970; Hofmann, 1978a, 1983, 1984a; Lotter & Boucherle, 1984).

In these cases the dynamics of the diversity mainly reflect climatic conditions.

During the postglacial period diversity may decline again, which generally indicates a disturbance of the community (Goulden, 1969). Crisman & Whitehead (1978) found a decline in chydorid diversity an equitability associated with increasing production in Berry Pond, Massachusetts.

In some cases where a change in diversity was connected with a change in the predominant species, an opportunity is afforded to specify the nature of the disturbance. For instance, in the Großer Segeberger See the predominating *Acroperus harpae* and *Eurycercus lamellatus* were replaced by *Alona rectangula*. In the uppermost layers all the dominant chydorids were species typical of polluted sites, most of them mud dwellers (Whiteside, 1970). Hence, there was a shift from species depending on macrophytes to those living in the mud.

A similar development has been observed in the eutrophic Eifel lake, Meerfelder Maar (Hofmann, 1978a, 1984a).

Such shifts in the chydorid community structure can be explained as a function of the increase of muddy areas at the expense of macrophytes in the littoral zone. This occurs in heavily polluted lakes characterized by extended algal blooms. Hence, the observed shift indicates a response to one effect of eutrophication.

However, chydorids react to eutrophication only if their littoral habitats are affected. Two north German lakes, the Großer Plöner See and Schöhsee, were subject to postglacial eutrophication as indicated by the profundal chironomid fauna (Hofmann, in press a). In these cases, however, eutrophication was not reflected by the chydorid assemblage. There was a rather uniform assemblage with minor internal shifts throughout the postglacial period, and only slight changes occurred in the percentages of 'polluted water species' and 'clear water species' (Whiteside, 1970). There were always a considerable number of species typical of oligotrophic lakes (following Flössner, 1972), indicating that suitable littoral habitats for species sensitive to the effects of eutrophication remained. Hence, the littoral zone was very little affected by eutrophication.

In general, it is not possible yet to explain minor shifts within the assemblages, even when they are rather distinct, because of the low indicator value of the individual species. Hence, an increase in a species typical of polluted conditions should by itself be considered an indication of eutrophication. Eutrophication of the littoral zone should be reflected by changes in the assemblage as a whole. Furthermore, one must consider which effects of eutrophication (or oligotrophication) may have occurred in the littoral zone and affected the composition of the chydorid fauna.

As chydorids are used as indicators of former environmental conditions in the littoral zone, one must be certain that all the species involved were living there. In polluted lakes *Chydorus sphaericus* invades the pelagic zone in high numbers and becomes superabundant in the chydorid assemblage of the sediment, consequently lowering the diversity (Hofmann, 1978a). In this case *Chydorus sphaericus* should not be included in a calculation of littoral diversity, because it mostly was not a member of the littoral community, i.e., here the decline in diversity was produced by mixing littoral and pelagic elements.

To summarize, analysis of the structure of chydorid assemblages from lake sediments can provide information on community dynamics and their environmental controls, such as climatic and trophic conditions.

The genus *Bosmina*

Frey (1962) found that chydorid species from the Eemian Interglacial of Denmark showed no morphological differences compared with recent populations. In contrast, the great variety of morphological forms in the subgenus *Eubosmina* has developed in the postglacial period (Rühe, 1913/14; Lieder, 1983a, c). This period is fully represented by sediments from lakes of glacial origin. The analysis of *Bosmina* remains from these sediments provides a direct, continuous observation of morphological variation in the period under discussion, and enables demonstration of the evolution of different morphs. This has been a major aspect of *Bosmina* analysis.

The results obtained from north German lakes in the vicinity of Plön can be summarized as follows (Fig. 1): The deep, stratified lakes share the same *Bosmina* (*Eubosmina*) succession. In the lateglacial period only *Bosmina longispina* was present. This species exhibited significant morphological variation, particularly in mucro length, producing *reflexa* morphs in the Subboreal and the Subatlantic. The species became extinct during the early Subatlantic and no longer exists in any lake in this area.

A second species, *B. coregoni* f. *kessleri* invaded the lakes in the Boreal. In this case successive mucro reduction led to a mucroneless *B. coregoni* f. *coregoni,* which still occurs in the lakes (Hofmann, 1978b, 1984b).

This provides the simplest explanation of the morphological variation found in the *Bosmina* material. However, transitional lines from *longispina* to *reflexa* and from *kessleri* to *coregoni,* as well as the consideration of *reflexa* as a morph of *longispina,* and *kessleri* as a morph of *coregoni,* contradict the classification of Lieder (1983a, c) based on recent populations.
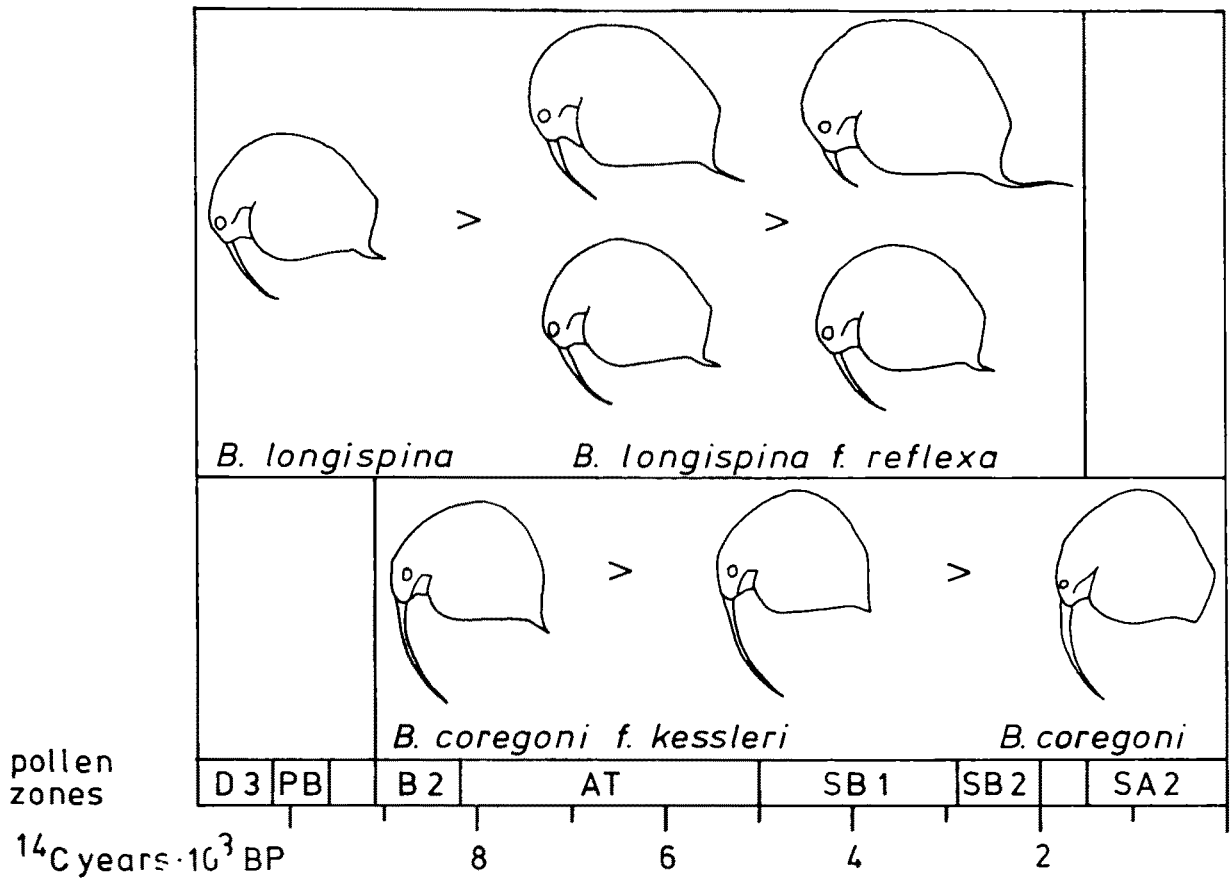
Fig. 1. Großer Plöner See (north Germany): synoptic view of the *Bosmina* (*Eubosmina*) fauna during late glacial and postglacial times (from Hofmann, 1984b).

Lieder (1983b) stresses the significance of hybridization between *B. longispina* and *B. corego-* mucroneless *B. coregoni*, which he believes produced the morphological variation in this subgenus.

However, analysis of the remains of *Bosmina* in the sediments shows:

1. There is no morphological indication of hybridization between *B. longipina* and *B. corego-ni*. Although these closely related species co-occurred for more than 6000 years, shells and antennulae were always separable. Furthermore, the morphological differences between them increased during the postglacial period because of divergent morphological variation in mucro length and in antennule characters.

2. There is no indication that *kessleri* was a product of hybridization between *longispina* and

coregoni, because *kessleri* occurred in the lakes before *coregoni* appeared. There was no temporal overlap between *longispina* and *coregoni*.

3. For the *Bosmina* in the lakes under discussion, the taxonomic treatment proposed by Lieder produces results that are inconsistent with the biological species concept, particularly his consideration that *kessleri* and *reflexa* are subspecies of *B. mixta*.

The present situation is that two different approaches have led to different results concerning *Bosmina* taxonomy. Further discussion and analysis of the problem is therefore desirable.

Two additional examples also indicate that species of the subgenus *Eubosmina* tend to exhibit enormous morphological variation. In a late glacial population of *B. longispina* from Lobsigensee (Swiss Plateau) from the Oldest Dryas to the Pre-

boreal, the number of antennule segments decreased in such a way that ultimately there was no overlap in this character with the original population (Hofmann, 1984c).

Some hypereutrophic north German lakes are inhabited by the backward-arched form *thersites* of *B. coregoni*. Analysis of *Bosmina* remains in short sediment cores showed that in the lowermost layers only typical *coregoni* specimens occurred. Above this zone there was gradual morphological transition both in shell and antennule characters, to the *thersites* form, so that in the uppermost layers only *thersites* was present. The *coregoni* phase and the *thersites* phase were connected by a period of polymorphism. It is not clear whether the polymorphism was induced by an immigrating population or whether it occurred within the original population (Hofmann, in press b).

The occurrence of different *Bosmina* species and morphs is related to the trophic state of the lakes (Patalas & Patalas, 1966) such that a change in this state should cause species succession.

The replacement of *Bosmina longispina* (in some cases called '*coregoni*' (Deevey & Deevey, 1971)) by *B. longirostris* as observed in several lakes, has to be considered a classical case of eutrophication-induced species succession (Deevey, 1942, 1969; Frey, 1955; Goulden, 1964; Crisman & Whitehead, 1978). Boucherle & Züllig (1983) showed the rate at which this replacement can occur – from *longispina* to *longirostris* and then back to *longispina* as the lakes recovered. In one lake the shift to *longirostris* seemed to occur in a single year. In the case of Rogers Lake, Deevey (1969) stressed the importance of invertebrate predation in bringing about this change.

Similarly in the north German lakes mentioned above, the succession from *B. longispina* to *B. coregoni* f. *kessleri* and finally to *B. coregoni* f. *coregoni*, is a succession of taxa typical of oligotrophic, mesotrophic, and eutrophic lakes (Patalas & Patalas, 1966). It is, however, not known which particular factor induced the *Bosmina* succession.

The existence of morphological transitions from *kessleri* to *coregoni*, and (finally?) to *thersites*, would lead to a transitional line between *kessleri* and *thersites* that is possibly initiated by eutrophication, implying that the different morphs are related to different trophic conditions. They would thus represent eco-phenotypes as mentioned by Lieder (1983c) for some *Bosmina* forms.

In the case of the Großer Plöner See and the Schöhsee, the results obtained from the faunal remains, including Chironomidae, *Bosmina*, and Chydoridae, have been summarized. The chironomid-indicated lake type succession is also reflected in the species succession within the subgenus *Eubosmina*. There was, however, no simultaneous development in the profundal and the pelagic zone (Hofmann, in press a).

The chydorids changed most dramatically at the beginning of the postglacial period. There were no distinct responses to eutrophication, with the exception of a slight change in the Subatlantic 2 of the Großer Plöner See (decreasing diversity and percentage of clear-water species, increase in polluted-water species). This correlates with recent conditions in the lakes, as the eutrophic character is more distinct in the Großer Plöner See than in the Schöhsee (Hofmann, in press a).

In conclusion, cladoceran analysis of lake sediments is indeed a method by which long term biological and ecological processes can be observed. There is, however, need for a better data background for correct interpretation. Furthermore, the use of equivalent analytical methods is desirable to compare developments in different lakes from different areas. This would lead not only to the recognition of typical developmental patterns and the separation out of local features, but would also lead to correlation of late-glacial and postglacial events between different areas, contributing to a more general view of Cladocera in space and time.

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