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Recent lake acidification and cladoceran dynamics: surface sediment and core analyses from lakes in Norway, Scotland and Sweden

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To interpret the remains of Cladocera in lake sediments in relation to pH history, fish abundance, vegetation change, trophic level change and other historic events, it is necessary to understand the balance of abiotic and biotic forces responsible for their present distribution, population dynamics and morphological types. Once these factors are understood, we can reverse the arguments to infer past lake conditions. Many cladoceran species are influenced by fish and invertebrate predation. Some species, especially in the plankton, also show a clear physiological relation to pH and aluminium levels in lakes. Moreover, several littoral–benthic species have a habitat distribution restricted to rock, sand, mud, vegetation, or a combination of some of these.

Remains of littoral and planktonic cladocerans were analysed in surface sediments of 18 Norwegian lakes with pH ranging from 4.5–7.5. In addition, sediment cores from four sites in Norway, four in Scotland and one in Sweden were analysed. The majority of sites showed evidence of recent acidification. In lakes with non-planktivorous fish, analyses of cladoceran remains gave no information on past fish populations, but indicated the pH history of the lakes. In lakes with present or past populations of planktivorous fish, the cladoceran record could be used to assess past fish status as well as past pH. In some lakes changes in the cladoceran communities could be related to changes in macrophyte distribution.

Introduction

Cladocera recovered from lake sediments in palaeolimnological studies are usually restricted to the primarily littoral–benthic dwelling family Chydoridae, whereas representation of planktonic species is usually restricted to *Bosmina* spp. (see, for example, Alhonen (1970)). Complex aquatic interactions are therefore impossible to reconstruct, especially as many species (e.g. copepods) are not preserved in the sediments.

Until recently, Cladocera remains have been mainly used to show development from oligo- to eutrophy in lakes. Species replacement within the Chydoridae and the genus *Bosmina* is very marked and easily assessed where there have been clear changes in lake trophy and fish predation (Whiteside 1970; Kerfoot 1974; Hofmann 1978; Boucherle & Züllig 1983).

The use of cladoceran remains to reconstruct acidification is a more difficult task. The changes in species abundance and composition over small pH ranges can be difficult to detect and demand a thorough knowledge of the ecology of the animals involved in the change (Nilssen 1978; Nilssen & Sandøy 1986). In addition, there are very few quantitative studies of crustaceans over a gradient of pH below 5.5.

Changes in cladoceran composition have been associated with acidification, but many, if not

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the majority, of these are related to predation and vegetation changes and thus only indirectly related to varying pH.

This study aimed to explore the use of cladoceran analysis in detecting changes in predation, pH, vegetation and other historic events in acid and acidified lakes (see Frey (1960)). We focus on the planktonic communities that are better pH indicators than the littoral communities and present results from a study of surface sediment samples for 18 lakes and of cores from nine lakes.

Sites, materials and methods

The cores were from Norway (Verevatn, Gulspettvann, Holmevatn, Röyrtjörna), Scotland (Loch Chon, Loch Tinker, Lochan Dubh, Lochan Uaine) and Sweden (Lilla Öresjön) (see Battarbee & Renberg, this symposium).

Sampling for surface sediments was done in 1985 and 1986 with a gravity corer, the Skogheim sampler (Skogheim 1979), usually at the deepest part of each lake. The sediment cores were extruded immediately on the shore of the lake, or within two days in the laboratory.

Samples of wet sediments were heated and stirred with a magnetic stirrer in 100 g l^{-1} KOH for about 1 h to deflocculate the sediment. The samples were then sieved through 90 μm and 20 μm mesh sizes, to retain small shell parts. Subsamples of a known volume were transferred with a pipette to a heated slide and mounted in glycerine jelly, then covered with a cover slip. Identification, counting and measurements were made under a microscope at times 80 magnification. For each sediment sample, the most abundant body part was chosen for each species to represent the number of individuals, weighted by the number potentially contributed by one individual in one mount. Except for a few samples with very low numbers of cladoceran remains, at least 200 individuals were counted.

In addition, we measured total shell length, rostrum and mucro on *Bosmina* spp., length of postabdomen on *Daphnia* spp., shell or postabdomen, or both, on the large-sized Chydoridae: *Alona affinis*, *Acroperus elongatus*, *A. harpae* and *Eurycercus lamellatus* to detect effects of fish predation in the littoral–benthic zone.

To identify unknown body parts, remains collected from the sediment surface were compared with animals sampled with a 90 μm plankton net. Two methods were used: cladoceran remains were digested with hydrochloric acid and the remaining parts studied under a microscope, or animals were mounted in polyvinyl lactophenol on a slide covered with a cover-slip. After two days they became transparent. Most of this work concentrated on planktonic animals, but non-chydorid littoral animals were also studied.

This method enabled all planktonic Cladocera and most non-chydorids in the littoral–benthic region (species not commonly included in palaeolimnological studies) to be counted. These analyses greatly increased processing time and led to difficult taxonomic problems. However, our simultaneous ecological studies in lake enclosures, pH-manipulated lakes and natural lakes over a wide pH gradient have made the analyses and interpretations easier.

Cluster analyses were done on a DEC VAX 8600 at the University of Oslo with the programme SPSS-X.

RESULTS AND DISCUSSION

(*a*) *Acidification of lakes and changes involving Cladocera*

The major processes that affect animals in acidified lakes change physiological, competitive and predatory interactions. Major pelagic taxa, like fish and daphnids, are physiologically vulnerable to acidic environments, whereas other species like the important invertebrate predators: copepods, corixids and *Chaoborus* can withstand considerable acidity (Nilssen *et al.* 1984). The changing species composition with decreasing pH seems in most cases to have only an indirect relation to pH. The most important factor for the species composition of zooplankton was found to be high aluminium concentrations and low food supply (Hörnström & Ekström 1983). During acidification below pH 5.2–5.5, fish have problems with reproduction and population densities decrease strongly. The invertebrate predators, both in the littoral and in the pelagic zones, increase with acidification (Nilssen 1980; Stenson 1985).

The benthic community becomes different from that in non-acidified lakes. The increase in the periphyton growth and the expansion of *Sphagnum* spp. and *Juncus bulbosus* f. *fluitans* imply an increase of the total plant biomass and a change in the physical structure of the habitat. Simultaneously, some macrophytes may decrease with acidification, e.g. isoëtids (Eriksson *et al.* 1983; Wallin & Renberg 1985).

There are problems in assessing cause–effect relations with changes in species composition and abundance in acidified lakes. Furthermore, it is evident that the alternations observed in the acidified systems have a multi-causal background. The effect of the many stresses produced by biotic and abiotic factors will vary between different organisms.

(*b*) *Habitat relations of the species recorded in this study*

The habitat relations of the littoral–benthic species recorded in this study are shown in figure 1. The expansion of *Sphagnum*, *Juncus bulbosus* f. *fluitans* and the increase of filamentous algae (reported in Nilssen (1980); Eriksson *et al.* (1983); Stenson (1985)) have created new habitats, microhabitats and new feeding niches, which may have contributed to the faunal development of Cladocera in the littoral and profundal parts of the lakes. Even if other macrophyte species have decreased due to low pH and competition from the new plants, the new habitats created by the colonizing plants may have allowed larger populations of littoral–benthic species of Cladocera to develop. If, conversely, the decreasing macrophytes are not replaced by new plant species, there will be fewer habitats available for the littoral–benthic species and the total diversity may decrease. If the macrophytes die out, the composite habitat of plants and soft mud will be replaced by a habitat of coarser mud, resulting in a change in littoral–benthic species composition (cf. figure 1.).

(*c*) *Predation and cladoceran remains*

Table 1 shows the general relations between fish predation and cladoceran abundances and communities. As the genus *Bosmina* is an important prey species both for fish (the larger specimens) and invertebrate predators (the smaller specimens), its morphology was investigated in detail. Large Chydoridae were also measured, but so far no clear relation with fish predation has been found (S. Sandøy & J. P. Nilssen, unpublished data).

Figure 2 shows the distribution of shell length and mucro length of small and large specimens of *Bosmina longispina*, respectively, comparing lakes with planktivorous fish (13, 15) and lakes

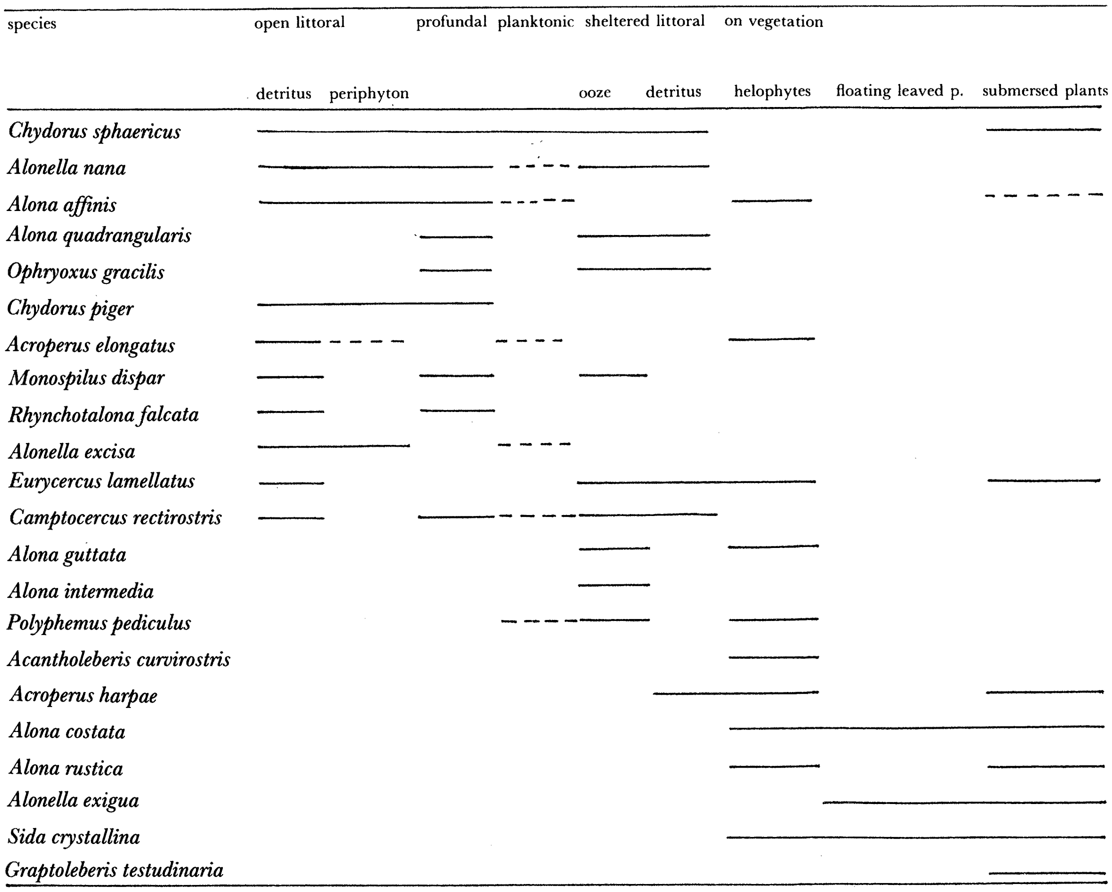

Figure 1. Habitat ecology of the littoral–benthic species recorded in this study (based on Fryer 1968; Whiteside 1970; Whiteside & Swindoll 1988; Flössner 1972; S. Sandøy & J. P. Nilssen, unpublished data). Most important habitats marked with continuous line, and occasional occurrence with dotted line. Comments on separate species: *E. lamellatus*, *C. rectirostris*, *A. affinis*, *A. harpae*, *A. quandrangularis*, *A. elongatus* (larger species, potentially subject to fish predation); species common in and between *Spagnum* spp.: *A. curvirostris*, *A. rustica*, *A. excisa*, *A. nana*, *C. piger*, *C. sphaericus*; sand: *M. dispar*; rock–sand: *A. elongatus*, *R. falcata*; mud: *C. piger*, *A. quadrangularis*, *A. intermedia*; vegetation: *G. testudinaria*, *S. crystallina*, *C. rectirostris*, *A. harpae*, *A. affinis*, *A. nana* (the last two species are less strongly associated with vegetation).

Table 1. Occurrence of Cladocera as related to fish abundance and lake pH

(Degree of planktivory among fish species depends upon lake size, share of littoral region and fish species competition. With pH below 5.0, fish and *Daphnia* spp. are usually not present if humic levels are low and aluminium is above 200 $\mu g\ l^{-1}$. Fish abundance and lake pH are based on literature and unpublished data (J. P. Nilssen & S. Sandøy).)

	planktivorous fish	
	absent	present
low pH	few or no *Daphnia*, no *Leptodora*, no *Bythotrephes* large-sized Chydoridae and Macrothricidae	uncommon combination in Scandinavia
high pH	large-sized *Daphnia* few small-sized plankton species	small *Daphnia*, small-sized species adaptation to invertebrate predators

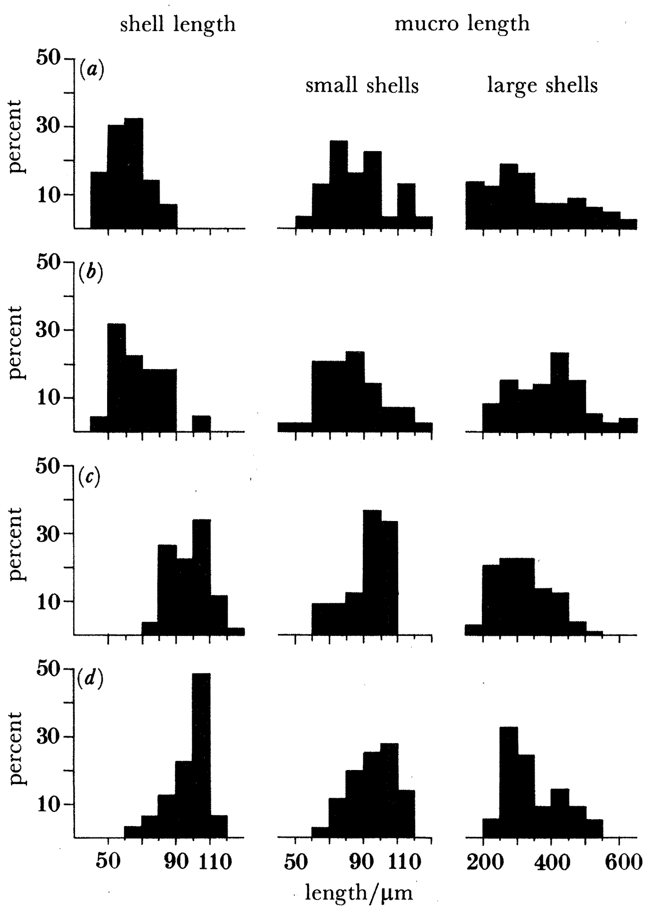

FIGURE 2. Size distribution of body shell and mucro of *Bosmina longispina* from animals of different size classes (small body shell length ⩽ 300 μm) related to pH and predation. Lakes 13 (*a*), 15 (*b*) have medium densities of planktivorous fish and pH 6.2 and 6.4, lakes 3 (*c*), 7 (*d*) are fishless and of pH 4.6 and 4.8.

without fish (3, 7). Generally the size range of *Bosmina* with planktivorous fish followed a normal (Gaussian) distribution, whereas acid fishless lakes showed a skewed size range pattern. Small specimens of *Bosmina* had comparably larger mucro length in acid fishless lakes, probably an adaptation to increased invertebrate predation. The change in the size distribution of *Bosmina* in Gulspettvann took place at the same time as pH decreased in this lake (around 4–5 cm depth) (figure 3). The mucro length of the small *Bosmina* showed comparable changes as indicated in figure 2. However, rostrum length remained constant throughout the core (S. Sandøy & J. P. Nilssen, unpublished data).

Laboratory and field studies have shown *Bosmina* to develop larger mucro and rostrum in response to copepod predation (Kerfoot 1977). In other studies, only the mucro length increased (Wong 1981). In all acid lakes in this study, mucro length increased in small-sized individuals, probably as a response to predation by invertebrates, such as *Heterocope* spp. (cf. Burckhart 1944).

We would have also expected an increase in body and rostrum size with acidification; the first as a response of decreased size-selective predation from fish and the latter due to increased invertebrate predation. In the less acidic lakes we recorded all size groups of *Bosmina*, whereas

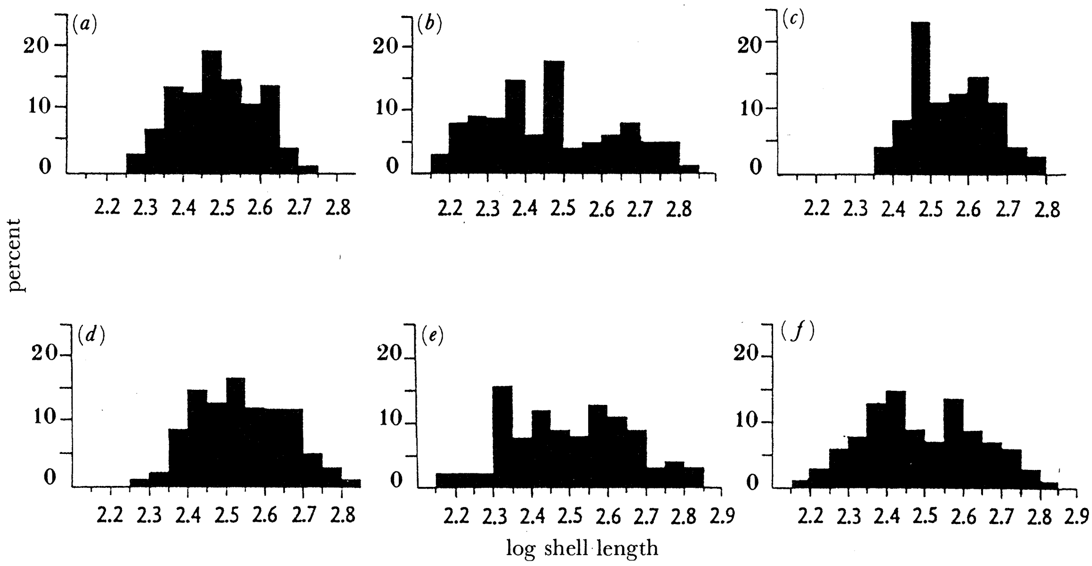

FIGURE 3. Size distribution of body shell of *Bosmina longispina* recovered from Gulspettvann (lake 6) at different depths, compared to lake 3 (*a*) (fishless) and lake 13 (*b*) (trout–perch lake); (*c*) 0–1 cm (present day: 1985); (*d*) 2–3 cm (around 1967), (*e*) 4–5 cm (around 1910), (*f*) 20–22 cm (more than 150 years) (dates from El-Daoushy, this symposium).

the most acidic lakes had comparably larger specimens but maximum sizes were smaller than in the lakes with planktivorous fish (figure 2).

For a lake with strong fish predation Nilssen (in preparation) recorded smaller body sizes in zooplankton than in a neighbouring acidic lake. It was also recorded that the acidic lake probably had a pH above 5.5 in earlier times and that the morphology of *Bosmina* had changed because older sediments contained specimens adapted to fish predation (Nilssen 1984).

(*d*) *Relations between Cladocera and lake* pH

The relation between lake pH and the Cladocera remains is shown in figure 4. The observation that a specific species decreases with decreasing pH does not mean in most cases that it cannot endure low pH. In general, species number and diversity in the planktonic community decrease with decreasing pH, but the littoral–benthic community diversity may decrease, remain stable or even increase depending upon changes in habitat (see above).

The interval of pH change is of critical importance for species succession and abundance patterns; a change from pH 6.0 to 5.0 has greater consequences for the communities than a change from pH 7.0 to 6.0. A particularly sensitive pH interval for many aquatic organisms seems to be pH 5.2–5.5, in the case of a clear water lake with aluminium content of about 150–200 μg l^{-1}. If the lake is strongly coloured, most toxic metal ions (e.g. aluminium) may be chelated and the changes in the lake community are less conspicuous.

With increasing acidification, there is an increasing tendency for some littoral species to be collected in the plankton: e.g., *Alonella nana*, *A. exisa*, *Acroperus harpae*, *A. elongatus*, *Alona affinis* and *Chydorus sphaericus*, together with some copepods. These species belong to the so-called pioneer species (early immigrants after ice withdrawal), common in a variety of environments.

The best pH indicators are the genus *Daphnia* (cf. Nilssen *et al.* 1984) and *Bosmina longirostris* (decrease or disappear at low pH) and *Acantholeberis curvirostris* (increases at low pH). Other

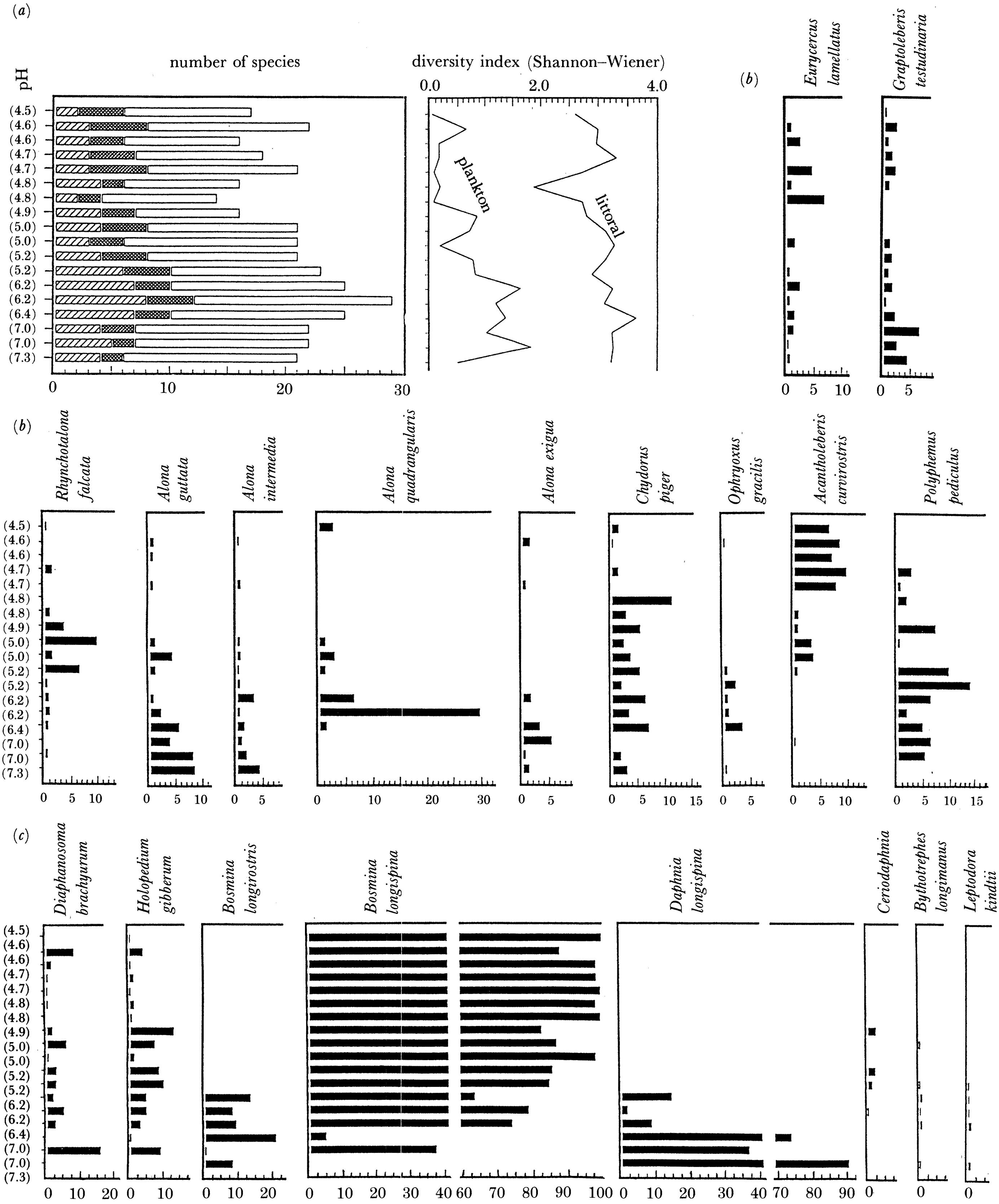

FIGURE 4. Results of analysis of cladoceran remains in surface sediment samples from 18 lakes with pH from 4.5 to 7.3; (*a*) number of species; (▨), planktonic Cladocera; (▩), non-chydorids; (▭), Chdoridae and diversity; (*b*) selected littoral species; (*c*) selected planktonic species.

indicator species are: *Alona intermedia*, *A. quadrangularis*, *A. guttata*, *Alonella exigua*, *Ophryoxus gracilis*, *Ceriodaphnia quandrangula*, *Bythotrephes longimanus*, *Leptodora kindtii* (usually decreasing with acidification) and *Alona rustica*, *Alonella exisa* (usually increasing with acidification).

(*e*) *Species changes in the Gulspettvann core*

As indicated above, the critical interval of pH change for cladoceran communities is pH 6.0 to pH 5.0. Diatom evidence (F. Berge, personal communication) for Gulspettvann indicate such a pH change.

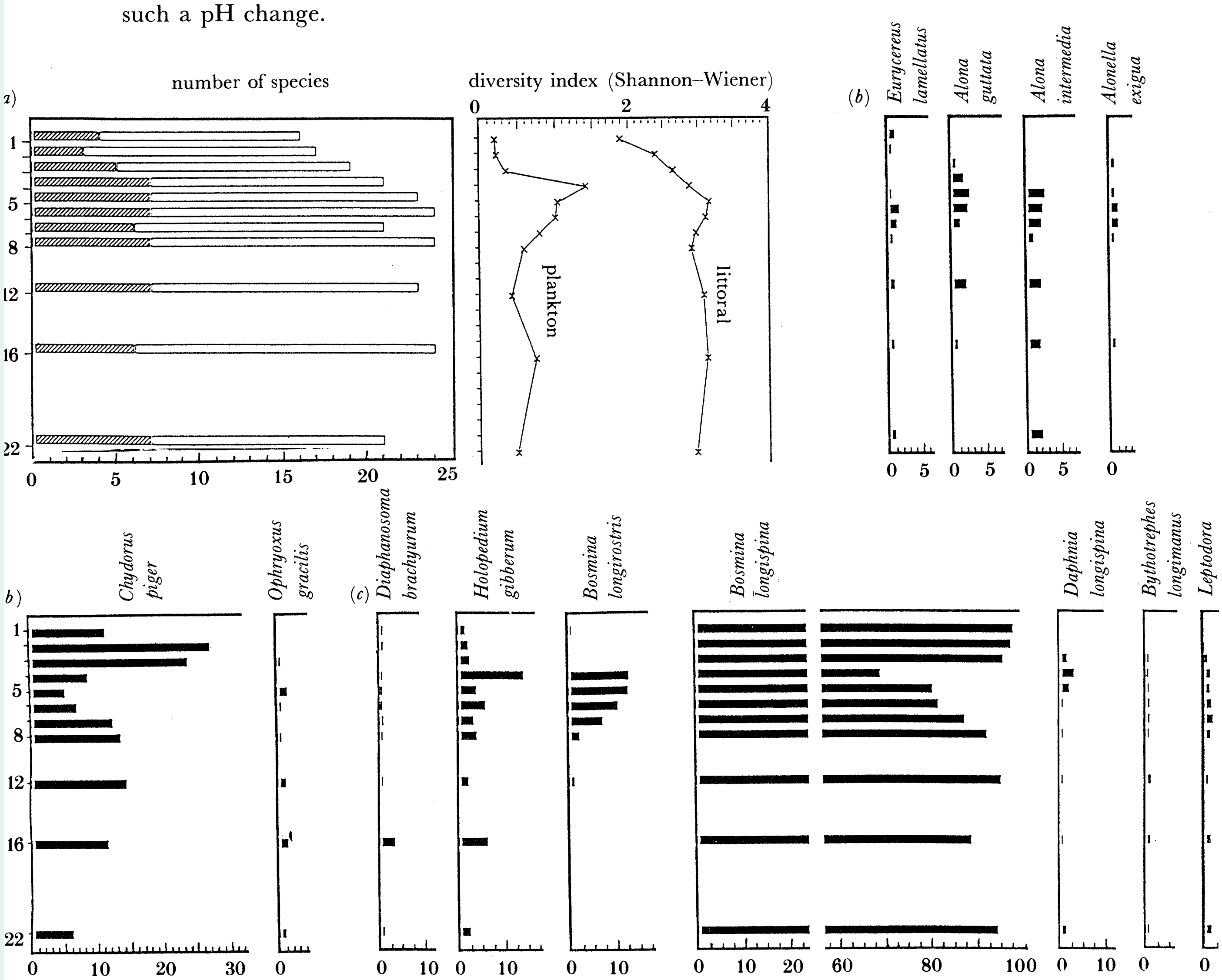

FIGURE 5. Results of analyses of cladoceran remains in a core from Gulspettvann; (*a*) number of species; (▨), planktonic Clodocera; (▭), littoral Cladocera and diversity; (*b*) selected littoral species; (*c*) selected planktonic species.

Characteristic changes within the littoral and planktonic community are shown in figure 5 based on data from Gulspettvann. Similar changes were seen in Lilla Öresjön (Renberg *et al.*, this symposium), Verevatn (Berge *et al.*, this symposium) and Loch Chon (Kreiser *et al.*, this symposium). The plankton community showed a disappearance of the acid-sensitive

D. longispina, *B. longimanus*, *L. kindtii* and *B. longirostris*. This agrees well with the distribution of animals from field studies (Sandøy & Nilssen 1986) and surface sediments (figure 4). The littoral species showed a disappearance of *A. intermedia*, *A. exigua*, *A. guttata* and *Ophryoxus gracilis*, comparable to the findings in the biogeographical samples and surface sediment samples. Crustacean changes took place at times comparable to changes in the diatom community (F. Berge, personal communication).

(*f*) *Cluster analyses and environmental reconstruction*

To reconstruct the pH history of Gulspettvann (figure 5) from the cladoceran remains, cluster analyses of both the core assemblages and the surface sediment dataset were done.

The dendrogram based on surface sediments of planktonic remains (not shown) divided the lakes into four different groups: acid fishless lakes, acid lakes with moderate fish populations, lakes with pH 6.2–6.4 and lakes with very small fish predation with pH ranging from 6.2 to 7.5. The dendrogram based on the littoral species (not shown) did not classify the lakes into so clearly delimited groups.

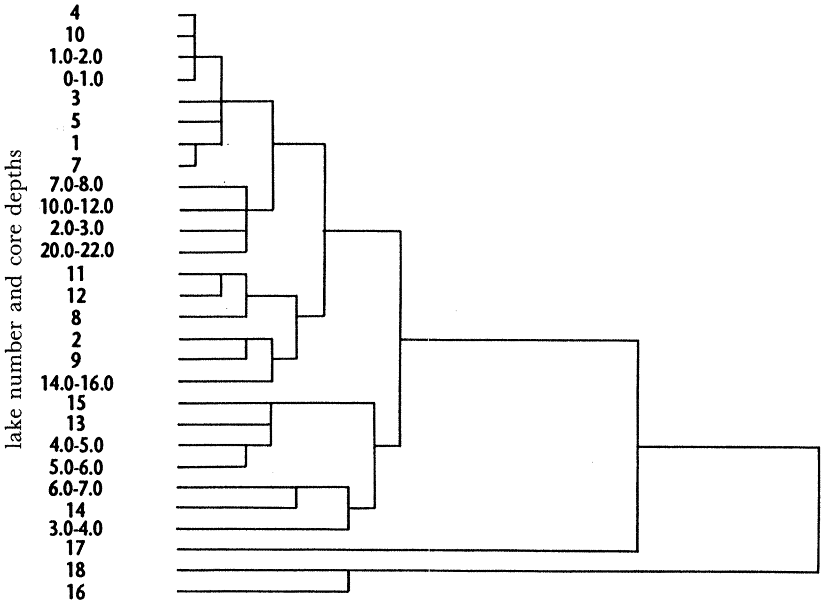

Figure 6. Cluster analyses (average linkage between groups) of planktonic species of the Gulspettvann core (0–22.0) and planktonic species in the surface sediment assemblages (lakes 1–18).

When surface sediment samples from the dataset and core samples from Gulspettvann were combined (figure 6), planktonic species from the upper 0–3 cm were grouped together with the most acidic lakes, whereas the strata from 3 to 7 cm were clustered with less acidic lakes in the same region. The littoral–benthic species did not show this relation, but were grouped in an isolated branch. This supports the suggestion that planktonic species may be more suited to study large geographical acidification patterns. Littoral assemblages may be more helpful to study single lakes, where other supporting data (e.g. from diatoms) are available.

CONCLUSIONS

1. Cladoceran remains are useful in reconstructing past environments and events in lakes. Changes in crustaceans occurred simultaneously with pH changes as assessed by diatoms or other palaeolimnological methods.

2. Interpretation of cladoceran remains demands a thorough knowledge of their ecology, including habitat selection and relation to predators and abiotic factors, like pH (cf. Nilssen & Sandøy 1986). Because acidification of lakes is a multi-causal phenomenon, in most cases species change is probably not directly related to pH.

3. The pelagic species assemblage gives information on general pH change, whereas the littoral community seems primarily useful in interpreting the more detailed history of a specific lake.

4. Knowledge of the changes in habitat structure (vegetation, sediment structure) of littoral species is necessary for a more thorough development of littoral species as indicators of past lake environment.

5. Cluster analyses on planktonic species can be used to detect changes during recent lake acidification.

6. Former predation patterns of planktivorous species can be assessed by analysing *Bosmina* remains. However, the contrasting effects of predation pressure from fish and invertebrate predators may make interpretation of the results difficult.

7. More work is necessary on habitat selection, population dynamics and predation relations of littoral–benthic species over a wide pH range (4.5–6.5) and over a large geographical region.

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