126 Raddum, G. G., Effects of low pH on insect larvae. SNSF-project, Oslo-Ås, Norway, IR *45/79* (1979) 1–58 (in Norwegian with English summary).
127 Raddum, G. G., Comparison of benthic invertebrates in lakes with different acidity, in: D. Drabløs and A. Tollan (eds)[29], pp. 330–331, 1980.
128 Raddum, G. G., and Fjellheim, A., Acidification and early warning organisms in freshwater in western Norway. Verh. int. Verein. Limnol. *22* (1984) 1973–1980.
129 Raddum, G. G., Hagenlund, G., and Halvorsen, G. A., Effects of lime treatment on the benthos of Lake Søndre Boksjø. Rep. Inst. Freshw. Res., Drottningholm *61* (1984) 167–176.
130 Raddum, G. G., and Sæther, O. A., Chironomid communities in Norwegian lakes with different degrees of acidification. Verh. int. Verein. Limnol. *21* (1981) 399–405.
131 Raddum, G. G., and Steigen, A. L., Reduced survival and calorific content of stoneflies and caddisflies in acid water, in: R. Singer (ed.)[141], pp. 97–101, 1981.
132 Ravera, O., Effects of experimental acidification in freshwater environments. Experientia *42* (1986) 507–516.
133 Roff, J. C., and Kwiatkowski, R. E., Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. *55* (1977) 899–911.
134 Rooke, J. B., and Mackie, G. L., Laboratory studies of the effects of Mollusca on alkalinity of their freshwater environment. Can. J. Zool. *62* (1984) 793–797.
135 Rooke, J. B., and Mackie, G. L., Growth and production of three species of molluscs in six low alkalinity lakes in Ontario, Canada. Can. J. Zool. *62* (1984) 1474–1478.
136 Rooke, J. B., and Mackie, G. L., Mollusca of six low-alkalinity lakes in Ontario. Can. J. Fish. aquat. Sci. *41* (1984) 777–782.
137 Russel-Hunter, W. D., Burky, A. J., and Hunter, R. D., Interpopulation variation in calcereous and proteinaceous shell components in the stream limpet, *Ferrissia rivularis*. Malacologia *20* (1981) 255–266.
138 Scheider, W., and Dillon, P. J., Neutralization and fertilization of acidified lakes near Sudbury, Ontario. Water Poll. Res. Canada *11* (1976) 93–100.
139 Schindler, D. W., Mills, K. H., Malley, D. F., Findlay, D. L., Shearer, J. A., Davies, I. J., Turner, M. A., Linsey, G. A., and Cruikshank, D. R., Long-term ecosystem stress: The effects of years of experimental acidification on a small lake. Science *228* (1985) 1395–1401.
140 Schindler, D. W., and Turner, M. A., Biological, chemical and physiological responses of lakes to experimental acidification. Water Air Soil Pollut. *18* (1982) 259–271.
141 Singer, R. (ed.), Effects of acidic precipitation on benthos. Proc., Symp. Hamilton, NY, August 8–9, 1980. North American Benthological Society, Hamilton, N.Y. 1981.
142 Singer, R., Notes on the use of shells of *Anodonta grandis* Say (Bivalvia; Unionidae) as a paleoecological indicator of trophic status and pH, in: R. Singer (ed.)[141], pp. 103–111, 1981.
143 Singer, R., Effects of acidic precipitation on benthos, in: Acid Precipitation. Effects on Ecological Systems, pp. 329–363. Ed. F. M. D'Itri. Ann Arbor Science, Ann Arbor 1982.
144 Singer, R., Benthic organisms, in: R. A. Linthurst (ed.)[80], pp. 5.14–5.37, 1984.
145 Singer, R., Macroinvertebrates, in: Biological and Chemical Field Survey of Small New Hampshire Lakes Sensitive to Acid Deposition, pp. 45–52. Eds C. W. Boylen, R. Singer and D. A. Roberts. EPA/NCSU Acid Deposition Program Contract Final Report No. APP-0313-1983. Fresh Water Institute Techn. Report 85–1, Troy, New York 1984.
146 Sutcliffe, D. W., Acid precipitation and its effects on aquatic systems in the English Lake District (Cumbria). Rep. Freshwat. biol. Ass. *51* (1983) 30–62.
147 Sutcliffe, D. W., and Carrick, T. R., Studies on mountain streams in the English Lake District. I. pH, calcium and the distribution of invertebrates in the River Duddon. Freshwat. Biol. *3* (1973) 437–462.
148 Svärdson, G., Survey of the activity of the laboratory with plan for 1974. Inform. Inst. Freshwat. Res. *1* (1974) 1–26 (in Swedish).
149 Swedish Ministry of Agriculture. Acidification today and tomorrow. The 1982 Stockholm Conference. Ministry of Agriculture Environment '82 Committee, Swedish Ministry of Agriculture, Stockholm, Sweden 1982.
150 Teichmann, W., Zeitpläne verschiedener *Gammarus*-Arten in Bächen des Schlitzerlandes. Diplomarbeit, FB Biologie, Univ. Giessen, 1977.
151 Townsend, C. R., and Hildrew, A. G., Longitudinal pattern in detritivore communities of acid streams: A consideration of alternative hypotheses. Verh. int. Verein. Limnol. *22* (1984) 1953–1958.
152 Townsend, C. R., Hildrew, A. G., and Francis, J., Community structure in some southern English streams: the influence of physicochemical factors. Freshwat. Biol. *13* (1983) 521–544.
153 Uutala, A. J., Composition and secondary production of the chironomid (Diptera) communities in two lakes in the Adirondack Mountain region, New York, in: R. Singer (ed.)[141], pp. 139–154, 1981.
154 Van der Borght, O., and Van Puymbroeck, S., Active transport of alkaline earth ions as physiological base of the accumulation of some radionuclides in freshwater molluscs. Nature *204* (1964) 533–534.
155 Vangenechten, J. H. D., and Vanderborght, O. L. J., Effect of acid pH on sodium and chloride balance in an inhabitant of acid freshwaters: The waterbug *Corixa punctata* (Illig.) (Insecta, Hemiptera), in: D. Drabløs and A. Tollan (eds)[29] pp. 342–343, 1980.
156 Wiederholm, T., and Eriksson L., Benthos of an acid lake. Oikos *29* (1977) 261–267.
157 Winterbourn, M. J., Hildrew, A. G., and Box, A., Structure and grazing of stone surface organic layers in some acid streams of southern England. Freshwat. Biol. *15* (1985) 363–374.
158 Witters, H., E., Vangenechten, J. H. D., Van Puymbroeck, S., and Vanderborght, O. L. J., The effect of pH and aluminium on the Na-balance in an aquatic insect *Corixa punctata* (Illig.), in: Acid Deposition and the Sulphur Cycle. Proc., Symp. Brussels 6 June, 1984, pp. 287–297. Ed. O. L. J. Vangenechten. Scope Belgium, 1984.
159 Zischke, J. A., Arthur, J. W., Nordlie, K. J., Hermanutz, R. O., Standen, D. A., and Henry, T. P., Acidification effects on macroinvertebrates and fathead minnows *(Pimephales promelas)* in outdoor experimental channels. Water Res. *17* (1983) 47–63.

0014-4754/86/050471-15$1.50 + 0.20/0

Impact of acidification on phytoplankton and zooplankton communities

by J. F. M. Geelen and R. S. E. W. Leuven

Laboratory of Aquatic Ecology, Catholic University, Toernooiveld, NL-6525 ED Nijmegen (The Netherlands)

Summary. Literature concerning the impacts of acidification on the phytoplankton and zooplankton composition has been reviewed. Available data on the species richness and composition of phytoplankton, attached algae and zooplankton of acidifying systems have been summarized. The effects of water acidification on the primary productivity and biomass of zooplankton have been discussed.
Key words. Acidification; phytoplankton; attached algae; zooplankton; primary productivity; diversity; biomass.

Introduction

Acidification of fresh waters due to acid precipitation has become a leading environmental concern in many parts of the world. Particularly in Scandinavia and the northeastern part of North America the pH and alkalinity of many soft water lakes is decreasing[4,29,31,38,48,63]. Recently, acidification of lakes and small water bodies has been observed in central Europe. In Scotland[94], Denmark[67], Western Germany[4,77,83] and some eastern European countries[4,99] several lakes have undergone a significant degree of acidification. The freshwater acidification in the Alpine zones in Switzerland[76] and Italy[57] is less serious than in Northern Europe because of the more favourable geological environment. However, many alpine lakes and tarns are already suffering a deterioration. In Belgium[87-89] and the Netherlands[6,15,18-20,35,36,52,69-71] acidification has been proved to have taken place in poorly buffered, oligotrophic waters on mineral sandy soils, i.e. moorland pools, some small lakes and dune pools.

The effects of acid precipitation on water acidity depend on the bedrock geology, the buffering capacity of the water and the sediment, hydrology and the potential acid deposition. There are many geomorphological differences between the susceptible surface waters. The acidified systems in northeastern North America and Scandinavia are large and deep, are often influenced by water inlet, and have quartz bearing bedrock and thin reactive sediment layers[29,48,63]. In the Netherlands and Belgium particularly small, shallow and isolated, poorly buffered waters are highly sensitive to acidification[52,89]. Acidification of the above-mentioned fresh waters is associated with a variety of physico-chemical changes like decreased turbidity, decreased availability of nutrients, and increased mobilization of (heavy) metals. The most conspicuous biological effects are the reduction and loss of fish populations, particularly salmon and trout. Changes which are less obvious, but not less severe, are the reduction and/or loss of amphibian populations, changes in phyto- and zooplankton, macro-invertebrate and macrophyte communities[29,41,48,52,69]. Generally there is a reduced species richness per unit area in acidified systems.

The mechanism of acidification appears to be very complex and is not yet fully understood. Because of many geomorphological differences one has to be careful in generalizing results from different areas. In many cases the impact of acidification cannot be ascribed to a pH decrease alone. Also the mobilization of (heavy) metals, changes in nutrient cycles (N,P,C) and food chains seem to influence the possibilities for life under acid circumstances.

The present paper reviews the available publications dealing with the impact of acidification on phytoplankton and zooplankton assemblages of lentic freshwater habitats.

Phytoplankton composition

Acidification may alter the structure of the phytoplankton communities on several levels i.e. species richness, species composition and dominance.

Several authors have discussed the changes in species composition connected with acidification. The first striking aspect is that with decreasing pH the number of species of Chlorophyta, Bacillariophyceae and Cyanophyta becomes reduced[41,42,66]. Lakes with pH values < 5.0 display a homogeneous and limited phytoplankton composition consisting of about ten species. The greatest changes in composition were found in the pH interval 5–6[2]. Due to distinct local geomorphological differences the reported phytoplankton composition in Canada differs from area to area. In the Sudbury area the number of species and number of individuals of Chlorophyta decreased, those of Chrysophyta varied little and the Cyanophyta just increased as pH declined[50]. In the La Cloche Mountain area a consistent pattern of decreasing species richness and diversity of phytoplankton with decrease in

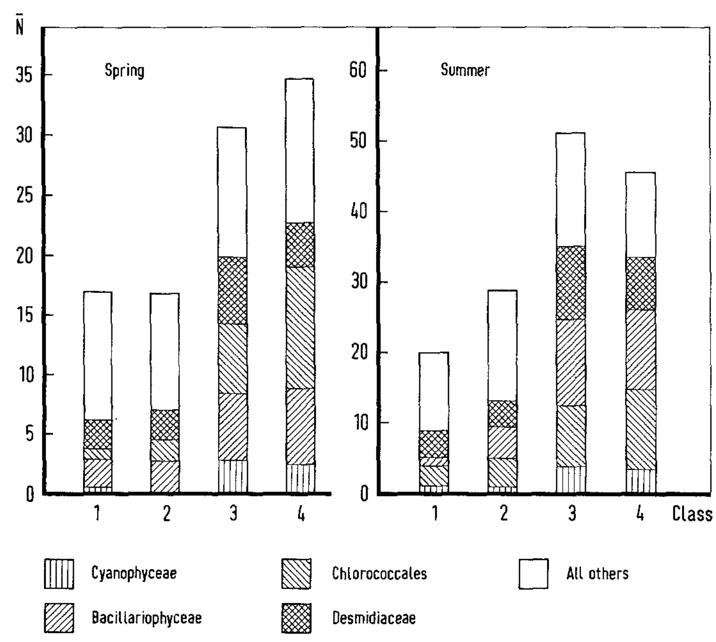

Figure 1. The mean number of phytoplankton taxa ($\bar{N}$) in poorly buffered waters within different pH-classes. Class 1: strongly acidified waters (pH < 5), class 2: slightly acid waters (pH 5.0–6.2), class 3: 'relatively' undisturbed waters (pH 6.2–9.2), class 4: eutrophicated waters (pH 6.6–10.4).

pH was observed. In acidic Florida lakes (USA) a decrease in the number of rare species was associated with decreasing pH[11].

The mean number of species for some phytoplankton groups in acidifying moorland pools in the Netherlands is illustrated in figure 1. In spring as well as in summer the mean species richness in strongly acidified waters is significantly lower than in the other waters and significantly fewer species of Cyanophyta, Bacillariophyceae, Chlorococcales and Desmidiaceae are observed.

The next phenomenon that has been noticed is that changes in the species spectrum take place. Many species found in circumneutral waters are absent or rare in acidic lakes. Van Dam et al.[18–20] studied the diatom assemblages of several moorland pools in the Netherlands. They concluded that in clear water pools the diversity decreases and the species spectrum shifts in the direction of acidobiontic organisms. Also, the dissimilarity among the pools has decreased in the last decades. This means that through acidification the diatom assemblages have become poorer in species and continually show more similarities. In the acidified systems the relative abundance of *Eunotia exigua* increases particularly strongly. The same phenomenon has been observed in Belgium, Denmark and Western Germany[21,86]. Also paleolimnological studies on diatoms give evidence for a continuous decrease in species number and a shift to acidobiontic species[5,9,13,22,26,33,68,83]. Coesel et al.[15] showed large changes in the desmid assemblages in Dutch acidified moorland pools also.

Nearly all acidified Dutch moorland pools were characterized by taxa indifferent to pH, i.e. mainly filamentous green algae *(Microspora, Oedogonium, Ulothrix)* and nanoplankton < 50 µm. A few strongly acidified pools[6] were characterized by desmids *(Cylindrocystis brebissonii, Bambusina brebissonii, Closterium striolatum, Closterium directum, Staurastrum jaculiferum)*, filamentous green algae *(Binuclearia tectorum, Microspora stagnorum)*, pyrrophytes *(Peridinium inconspicuum)* and chrysophytes *(Dinobryon divergens)*. The observed desmids belong to a fairly common community, poor in species, which is characteristic for extremely oligotrophic, occasionally slightly disturbed, *Sphagnum*-rich waters with a pH of 4–5[14]. According to Rosén[73] *Peridinium inconspicuum* is often a characteristic species in acidified lakes (pH < 5.5) and may establish large populations (> 1 mg·l^{-1}).

Also during acidification the phytoplankton assemblages become dominated by special phytoplankton groups or species. In acidified lakes in Sweden dinoflagellates (*Peridinium inconspicuum* and *Gymnodinium* spp.) become dominant[2,43,46,73]. In the Jasne Lake, Poland, at a mean pH of 4.3, phytoplankton is composed exclusively of nanoplankton: *Cryptomonas marssonii* and *C. erosa* var. *reflexa* dominate in the metalimnion[99]. Chrysophyceae and *Chlamydomonas* are most abundant in all high mountain lakes in Switzerland with pH 5.2–6.0 and 9–14 species of phytoplankton per lake[74].

In the Sudbury area in Canada *Dinobryon tabellariae* was dominant in the most acidic lakes, while *Synura uvella, Dinobryon divergens* and *Chromulina* spp. were dominant in the less acidic lakes[50]. Dillon et al.[28] noted for the acidic Sudbury lakes and Bleiwas et al.[7] for the poorly buffered lakes in the La Cloche Mountain area that they were dominated by dinoflagellates in contrast to the circumneutral shield lakes, which were dominated by diatoms and/or chrysophytes. However, the dominance of Dinophyceae and Cryptophyceae in Carlyle Lake in Sudbury, with a pH of 4.5–6.0[96] is similar to the situation in Swedish lakes with pH levels of about 5[46]. Also lakes in the Sault Ste. Marie District were dominated by Chrysophyceae *(Chromulina)*, while dinoflagellates were unimportant[49]. In three acid-stressed lakes in Nova Scotia, phytoplankton communities were even more diverse; one lake was dominated by diatoms, one by chrysophytes and green algae and one by cyanophytes[8]. In acidic Florida lakes (USA) blue-green algae were replaced by green algae, which made up 60% of the total phytoplankton[11,17]. In two acidic Adirondack Mountain lakes (USA) Chrysophyceae dominated both in terms of species number and biomass all year. The Dinophyceae, particularly *Peridinium inconspicuum*, made up a significant portion of the biomass. Dinophyceae become increasingly impor-

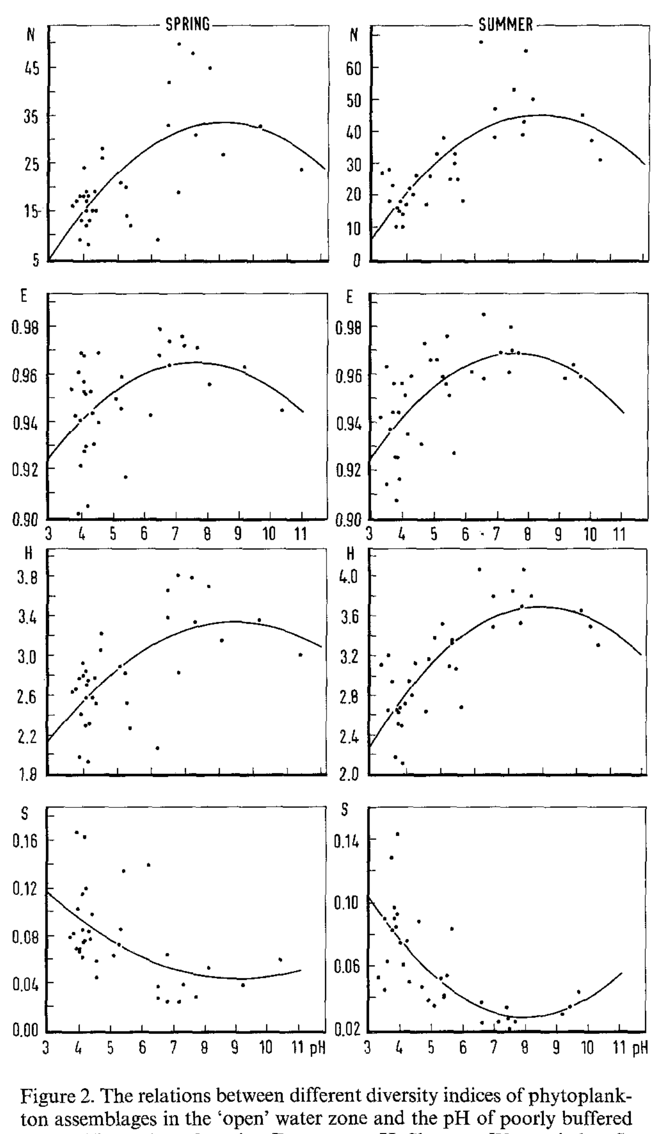

Figure 2. The relations between different diversity indices of phytoplankton assemblages in the 'open' water zone and the pH of poorly buffered waters. N: number of species; E: evenness; H: Shannon-Weaver index; S: Simpson Index.

tant contributors to the communities with decreasing pH, but do not dominate as is reported for some acidic lakes[40]. In the Dutch acidified moorland pools[6] only six taxa are dominant: *Binuclearia tectorum, Microspora* spec., *Mougeotia* spec., *Closterium striolatum, Cryptomonas erosa* and *Cryptomonas ovata*. Only the dominance of *Binuclearia tectorum, Closterium striolatum* and *Microspora* spec. is pH-dependent. *Cryptomonas erosa* and *C. ovata* are indifferent to pH.
The relations between the pH and several diversity indices are illustrated in figure 2. Apparently phytoplankton assemblages in poorly buffered circumneutral waters possess both in spring and in summer a large number of species (N), a high evenness (E), a high Shannon-Weaver index (H) and a low Simpson index (S). This means that relatively undisturbed, poorly buffered waters show a large species richness and an equal distribution of abundances over the species. Changes in pH in these waters result in a strong decrease of diversity (low N and H) and an increase of the dominance of a few species (low E and high S).
One may conclude that there is general agreement that phytoplankton species composition changes and richness decreases at low pH, in spite of considerable differences between the lakes examined, and in the methodology used in plankton analysis.

Attached algae

Reports in the Scandinavian literature indicate that in acidic lakes attached filamentous algae such as *Mougeotia, Batrachospermum, Lyngbya, Oscillatoria,* and *Pseudoanabaena* become abundant[37,41,51]. Hendrey et al.[41] observed that *Binuclearia tectorum, Mougeotia* spp., *Eunotia lunaris, Tabellaria flocculosa* or *Dinobryon* spp. at any sampling date constituted at least 20% of the microflora. Filamentous algae grow densely over macrophytes; dense mats of benthic algae and undecomposed plant litter are recorded from Sweden. In Lake Colden, N.Y., similar mats of algae occur. The primary species are *Phormidium tenue, Tabelleria fenestrata, Fragilaria virescens* and *Diatoma*. The aquatic macrophytes are heavily covered by filamentous algal clouds of *Mougeotia* and *Tabellaria fenestrata*[43]. *Mougeotia scalaris* has also frequently been observed free-floating in the pelagial of many acidified lakes; this species is apparently well adapted to acid waters[2]. With increasing acidification filamentous algae such as *Mougeotia, Microspora* and *Binuclearia* become dominant[61]. The same phenomenon has been observed in Dutch moorland pools[6].
According to Brock[12] benthic blue-green algae are completely absent at a pH < 4, while Lazarek[51] found mats of blue-green algae in acidified Swedish lakes. Blue-green algae are indeed more sensitive to a low pH, but particularly Oscillatoriaceae can become dominant in acidifying waters, owing to raised mucilage production[51].
In the Jasne Lake, Poland, the bottom is overgrown with a dense meadow of the moss *Drepanocladus fluitans*, covered with abundantly growing filamentous algae[99]. The extensive growth of attached algae may inhibit the transport of nutrients from sediments to the overlying water; also, the nutrients of these algae may not be recycled through the system at a normal rate[40].

Biomass and productivity of algae

The primary production and/or biomass of (free-floating) algae can be affected by the tolerance of individual species with respect to water quality, seasonal succession and interactions between species (i.e. ability to compete for nutrients, grazing), nutrient availability and light penetration. It is evident that all of these factors are altered by acidification. However, no consistent pattern emerges for the net effect of all changes.
In some studies phytoplankton biomass has been shown to be reduced by lake acidification[7,17,37,41]. On the other hand, in acidifying oligotrophic lakes in Norway[66], and moorland pools in the Netherlands[6,52] no significant correlations between chlorophyll a content and the pH of the water were apparent. Several other studies gave no indications for a decrease or drastic change in phytoplankton biomass or primary production rate[3,28,50,56]. During artificial acidification of a Canadian Shield lake a slight elevation of chlorophyll a and increased algal production and biomass was observed[32,75]. It is clear that the literature on this point is far from unanimous. Fortunately the discrepancies in data have been explained[28,50,95]. Single surface samples of phytoplankton may not be sufficient to characterize productivity or biomass in acid lakes. Under acidic conditions the depth of the euphotic zone increases, and column samples through the whole photic zone are required for calculations of primary productivity or standing crop[50,75]. For example Kwiatkowski and Roff[50] noticed that primary production expressed volumetrically ($mg\ C \cdot m^{-3} \cdot h^{-1}$) was reduced in lakes with a pH below 5.5, whereas production expressed on an area basis ($mg\ C \cdot m^{-2} \cdot h^{-1}$) remained high in waters with a pH down to 4.4. Also Raddum et al.[66] suggested that the changes in transparency in lakes could be important. This has been proved by a good correlation between the ratio phaeopigment/chlorophyll a and Secchi-disc transparency.
Furthermore, some authors state that there is little evidence that low pH per se can directly reduce phytoplankton biomass or productivity. Dillon et al.[28] reported that phytoplankton biomass and productivity of acid lakes were similar to those of circumneutral lakes of the same nutrient status. Generally phytoplankton community biomass is better correlated with phosphorus concentration than with pH[17,28,95]. Crisman et al.[17] mentioned that chorophyll values displayed a pronounced increase with increasing phosphorus concentrations for all pH-intervals (0.5 pH units) in poorly buffered waters with a pH above 5.6, while the responses in more acidic lakes were diminished. Phosphorus additions in enclosures of an acid lake indeed showed that chlorophyll and phytoplankton biomass significantly increased; no large changes in H^+ concentrations were observed during the experimental manipulations[25,91]. Also in acid Sudbury lakes of Canada small additions of phosphorus caused significant increases of the mean phytoplankton biomass[28].
Grahn et al.[37] already stated that the primary production in acid lakes may be influenced by reduced nutrient levels. They suggested that the primary biological effects, on individuals and populations, of a continuous supply of acid substances to a lake induce profound, long-term

changes, forcing the lake into an increasingly more oligotrophic state. This oligotrophication of lakes generally tends – by means of a feedback mechanism – to accelerate further the process of acidification. Some other authors[27,40] stated that acidification may lead to a reduced availability of nutrients, for instance that soil acidification results in high concentrations of aluminium, iron and other metals, which can form precipitates of phosphate in the water column. Thus atmospheric deposition of acid might lead to reduced phytoplankton production and biomass by altering the availability of critical nutrients, such as phosphorus.

Johnson et al.[47] concluded that high acidity also limited the availability of inorganic carbon, resulting in a reduction of primary production of phytoplankton. Roelofs et al.[69–71] pointed out that changes in inorganic carbon content, which occur as a result of acidification, also play a very important role in the changes of macrophyte communities. The increase in the (heavy) metal content of acidifying systems can affect the biomass of phytoplankton. In moorland pools in the Netherlands a negative correlation between chlorophyll a and aluminium content exists[6].

In acidic clear water lakes a very extensive growth of attached algae is ubiquitous. Particularly dense mats of benthic algae were observed, whereas filamentous algae overgrow macrophytes[37,40,43,51,61].

There are several explanations for the increase in biomass of attached algae. Removal of algae by grazing of fish, macroinvertebrates and zooplankton is probably diminished[37,39,41,43,61,84]. Benthic and epiphytic algae are less dependent on environmental fluctuations. Dead cells remain within the algal community, so that the released nutrients can be re-used. Such a community possesses an effective survival strategy under nutrient-poor circumstances[51]. Many filamentous algae display a raised mucilage production at high acidity. Through this adaptation they may possibly become resistant to the high acidity and the higher concentrations of (heavy) metals and aluminium[34,51,61].

Epiphytic algae probably take advantage of CO_2 excreted by macrophytes[51]. When poorly buffered waters are acidified and the sediment contains carbonate, a temporary increase of the CO_2-concentrations in the sediment will occur[69,71]. Benthic algae may profit by the diffusion of CO_2 from the sediment to the water layer. To explain the unusual accumulation of several algae, a number of authors e.g. Evans[31] and Hendrey et al.[41] cite the statement of Moss[60] that the intolerance of various species to low pH or to consequent chemical changes will allow just a few algal species to utilize the nutrients available in these predominantly oligotrophic waters. However, Shoesmith and Brook[78] warned that the experiments of Moss[58–60] must be viewed with due caution, because he based his conclusions on the behaviour of cultured algae. Besides, the remaining species may have a better ability to ingest nutrients, and possess morphological adaptations to escape predation such as large cells, long filaments, durable cell walls or gelatinous sheats that preclude ingestion or digestion by zooplankton[55,65].

Zooplankton composition

A negative relationship between zooplankton species diversity and lake pH has been reported for Scandinavian countries[2,42,56,66], for Canada[7,8,72,81,82,97] and for Florida[11,16,17]. These studies present evidence that the low pH of some lakes is a recent condition associated with acid rain (pH < 5.6). In some previous studies[72,81] an effect of pH on zooplankton was not observed until lake pH dropped below values of 5–5.5. In lakes of the La Cloche Mountains (Canada) with pH < 5.0 many species are completely eliminated and even tolerant species become progressively rarer. In some lakes only a single species *(Diaptomus minutus)* remains[81].

In figure 3 the mean diversity indices (N,S,E and H) for

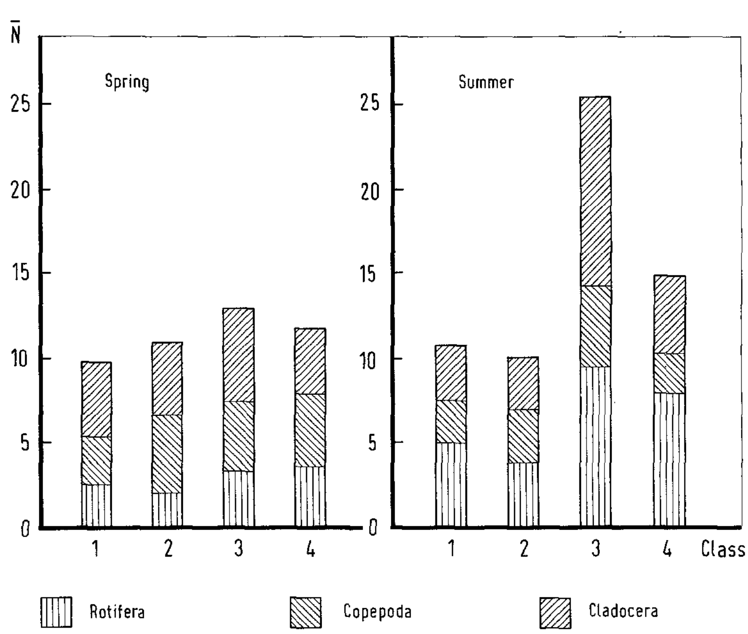

Figure 3. The mean number of zooplankton taxa (N̄) in poorly buffered waters within different pH-classes. Class 1: strongly acidified waters (pH < 5), class 2: slightly acid waters (5 ≦ pH < 6), class 3: 'relatively' undisturbed waters (6 ≦ pH < 7), class 4: alkaline waters (pH ≧ 7).

the zooplankton communities of Dutch moorland pools are represented[6,52]. In the relatively undisturbed poorly buffered waters (class 3) on an average more species (N), a higher evenness (E) and a higher Shannon-Weaver index (H) and a lower Simpson index (S) were found compared to the other systems (class 1, 2 and 4). The zooplankton communities in the undisturbed waters thus show, just like the phytoplankton communities, a large diversity and an equal distribution of the number of individuals over the species. In the acidified waters (class 1 and 2) and the poorly buffered waters with high pH (class 4) the species richness is clearly lower and some species become dominant.

In the relative undisturbed waters (class 3) on an average more species of rotifers and cladocerans are observed (fig. 4). This is particularly the case in summer, when a macrophyte vegetation occurs. In spring only a little difference can be observed in the mean numbers of zooplankton species in waters with different pH.

There is a significant relationship between the diversity of zooplankton in the open water and amongst the vegetation, indicating that high diversity indices in the vegetation are related to high diversities in the open water and vice versa. There are correlative relations between the physico-chemical parameters and the diversity of the zooplankton communities in the open water too. The diversity of the zooplankton community as a whole, in spring, is only correlated with aluminium, whereas in summer positive correlations ($p < 0.05$) with Al^{3+}, NO_2^-, DOC, pH, alkalinity, Ca^{2+} and acidity are found. At high (toxic) aluminium concentrations the diversity is lower,

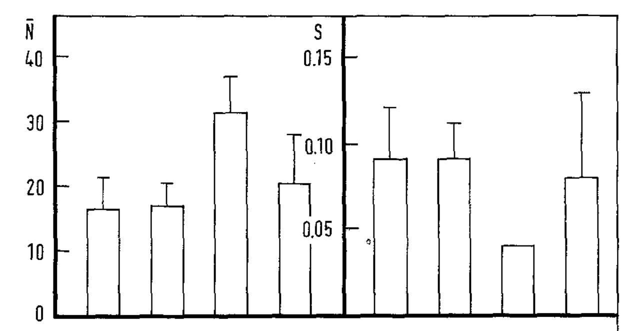

Figure 4. The mean values (+S.D.) of different diversity indices of zooplankton communities in poorly buffered waters with different pH. N: number of species; E: evenness; H: Shannon-Weaver index; S: Simpson index. Class 1: strongly acidified waters ($pH < 5$), class 2: slightly acid waters ($5 \leqq pH < 6$), class 3: 'relatively' undisturbed waters ($6 \leqq pH < 7$), class 4: alkaline waters ($pH \geqq 7$).

while in these waters some species become dominant e.g. at an aluminium content of 10–20 $\mu mol \cdot l^{-1}$ *Chydorus sphaericus* and *Scapholeberis mucronata* ($p < 0.001$) and *Keratella serrulata* ($p < 0.01$)[6,52].

The diversity of the phytoplankton and that of the zooplankton of the Dutch moorland pools are strongly correlated with each other. When a high phytoplankton diversity was found, the zooplankton diversity was also high, and conversely. These correlations are probably direct as well as indirect. The zooplankton will influence the diversity of the phytoplankton directly by predation. The indirect correlation is the decreasing diversity of both biota under the influence of acidification.

Copepods, cladocerans and rotifers all contribute to the reduced number of species, but the cladocerans are apparently most affected[45]. However, acidic lakes in Scandinavia and Canada are characterized by a dominance of Bosminidae and a scarcity of Daphnidae and Rotifera[2,7,38,66,81,97]. The data of Morling[56] and Brezonik[11] contrast with the above-mentioned data. In western Swedish lakes most zooplankton species were observed during the whole acidification period[56]. In Florida more acidic lakes had more species than less acidic lakes had, but three measures of species diversity showed no significant differences between the two types of lakes[11].

In strongly acidified moorland pools in the Netherlands about ten zooplankton species were encountered (fig. 4). Species which were observed frequently and are sometimes dominant are the cladocerans *Alonella excisa, Bosmina longispina, Chydorus sphaericus, Daphnia obtusa, Scapholeberis mucronata, Polyphemus pediculus* and the rotifers *Keratella serrulata* and *Lecane* spp. Only calanoid copepodites become dominant.

According to Raddum et al.[66] only two species are characteristic for acid waters, viz. *Bosmina longirostris* and *Keratella serrulata*, the last species being considered to be an indicator of acidification. The Dutch zooplankton community is obviously composed of small species[6], as has been observed also in northeastern North America[16,81,97]. This is in contrast to an increase of large copepods, particularly *Heterocope saliens*, as observed in Scandinavia, as a result of increased predation by invertebrate predators, e.g. *Chaoborus*, whose densities increase following the extinction of fish[30,40,66].

Most species of Copepoda and Cladocera are able to tolerate considerable variations of pH. This does not justify the conclusion that pH is without influence. There is probably an optimum pH for every single species[54]. The influence of pH on survival of some cladoceran species has been investigated. Experimentally it has been demonstrated that a $pH < 6$ is unfavourable for *Daphnia longispina* and at a pH 5.3 the harmful effect is evident. At pH 3.0 *D. longispina, D. pulex* and *Bosmina longispina* and at a pH 2.8 *Chydorus sphaericus* die in a few hours[80]. Experiments in which the pH tolerance of *Daphnia pulex* was studied[23] showed that this species was able to survive between pH 4.3 and 10.4, but the potential for reproduction was limited to pH 7.0–8.7. Experimental studies with *Daphnia magna* show that this species tolerates low pH for short periods; however, chronic exposure indicates that continuous survival is unlikely at a pH below 5.0[64]. These experiments have been criticized by Walton et al.[90], particularly because of a lack of detailed analysis of reproductive capabilities. A chronic 21 days life table test indicated a gradually increasing impairment of population growth rate potential (r) at pH $\leq$ 5.0. This was due primarily to reduced survival and delayed onset of reproductive maturity[90]. According to Brehm and Meijering[10] *Daphnia magna* is more sensitive to low pH than *D. pulex*. Mortality increased in close relation to reduction of pH (< 5) and is mainly caused by the increasing concentration of free hydrogen ions. For survival a pH of 5.3–4.5 for *D. magna* and a pH of 4.9–3.9 for *D. pulex* is critical. Primarily the respiration is influenced, as has been shown by Alibone and Fair[1]. The effect of low pH values on *Daphnia magna* severely depresses the O_2 uptake rates. At low pH the CO_2 concentration inhibits the diffusion of CO_2 from the gills, and the CO_2 tension of the blood increases, raising the acidity of the blood, which decreases the blood's affinity for O_2[1].

Zooplankton biomass

It has been proved in the previous paragraphs that in acidifying freshwater systems the species composition of both phytoplankton and zooplankton changes, and due to an altered predator-prey system a dominance of only a few species, tolerant to low pH, may occur. The net effect of all these factors will determine the zooplankton biomass. However, studies of zooplankton have not been sufficiently intensive to assess whether acidification results in reduction of zooplankton standing stocks[31].

Acidification has had a strong effect on zooplankton biomass in northeastern North American lakes. In lakes in northern Ontario (Canada) zooplankton showed a significant reduction in species and numbers at the lower pH levels; the Rotifera showed the greatest changes. Significant relationships were found between the zooplankton standing crop and chlorophyll a concentrations and between the zooplankton standing crop and areal primary productivity. Dry weights for *Holopedium gibberum* and *Diaptomus minutus* were lowest in the most acidic lakes[72]. The results suggest a continuous change in biomass over the entire range of pH (4.5–7.2)[16]. In contrast with this observation, in the La Cloche area (Ontario, Canada) zooplankton biomass was not correlated with pH[7]. The mean abundance of zooplankton in Florida decreased from 145 specimens per litre in nonacidic lakes to 75 specimens per litre in acidic lakes[11,17]. In West-Swedish lakes, Morling[56] observed small changes in species composition, but the frequencies of zooplankton organisms were mostly reduced. The reduction was most pronounced for Cladocera; particularly *Ceriodaphnia quadrangula* and *Daphnia longispina* occur sparsely in some lakes, while acidification reduced their numbers to extremely low values. Also *Holopedium gibberum* and *Polyphemus pediculus* almost disappeared from some lakes. In contrast to the general trend of frequency reduction, some rotifers increased in numbers e.g. *Keratella serrulata* and *Conochilus unicornis*.

In the Adirondack (USA) lakes the number of rotifers declined with decreasing pH. However, their density in humic lakes was usually high. It appears that the organic substances in the humic lakes may complex much of the dissolved matter, mitigating metal toxicity. Siegfried et al.[79] assumed that the differences in the structure of the rotifer communities in relation to pH may also represent an indirect relationship. Because in acidifying systems many structural and functional changes occur, there may be other factors influencing the diversity of rotifers. These statements also hold for other zooplankton communities[16]. Simplification of the plant communities in lakes reduces the variability of food available to the next higher trophic level, while changes in phytoplankton biomass may decrease the food supply to herbivorous zooplankton[41].

Many authors assume that the size and composition of the zooplankton communities are also in large part regulated by the kind of predators[24,30,44,45,53,62,92,97,98]. The change from a predator-prey system dominated by fish to one dominated by invertebrates may be responsible for several ecological changes reported from acidified lakes.

Conclusions

In spite of geomorphological differences between acidifying systems and discrepancies in methods of plankton analysis, this review allows some general conclusions. In acidifying systems there is a strong decrease in the diversity of phytoplankton communities, whereas a few species become dominant. There are no clear indications for changes in the biomass and primary productivity of phytoplankton, however, the biomass of attached algae tends to increase. The scarce data on zooplankton indicate a decrease in standing stock.

It is evident that not only the pH, but also some other environmental factors are responsible for the structural and functional changes in acidifying systems. Decreased nutrient availability, changes in trophic relationships between primary and secondary producers and altered predator-prey systems may contribute to the simplification of acidifying aquatic ecosystems. Unfortunately the importance of the key factors involved, and the mechanism of acidification processes, are not yet fully understood.

Acknowledgments. A part of this study has been financed by the Ministry of Housing, Physical Planning, and Environment. The authors are greatly indebted to Prof. Dr. C. den Hartog for critical remarks, and to the Department of Illustration for preparing the drawings.

1 Alibone, M. R., and Fair, P., The effects of low pH on the respiration of *Daphnia magna* Straus. Hydrobiologia *85* (1981) 185–188.
2 Almer, B., Dickson, W. T., Ekström, C., Hörnström, E., and Miller, U., Effects of acidification on Swedish lakes. Ambio *3* (1974) 30–36.
3 Almer, B., Dickson, W. T., Ekström, C., and Hörnström, E., Sulphur pollution and the aquatic ecosystem, in: Sulphur in the Environment, pp. 272–311. Ed. I. O. Nriagu. Wiley, New York 1978.
4 Anonymus, Acid rain: a review of the phenomenon in the EEC and Europe. Ed. Environmental Resources Ltd., Graham and Trotman, London 1983.
5 Battarbee, R. W., and Flower, R. J., The inwash of catchment diatoms as a source of error in the sediment-based reconstruction of pH in an acid lake. Limnol. Oceanogr. *29* (1984) 1325–1329.
6 Bie, J. E. G. M. de, and Maenen, M. M. J., Een onderzoek naar de effecten van zure neerslag op microflora en -fauna in zwak gebufferde wateren op kalkarme zandgronden. Report 178. Lab. Aquatic Ecology, Nijmegen 1984.
7 Bleiwas, A. S. H., Stokes, P. M., and Olaveson, M. M., Six years of plankton studies in the La Cloche region of Ontario, with special reference to acidification. Verh. int. Ver. Limnol. *22* (1984) 332–337.
8 Blouin, A. C., Lane, P. A., Collins, T. M., and Kerekes, J. J., Comparison of plankton-water chemistry relationships in three acid-stressed lakes in Nova Scotia, Canada. Int. Rev. ges. Hydrobiol. *69* (1984) 819–842.

9 Brakke, D.F., Acidification history and prediction using biological indices. Verh. int. Ver. Limnol. *22* (1984) 1391–1395.

10 Brehm, J., and Meijering, M.P.D., Zur Säure-Empfindlichkeit ausgewählter Süsswasser-Krebse (*Daphnia* und *Gammarus*). Arch. Hydrobiol. *95* (1982) 17–27.

11 Brezonik, P.L., Crisman, T.L., and Schulze, R.L., Planktonic communities in Florida softwater lakes of varying pH. Can. J. Fish. aquat. Sci. *41* (1984) 46–56.

12 Brock, T., Lower pH limit for the existence of blue-green algae: evolutionary and ecological implications. Science *179* (1973) 480–482.

13 Charles, D.F., Recent pH history of Big Moose Lake (Adirondack Mountains, New York, USA) inferred from sediment diatom assemblages. Verh. int. Ver. Limnol. *22* (1984) 559–566.

14 Coesel, P.F.M., The relevance of desmids in the biological typology and evaluation of freshwaters. Hydrobiol. Bull. *9* (1975) 93–101.

15 Coesel, P.F.M., Kwakkestein, R., and Verschoor, A., Oligotrophication and eutrophication tendencies in some Dutch moorland pools, as reflected by their Desmid flora. Hydrobiologia *61* (1978) 21–31.

16 Confer, J.L., Kaaret, Th., and Likens, G.E., Zooplankton diversity and biomass in recently acidified lakes. Can. J. Fish. aquat. Sci. *40* (1983) 36–42.

17 Crisman, T.L., Schulze, R.L., Brezonik, P.L., and Bloom, S.A., The biotic response in Florida lakes, in: Ecological Impact of Acid Precipitation, pp. 296–297. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.

18 Dam, H. van, and Kooyman-van Blokland, H., Man-made changes in some Dutch moorland pools, as reflected by historical and recent data about diatoms and macrophytes. Int. Rev. ges. Hydrobiol. *63* (1978) 587–607.

19 Dam, H. van, Suurmond, G., and ter Braak, C.J.F., Impact of acid precipitation on diatoms and chemistry of Dutch moorland pools, in: Ecological Impact of Acid Precipitation, pp. 298–299. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.

20 Dam, H. van, Suurmond, G., and ter Braak, C.J.F., Impact of acidification on diatoms and chemistry of Dutch moorland pools. Hydrobiologia *83* (1981) 425–459.

21 Dam, H. van, and Beljaars, K., Nachweis von Versauerung in West-Europäischen kalkarmen stehenden Gewässern durch Vergleich von alten und rezenten Kieselalgenproben, in: Gewässerversauerung in der Bundesrepublik Deutschland, pp. 184–188. Eds J. Wieting, B. Lenhart, C. Steinberg, A. Hamm and R. Schoen. Proc. Seminar Umweltbundesamt. Schmidt, Berlin 1984.

22 Davis, R.B., and Berge, F., Atmospheric deposition in Norway during the last 300 years as recorded in SNSF lake sediments. II Diatom stratigraphy and inferred pH, in: Ecological Impact of Acid Precipitation, pp. 270–271. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.

23 Davis, P., and Ozburn, G., The pH tolerance of *Daphnia pulex* (Leydig emend Richard). Can. J. Zool. *47* (1969) 1173–1175.

24 De Costa, J., and Janicki, A., Population dynamics and age structure of *Bosmina longirostris* in an acid water impoundment. Verh. int. Ver. Limnol. *20* (1978) 2479–2483.

25 De Costa, J., Janicki, A., Shellito, G., and Wilcox, G., The effect of phosphorus additions in enclosures on the phytoplankton and zooplankton of an acid lake. Oikos *40* (1983) 283–294.

26 Dickman, M., and Fortescue, J., Rates of lake acidification inferred from sediment diatoms for 8 lakes located north of Lake Superior, Canada. Verh. int. Ver. Limnol. *22* (1984) 1345–1356.

27 Dickson, W., Properties of acidified waters, in: Ecological Impact of Acid Precipitation, pp. 75–83. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.

28 Dillon, P.J., Yan, N.D., Schneider, W.A., and Conroy, N., Acidic lakes in Ontario: characterization, extent, and responses to base and nutrient additions. Arch. Hydrobiol. Beih. Ergebn. Limnol. *13* (1979) 317–336.

29 Drabløs, D., and Tollan, A., (Eds), Ecological Impact of Acid Precipitation. Proc. Int. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.

30 Eriksson, M.O.G., Henrikson, L., Nilsson, B.-I., Nyman, G., Oscarson, H.G., and Stenson, A.E., Predator-prey relations important for the biotic changes in acidified lakes. Ambio *9* (1980) 248–249.

31 Evans, L.S., Botanical aspects of acidic precipitation. The Botanical Review *50* (1984) 449–490.

32 Findlay, D.L., Effects on phytoplankton biomass, succession and composition in lake 223 as a result of lowering pH levels from 5.6 to 5.2. Data from 1980 to 1982. Can. Manuscr. Rep. Fish. aquat. Sci. *1761* (1984) 1–10.

33 Flower, R.J., and Battarbee, R.W., Diatom evidence for recent acidification of two Scottish lochs. Nature *305* (1983) 130–133.

34 Foster, P.L., Species associations and metal contents of algae from rivers polluted by heavy metals. Freshwater Biol. *12* (1982) 17–39.

35 Geelen, J.F.M., Leuven, R.S.E.W., de Bie, J.E.G.M., and Maenen, M.M.J., Impact of acidification and eutrophication on microflora and microfauna assemblages of 'Littorellion' dominated systems. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen (1983) 68–72.

36 Geelen, J.F.M., Leuven, R.S.E.W., de Bie, J.E.G.M., and Maenen, M.M.J., Effecten van waterverzuring op microflora en microfauna van Littorelliongemeenschappen, in: Zure regen, oorzaken, effecten en beleid, pp. 182–183. Eds E.H. Adema and J. van Ham. Proc. Symp. Zure regen, 's Hertogenbosch, 17–18 November 1983. Pudoc, Wageningen 1984.

37 Grahn, O., Hultberg, H., and Landner, L., Oligotrophication a self-accelerating process in lakes subject to excessive supply of acid substances. Ambio *3* (1974) 93–94.

38 Haines, T.A., Acid precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. *110* (1981) 669–707.

39 Hall, R.J., Likens, G.E., Fiance, S.B., and Hendrey, G.R., Experimental acidification of a stream in the Hubbard Brook Experimental Forest, New Hampshire. Ecology *6* (1980) 967–975.

40 Hendrey, G.R., Effects of acidification on aquatic primary producers and decomposers, in: Acid rain/Fisheries, pp. 125–135. Ed. R.E. Johnson. Proc. Int. Symp. Acid Precip. Fish. Imp. Am. Fish. Soc., Bethesda, Maryland 1982.

41 Hendrey, G.R., Baalsrud, K., Traaen, T.S., Laake, M., and Raddum, G., Acid precipitation: some hydrobiological changes. Ambio *5* (1976) 224–227.

42 Hendrey, G.R., and Wright, R.F., Acid precipitation in Norway: effects on aquatic fauna. J. Great Lakes Res. *2* (1976) 192–207.

43 Hendrey, G.R., and Vertucci, F.A., Benthic plant communities in acidic Lake Colden, N.Y.: *Sphagnum* and the algal mat, in: Ecological Impact of Acid Precipitation, pp. 314–315. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.

44 Henrikson, L., Oscarson, H.G., and Stenson, J.A.E., Does the change of predator system contribute to the biotic development in acidified lakes?, in: Ecological Impact of Acid Precipitation, pp. 316–317. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980. SNSF project, Oslo–Aas 1980.

45 Hobaek, A., and Raddum, G.G., Zooplankton communities in acidified lakes in South Norway. SNSF project I.R. *75/80* (1980) 132ff.

46 Hörnström, E., Ekström, C., Miller, U., and Dickson, W., Forsurningens inverkan pa vastkustsjoar. Information fran Sotvattenslaboratoriot. Drottningholm No. *4* (1973) 1–81.

47 Johnson, M.G., Michalski, M.F.P., and Christie, A.E., Effects of acid mine wastes on phytoplankton communities of 2 northern Ontario lakes. J. Fish. Res. Bd. Can. *27* (1970) 425–444.

48 Johnson, R.E., (Ed.), Acid rain/Fisheries. Proc. Int. Symp. on Acidic Precipitation and Fishery Impacts in Northeastern North America. Cornell Univ. Ithaca N.Y. August 2–5, 1981. Am. Fish. Soc., Bethesda, Maryland 1982. 357ff.

49 Kelso, J.R.M., Love, R.J., Lipsit, J.H., Dermott, R., Chemical and biological status of headwater lakes in the Sault Ste Marie district, Ontario, in: Acid precipitation. Effects on Ecological Systems. Status of Lakes in the Sault Ste Marie District, pp. 165–207. Ed. F.M. D'Itri. Ann Arbor Science, 1980.

50 Kwiatkowski, R.E., and Roff, J.C., Effects of acidity on the phytoplankton and primary productivity of selected northern Ontario lakes. Can. J. Bot. *54* (1976) 2546–2561.

51 Lazarek, S., Structural and functional aspects of epiphytic and benthic algae in the acidified Lake Gårdsjön, Sweden. Ph.D. Thesis. Inst. of Limnology, Univ. of Lund 1983.

52 Leuven, R.S.E.W., and Schuurkes, J.A.A.R., Effecten van zure, stikstof en zwavelhoudende neerslag op zwak gebufferde en voedselarme wateren. Publikatiereeks Lucht 47. Ministry of Housing, Physical Planning and Environment 1984.

53 Lewis, W.M., Zooplankton community analyses. Springer, Berlin 1979.

54 Lowndes, A.G., Hydrogen ion concentration and the distribution of freshwater entomostraca. A. Mag. nat. Hist. ser. 12, *5* (1952) 58–65.

55 McCauley, E., and Briand, F., Zooplankton grazing and phytoplankton species richness: Field tests of the predation hypothesis. Limnol. Oceanogr. *24* (1979) 243–252.

56 Morling, G., Acidification and plankton in West-Swedish lakes 1966–1983. Ph.D. Thesis. Inst. of Limnology, Univ. of Lund 1984.
57 Mosello, R., and Tartari, G., Effects of acid precipitation on subalpine and alpine lakes. Water Quality Bull. *8* (1982) 96–110.
58 Moss, B., The influence of environmental factors on the distribution of freshwater algae: an experimental study. 1. Introduction and the influence of calcium concentration. J. Ecol. *60* (1972) 917–932.
59 Moss, B., The influence of environmental factors on the distribution of freshwater algae: an experimental study. 2. The role of pH and carbon dioxide-bicarbonate system. J. Ecol. *61* (1973) 157–177.
60 Moss, B., The influence of environmental factors on the distribution of freshwater algae: an experimental study. 4. The growth of test species in natural lake waters, and conclusion. J. Ecol. *61*, 193–211.
61 Müller, P., Effects of artificial acidification on the growth of periphyton. Can. J. Fish. Aquat. Sci. *37* (1980) 355–363.
62 Nilssen, J.P., Østdahl, T., and Potts, W.T.W., Species replacements in acidified lakes: Physiology, predation or competition? Verh. int. Ver. Limnol. *22* (1984) 699.
63 Overrein, L.N., Seip, H.M., and Tollan, A. (eds), Acid precipitation – Effects on forest and fish. Final Report SNSF project 1972–1980, 2nd edn. Oslo 1980.
64 Parent, S., and Cheetham, R.D., Effects of acid precipitation on *Daphnia magna*. Bull. Environ. Contam. Toxicol. *25* (1980) 298–304.
65 Porter, K.G., The plant-animal interface in freshwater ecosystems. Am. Sci. *65* (1977) 159–170.
66 Raddum, G.G.A., Hobaek, A., Lømsland, E.R., and Johnsen, T., Phytoplankton and zooplankton in acidified lakes in South Norway, in: Ecological Impact of Acid Precipitation, pp. 332–333. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.
67 Rebsdorf, A., Acidification of Danish softwater lakes, in: Ecological Impact of Acid Precipitation, pp. 238–239. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid Precip., Norway 1980, SNSF project, Oslo–Aas 1980.
68 Renberg, I., and Hellberg, T., The pH history of lakes in southwestern Sweden, as calculated from the subfossil diatomflora of the sediments. Ambio *11* (1982) 30–33.
69 Roelofs, J.G.M., Impact of acidification and eutrophication on macrophyte communities in soft waters in the Netherlands. I. Field observations. Aquat. Bot. *17* (1983) 139–155.
70 Roelofs, J.G.M., and Schuurkes, J.A.A.R., Impact of acidification and eutrophication on macrophyte communities in soft waters. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, (1983) 197–202.
71 Roelofs, J.G.M., Schuurkes, J.A.A.R., and Smits, A.J.M., Impact of acidification and eutrophication on macrophyte communities in soft waters. II Experimental studies. Aquat. Bot. *18* (1984) 389–411.
72 Roff, J.C., and Kwiatkowski, R.E., Zooplankton and zoobenthos of selected northern Ontario lakes of different acidities. Can. J. Zool. *55* (1977) 899–911.
73 Rosén, G., Phytoplankton indicators and their relation to certain chemical and physical factors. Limnologica *13* (1982) 263–290.
74 Schanz, F., Chemical and algological characteristics of five high mountain lakes near the Swiss National Park. Verh. int. Ver. Limnol. *22* (1984) 1066–1070.
75 Schindler, D.W., Evolution of the experimental lakes project. Can. J. Fish. aquat. Sci. *37* (1980) 313–319.
76 Schnoor, J.L., Sigg, L., Stumm, W., and Zobrist, J., Saure Niederschläge und ihr Einfluss auf die Schweizer Seen. Mitt. E.A.W.A.G. *15* (1983) 6–14.
77 Schoen, R., Wright, R., and Krieter, M., Gewässerversauerung in der Bundesrepublik Deutschland. Naturwissenschaften *71* (1984) 95–97.
78 Schoesmith, E.A., and Brook, A.J., Monovalent – divalent cation ratios and the occurrence of phytoplankton, with special reference to the desmids. Freshwater Biol. *13* (1983) 151–155.
79 Siegfried, C.A., Sutherland, J.W., Quinn, S.O., and Bloomfield, J.A., Lake acidification and the biology of Adirondack lakes I Rotifer communities. Verh. int. Ver. Limnol. *22* (1984) 549–558.
80 Skadowksi, S.N., Über die aktuelle Reaktion der Süsswasserbecken und ihre biologische Bedeutung. Verh. int. Ver. Limnol. *3* (1926) 109–144.
81 Sprules, W.G., Midsummer crustacean zooplankton communities in acid-stressed lakes. J. Fish. Res. Bd. Can. *32* (1975) 389–395.
82 Sprules, W.G., Factors affecting the structure of limnetic crustacean zooplankton communities in central Ontario lakes. Verh. int. Ver. Limnol. *19* (1975) 635–643.
83 Steinberg, C., Arzet, K., and Krause-Dellin, D., Gewässerversauerung in der Bundesrepublik Deutschland im Lichte paläolimnologischer Studien. Naturwissenschaften *71* (1984) 631–634.
84 Sutcliffe, D.W., and Carrick, T.R., Studies on mountain streams in the English Lake District. I pH, calcium, and the distribution of invertebrates in the River Duddon. Freshwater Biol. *3* (1973) 437–462.
85 Sutcliffe, D.W., Carrick, T.R., Heron, J., Rigg, E., Talling, J.F., Woof, C., and Lund, J.W.G., Long-term and seasonal changes in the chemical composition of precipitation and surface waters of lakes and tarns in the English Lake District. Freshwater Biol. *12* (1982) 451–506.
86 Symoens, J.J., Janssen, S., Remels, L., and van de Gucht, D., Algae as indicators of water quality in a lowland fen nature reserve. Verh. int. Ver. Limnol. *21* (1981) 1472–1475.
87 Vangenechten, J.H.D., Interrelations between pH and other physicochemical factors in surface waters of the Campine of Antwerp (Belgium): with special reference to acid moorland pools. Arch. Hydrobiol. *90* (1980) 265–283.
88 Vangenechten, J.H.D., Van Puymbroeck, S., Vanderborght, O.L.J., Bosmans, F., and Deckers, H., Physico-chemistry of surface waters in the Campine region of Belgium, with special reference to acid moorland pools. Arch. Hydrobiol. *90* (1981) 369–396.
89 Vangenechten, J.H.D., Van Puymbroeck, S., and Vanderborght, O.L.J., Acidification in Campine boglakes, in: Scope Belgium. Proc. Acid. deposition and sulphur cycle, pp. 251–262. Ed. O.L.J. Vanderborght. Brussels 1984.
90 Walton, W.E., Compton, S.M., Allan, J.D., and Daniels, R.E., The effect of acid stress on survivorship and reproduction of *Daphnia pulex*. (Crustacea: Cladocera). Can. J. Zool. *60* (1982) 573–579.
91 Wilcox, G., and DeCosta, J., The effect of phosphorus and nitrogen addition on the algal biomass and species composition of an acidic lake. Arch. Hydrobiol. *94* (1982) 393–424.
92 Williams, J.B., A study of summer mortality factors for natural populations of Chydoridae (Cladocera). Hydrobiologia *107* (1983) 131–139.
93 Wright, R., and Gjessing, E.T., Acid precipitation: changes in the chemical composition of lakes. Ambio *5* (1976) 219–223.
94 Wright, R.F., Harriman, R., Henriksen, A., Morrison, B., and Caines, L.A., Acid lakes and streams in the Galloway area, southwestern Scotland, in: Ecological Impact of Acid Precipitation, pp. 248–249. Eds D. Drabløs and A. Tollan. Proc. Int. Conf. Ecol. Impact Acid. Precip., Norway 1980, SNSF project, Oslo–Aas 1980.
95 Yan, N.D., Phytoplankton community of an acidified heavy metal-contaminated lake near Sudbury, Ontario: 1973–1977. Water, Air and Soil Pollution *11* (1979) 43–55.
96 Yan, N.D., and Stokes, P., Phytoplankton of an acidic lake and its response to experimental alterations of pH. Envir. Cons. *5* (1978) 93–100.
97 Yan, N.D., and Struss, R., Crustacean zooplankton communities of acidic metal contaminated lakes near Sudbury, Ontario. Can. J. Fish. aquat. Sci. *37* (1980) 2282–2293.
98 Zaret, T.M., A predation model of zooplankton community structure. Verh. int. Ver. Limnol. *20* (1978) 2496–2500.
99 Zytkowicz, R., Characteristics of the environment of the Jasne Lake. A.U.N.C., Limnol. Pap. *13* (1982) 51–63.

0014-4754/86/050486-09$1.50 + 0.20/0