The effects of acid deposition on benthic animals in lakes and streams

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Introduction

Acidification of lakes and streams has taken place recently in parts of Europe and North America[33,80,122,149]. Acidification in fresh water is particularly linked to atmospheric depositions but may also have terrestrial origins, and be related to effluents from mining industries. Effects on benthic animals have been brought into focus[141] and previously reviewed by e.g. Haines[47], National Research Council Canada[105], Burton et al.[22] and Singer[143,144].

Lakes and streams have a wide variety of benthic animals, here defined as macroinvertebrates such as crayfish, snails and insects. They are found on stones and macrovegetation in shallow water or living on and in sediments. Animals capable of swimming, for example some crustaceans and insects, are also considered as part of the benthic community since they often come to rest on the bottom or seek shelter among stems and leaves of aquatic macrovegetation.

We may distinguish between four viewpoints of importance for analysing effects of acidification on benthic animals (fig. 1): 1) External environmental factors, 2) Internal metabolism of the species, 3) Time variation, and 4) Interactions: one factor or condition influencing the effect of another. A simplified version of this conceptual

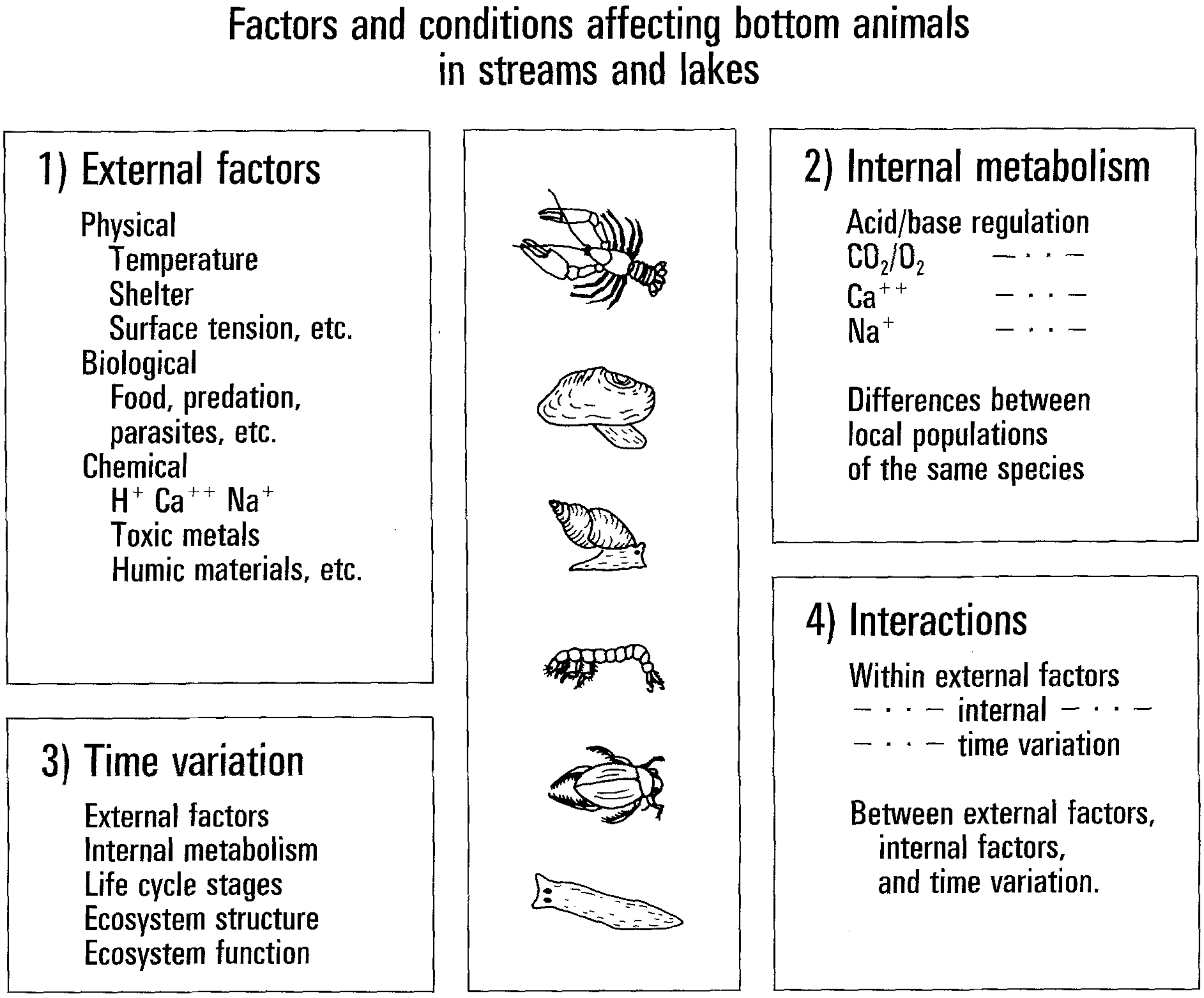

Figure 1. Effects of acidification upon benthic animals in fresh water are spread among a multitude of cause-effect pathways. In the present conceptual framework we distinguish between four viewpoints of importance for analysing the problem concerned: 1) external environmental factors of importance for the presence and well-being of the species, 2) internal metabolism of the species, 3) time variation, and 4) interactions: one factor or condition influencing the effect of another.

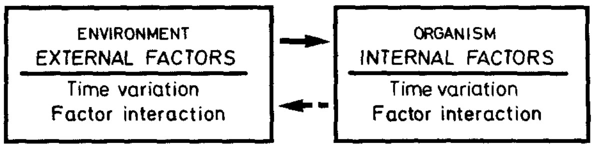

Figure 2. Acidification of lakes and streams brings about changes in the external factors on which organisms are dependent. These external factors vary in time and interact. Effects induced in the internal metabolism of the organisms (solid arrow) are also dependent on situation in time and interrelated factors in physiological processes. Feed-back mechanisms from the internal metabolism occur through excreted products or materials released after the death of the organism.

framework is shown in figure 2 stressing the cause-effect relation between environment and organism and taking time variation and factor interaction into account. A slight feed-back mechanism from organism to environment is indicated and explained in the legend. At present most of our knowledge refers to situations where attempts have only been made to evaluate H^+ concentration or, at best, a few additional factors, in a situation with many unknown variables.

Localities susceptible to acidification have low alkalinity and low concentration of calcium. Linthurst[80] considers waters with alkalinity below 200 μeq/l as susceptible and Henriksen[58] those below 6 mg Ca/l. A variety of benthic animals inhabit this type of water as well as environments considered as highly susceptible (alkalinity < 40 μeq/l and calcium < 3 mg Ca/l). There are four main approaches for studying effects of acidification upon these invertebrates: 1) Time-trend studies, 2) Field experiments, 3) Laboratory experiments, and 4) Field surveys of selected species or benthic communities in localities with different levels of acidity. Field experiments are reviewed in detail by Ravera[132]. All approaches are to some extent included in this presentation. There is considerable research activity throughout America and Europe and data presented on the following pages are likely to be supplemented rapidly.

Freshwater 'shrimps' (Gammarus) and other amphipods

Future damage in German forests may, according to Pieper and Meinel[124], be forecast by using species of *Gammarus* as early warning signals. The indicator value of these species is well established[95–98]. In the Kaufunger Wald in Hessen, West Germany, Meijering[96] noted that the *Gammarus* species disappeared from 16 out of 99 places investigated from 1968 to 1982, in the upper reaches this was due to acidification, and in the lower parts due to increasing organic pollution. In this forest *G. fossarum* and *G. pulex* occurred down to pH 5.7, and also at a single locality with pH 5.35 with a relatively high electrolytic conductivity. In one stream in the same area Teichmann[150] noted that heavy precipitation caused a drop in pH to 4.4–4.5 with subsequent death of all 'shrimps' within one week.

Gammarus fossarum is usually absent below pH 6.0; *G. pulex* is slightly more tolerant, having once been found down to pH 4.8[94]. A higher sensitivity of *G. fossarum* to low pH was also corroborated experimentally by Brehm and Meijering[19] who noted that acid stress on both species was caused mainly by H^+ ions while various anions were less important. For *G. fossarum* the upper part of figure 3 shows decreased survival rates with decreasing pH. For the same species Meinel et al.[99] showed that increased Na concentration enhanced survival rate at low pH and Matthias[88] observed the same mortality rates for fed and unfed specimens kept at low pH, concluding that chemical factors were responsible for the absence of *Gammarus* species in acid German streams.

A lower survival rate for *Gammarus pulex* in acid water was also observed experimentally by Minshall and Minshall[100] in Great Britain where the species is absent from places with pH < 5.7[44, 146, 147]. Townsend et al.[152] noted that pH was the most important environmental factor for determining its presence in 34 English streams. In a survey of 300 streams in South Sweden *G. pulex* occurred regularly down to pH 6.0 and occasionally down to pH 5.7[121].

Another species of *Gammarus* mainly inhabiting lakes (*G. lacustris*) is known from more than 1000 localities in Norway[116]. In warmer lowland areas K. A. Økland[117] showed that this northern circumpolar species was stressed by high temperature and was restricted to lakes with a relatively high total hardness (> 0.5°dH ≈ 2.7 mg

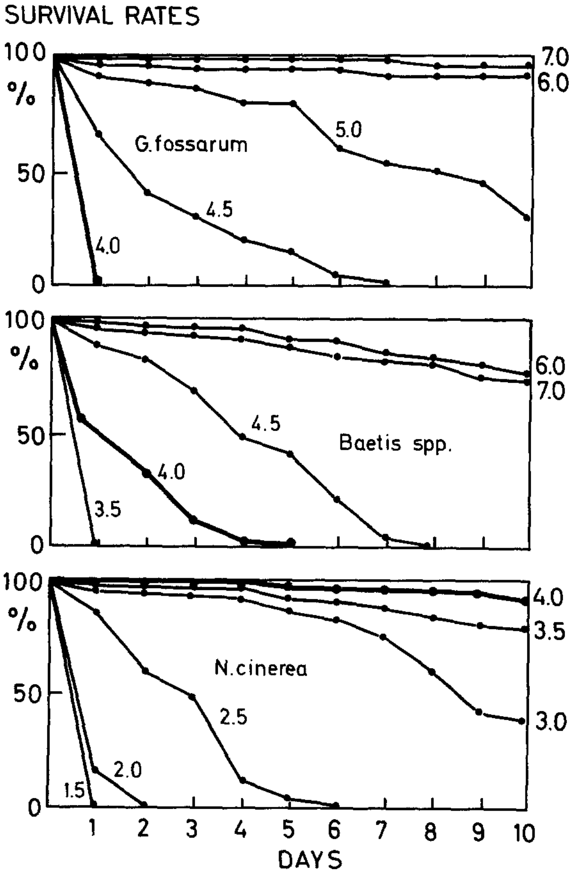

Figure 3. Survival rates in acidified stream water (taken from a neutral stream in West Germany) for the freshwater 'shrimp' *Gammarus fossarum*, larvae of mayflies *Baetis* spp., and the stonefly species *Nemoura cinerea*. In the field the first species is rarely encountered at places with pH below 6.0, the latter having been found down to pH 3.7. Modified from Matthias[88]. With permission from E. Schweizerbart'sche Verlagsbuchhandlung.

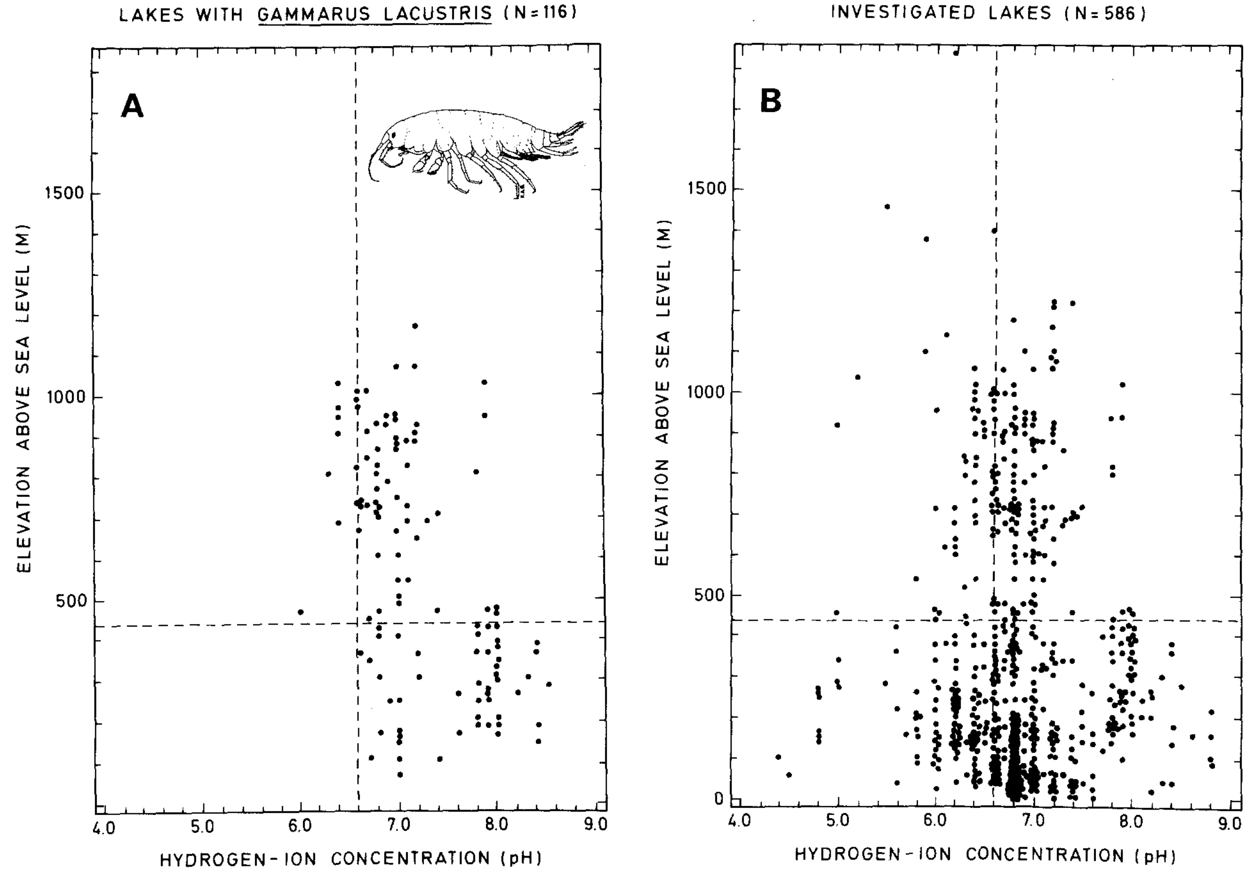

Figure 4. Elevation above sea level and pH in (A) lakes with presence of the freshwater 'shrimp' *Gammarus lacustris* and (B) investigated lakes in southeastern Norway. Each dot represents one lake, showing summer pH values from surface water. In lowland areas this circumpolar species is stressed by high temperature and presence is restricted to lakes with pH ≥ 6.6. At elevations above 440 m pH down to 6.0 is tolerated. Modified from K. A. Økland[117]. With permission from the SNSF-project.

Ca/l+0.6 mg Mg/l), which in this area maintains a high pH (≥ 6.6), cf. figure 4. At elevations above 440 m temperature is more favourable and lower total hardness (down to 0.1°dH ≈ 0.6 mg Ca/l+0.04 mg Mg/l) and lower pH (down to 6.0) is tolerated (cf. also fig. 17). The lowest pH values tolerated were reached in mountain lakes where calcium content was far above the minimum[120]. Other studies from Norway confirm a lower tolerance limit of pH 6.0 for *G.lacustris*[128]. Experimentally, Borgstrøm and Hendrey[18] showed that adult specimens had a low tolerance to pH values below 5.5 even for short exposure periods, the higher temperature in June (7–16°C) giving a higher mortality as compared with an experiment in September (11–6°C). In Sweden Engblom and Lingdell[30] noted occurrence in the field down to pH 5.6 for *Gammarus (lacustris* and/or *pulex)* and observed death within one week at pH 5.5.

In Sweden Mossberg[101] noted that another amphipod *(Pallasea quadrispinosa)* occurred in Lake Skärsjön in 1943 (pH 6.9) but could not be found again in 1977 following acidification to pH 5.4–6.1.

In North America, amphipods are known to endure much more acidic stress than that found for most European populations, Kelso et al.[77] noted the occurrence of *Hyalella azteca* and *Crangonyx richmondensis* down to pH 4.8 in some Canadian lakes.

Crayfish

The crayfish *Astacus astacus* is regarded as a delicacy in Scandinavia where it mainly occurs in waters with a summer pH above 6.0, some populations thriving down to about pH 5.5[81], [148]. The eggs are carried by the females from October to June–July and are exposed to short-term acidification during heavy rainfall and run-off in autumn and snow melt in spring[10, 43]. Appelberg[10] demonstrated a drastic loss of eggs during egg attachment on the female when specimens were kept at pH 5.0 as compared with those kept at 6.0 and 7.0 (fig. 5). The mortality rate during embryonal development was higher at pH 5.5 and below, compared with neutral water. At the moment of hatching, mortality increased drastically and remained high during early post-hatching stages at low pH (fig. 6). Acidification of Swedish lakes and streams is considered the most important environmental factor restricting the presence and well-being of the crayfish, next to the influence of the fungal parasite *Aphanomyces astaci*[8].

When a Canadian lake was artificially acidified from pH 6.7 to 5.0 over a period of eight years Schindler and Turner[140] and France[41] reported reduced calcification of the exoskeleton of the crayfish *Orconectes virilis* at pH 5.6 and increased infestation by parasites. At pH 5.4 recruitment failures and diminished population numbers be-

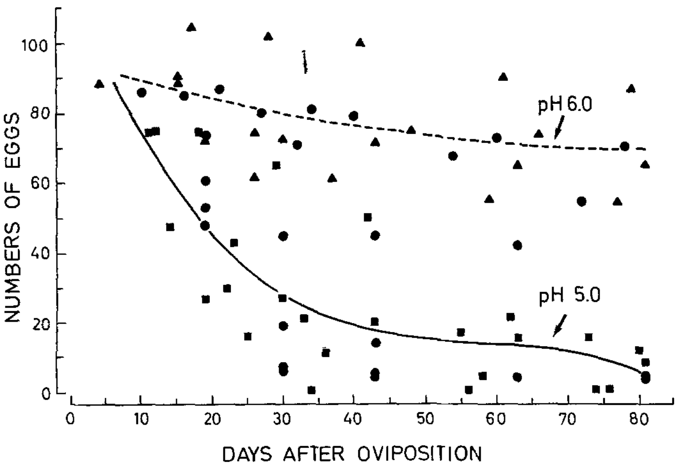

Figure 5. Number of attached eggs to females of the crayfish *Astacus astacus* from Sweden during a period of 80 days after egglaying. ● pH 7.0, ▲ pH 6.0, ■ pH 5.0. Curves fitted by cubic regression at pH 6.0 and 5.0. Modified from Appelberg[10]. With permission from Institute of Freshwater Research, Drottningholm.

came evident. Later, the crayfish disappeared completely[139].

Acid stress causes haemolymph acidosis and failure in body salt regulation in several species of crayfish[9,86,92], Malley[86] found inhibition of Ca uptake at low pH (below 5.75, cf. fig. 7) in the crayfish *Orconectes virilis* collected in a lake in Canada. Appelberg[10] showed a rapid, pH-dependent accumulation of Ca after hatching for *Astacus astacus* in Sweden. Acid exposure caused both a depression of mean total Ca content and net accumulation rate. A reduced calcium content in the exoskeleton after molt in acid water compared with neutral water of the same calcium concentration was also evident[6]. Oxygen uptake in eggs was influenced by acid stress[7], and for adult specimens of *A. astacus* an aluminum content of 250 µg Al/l disturbed ion regulation although not as drastically as was reported for fish[9]. A similar reaction to aluminum was also reported for a Swedish strain of the crayfish *Pacifastacus leniusculus*[9].

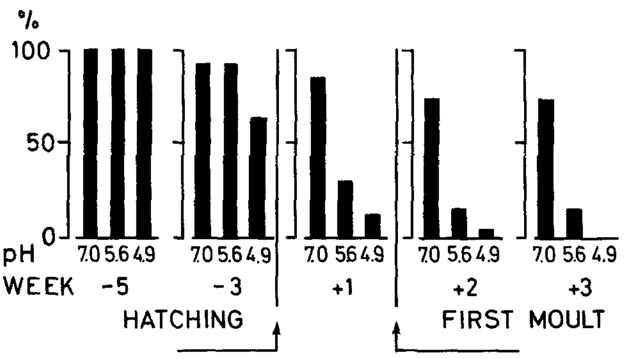

Figure 6. Percent survival of eggs of the crayfish *Astacus astacus* exposed to different pH-levels (7.0, 5.6, and 4.9) in Sweden during a period of five weeks before hatching and three weeks past hatching. From hatching and onwards survival decreases with decreasing pH. Modified from Appelberg[10]. With permission from Institute of Freshwater Research, Drottningholm.

Specific species tolerances and/or local conditions are of importance for determining H^+ tolerances of crayfish. As reviewed by Appelberg[6] there are American species found in waters of pH 4.0 and a Tasmanian one normally living at pH 4.5. Collins et al.[23] noted that *Cambarus bartoni* maintained reproducing populations at pH < 4.9 in three Canadian lakes.

Other crustaceans

In the Canadian lake-acidification experiment mentioned above, Schindler and Turner[140] report that the opossum shrimp *Mysis relicta* was eliminated at 5.8–6.0. Borgstrøm et al.[17] did not find the tadpole shrimp *Lepidurus arcticus* in lakes with a pH below 6.1 in Norway. This species was tested experimentally by Borgstrøm and Hendrey[18] for pH tolerance of the first larval stages. They observed increased mortality and delayed moulting at pH 5.5 and below. Experiments with *L. arcticus* in Canada by Havas and Hutchinson[53] revealed a significant increase in mortality below pH 4.5. The better ability to endure high acidity, as compared with Norwegian studies, was connected with the high calcium content in the water (250 mg Ca/l). Water from an acidic pond (pH 2.8) was markedly more toxic than water from an alkaline pond (pH 8.2) when both were adjusted to pH 4.5, probably owing to the elevated concentrations of aluminum. In a later study they reported decreased internal levels of Na and Cl under acid stress[54].

In Sweden, Mossberg[101] reports that the population density of the freshwater louse *Asellus aquaticus* decreased significantly from 1943 to 1977 in Lake Hovtjärn following acidification from pH 5.6–5.7 to pH 4.8–5.4. The lower pH limit in Sweden seems to be 4.3–4.4, with extremely low population density at the most acid sites[72,101,103,121]. In southeastern Norway K. A. Økland[117]

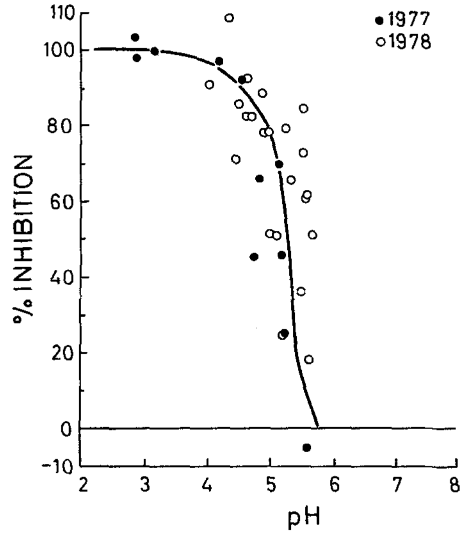

Figure 7. Low pH induces a progressive inhibition of calcium uptake in the crayfish *Orconectes virilis* from a Canadian lake. Percent inhibition is plotted against the mean pH of the medium during the experimental period. Data from two years are shown. Modified from Malley[86]. With permission from Canadian Journal of Fisheries and Aquatic Sciences.

reported frequent occurrence of *A. aquaticus* in lakes with pH > 5.2, and a more scattered presence in lakes down to pH 4.8 (fig. 17).

There are several species of Cladocera (water fleas etc.) which belong partly or completely to the benthic fauna. There is evidence, mainly based on plankton studies[4, 24, 122, 133] of reduced well-being of Cladocera in acid environments; the genus *Daphnia* is generally absent below pH 5.0–5.5. Collins et al.[23], however, reported increased densities of benthic cladocerans (primarily *Latona* sp.) in two of three acidified lakes (pH 4.6–4.8) investigated in Canada as compared with those of higher pH (> 5.9). As reviewed by Havas[52], several physiological mechanisms break down when cladocerans are under acid stress, particularly those necessary for maintaining a proper Na-balance.

Mollusca: snails (Gastropoda) and mussels/clams (Bivalvia)

For waters relatively poor in calcium a high H^+ concentration is a major factor for restricting the distribution of molluscs. This was noted e.g. in South Sweden by Hubendick[70]. In this area Mossberg[101] reports changes in mollusc populations in parallel with acidification trends: 1) From 1943 to 1973, the pH dropped from 6.3 to 5.2–5.3 in Lake Västra Skälsjön. The snail *Valvata macrostoma* disappeared and populations of small mussles (*Pisidium* spp.) were drastically diminished. 2) In Lake Grimsgöl *Pisidium* sp. disappeared when the pH dropped from 6.2 (1940's) to 4.8–5.5 (1977). Studies by Eriksson et al.[37–39] showed that it was not possible to confirm the presence of the pearl mussel *Margaritifera margaritifera* and the snail *Ancylus fluviatilis* in some rivers in 1980. 'Empty' rivers had a significantly lower pH as compared with localities where the species still occurred. *M. margaritifera* is known in Europe down to pH 5.1[76] and *A. fluviatilis* down to 5.7[147]. Effects of low pH on the snail *Amnicola limosa* may also be inferred by the evidence Rooke and Mackie[135] presented from Heeney Lake in Canada: failure of reproduction in a lake subject to acid precipitation and a spring depression of pH down to 4.7[85]. In an acidification experiment in the USA, Burton et al.[22] also confirmed the sensitivity of molluscs to low pH when the snail *Physa heterostropha* was eliminated by acidification from pH 7.4 to 4.0.

Comparison of molluscan faunas and pH generally reveals a decreasing number of species with decreasing pH. The largest sets of data are those from Norway, based on 959 lakes investigated for snails by J. Økland[109–111], and 593 lakes investigated for small mussels (Sphaeriidae) by K. A. Økland[117] and Økland and Kuiper[118, 119]. For both molluscan groups there is a decreasing number of species with decreasing pH, no snails having been found below pH 5.2 (fig. 8) and no mussels below pH 4.7 (fig. 9). Both sets of data refer to summer surface pH values. A decreasing number of species with decreasing pH has also been reported from other studies in Norway[68, 69, 107, 115] as well as in Sweden[70], Finland[1], England[147], Canada[133] and the USA[26, 145]. Some studies in Canada[90, 91] and the USA[28] have failed to prove decreasing molluscan populations with decreasing pH owing to lack of particularly acid sites.

The need for calcium to build up a shell is probably the main reason why this element is the most important chemical parameter in molluscan ecology (reviewed by e.g. Hunter[73] and McKillop[90]). Field studies separating the effect of pH from that of calcium are particularly significant since these factors are interrelated. For low total hardness-lakes in southeastern Norway (hardness up to 0.4° dH ≈ 2.2 mg Ca/l+0.4 mg Mg/l) J. Økland[109, 110]

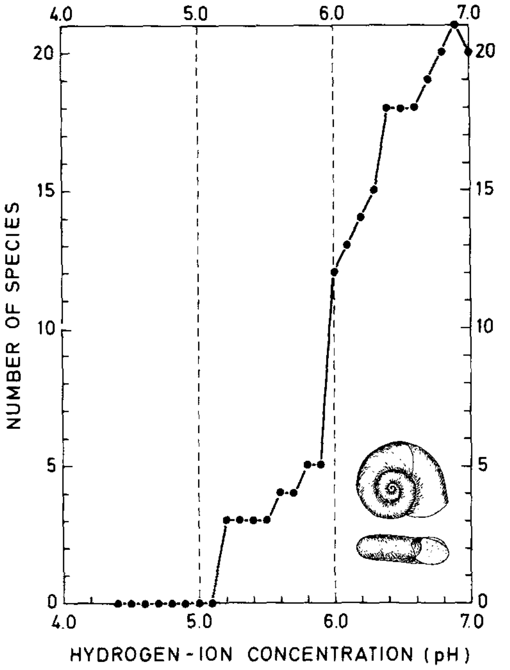

Figure 8. For freshwater snails species tolerance to pH within the range 4.0–7.0 is indicated, based on studies of 959 lakes in Norway (summer surface values). There is a rapid drop in number of species around pH 6.0. No species occurred below pH 5.2. Modified from J. Økland[110]. With permission from the SNSF-project.

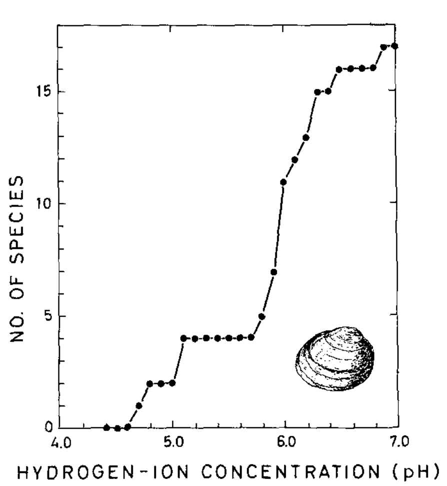

Figure 9. For small mussels (Sphaeriidae) species tolerance to pH within the range 4.0–7.0 (summer surface values) is indicated, based on studies of 593 lakes in Norway. There is a rapid drop in number of species around pH 6.0. No species occurred below pH 4.7. Modified from K. A. Økland[117]. With permission from the SNSF-project.

demonstrated that both the number of species and the time-catch abundance of snails decreased with decreasing values for pH within the same level of total hardness. Figure 10 presents the phenomenon visually for presence/absence of snails. A decreasing number of species of small mussels (Sphaeriidae) with decreasing pH for the same level of total hardness was also shown in Norway by Økland and Kuiper[118] for lakes of low total hardness (fig. 11). Studies by Raddum[127] and Raddum and Fjellheim[128] also separate the deleterious effect of low pH from that of calcium in other groups of Norwegian lakes. A decreasing number of snail species with decreasing pH in lakes of roughly the same calcium concentration has also been observed by Aho[1] in Finland and by Collins et al.[23] in Canada.

Effects of low pH and acidification upon snail populations in waters of the same calcium content are also manifested by average tendencies in county regions in Norway as shown by J. Økland[109]. Large parts of western South Norway have lakes with low total hardness (below 0.5° dH ≈ 2.7 mg Ca/l+0.6 mg Mg/l). The southern part of this vast area is heavily influenced by acid precipitation[122] and lakes are generally much more acid (pH 4.4–5.9) as compared with the northern ones (pH 6.0–7.3). Going from north to south the number of species of snails in the various regions decreases from 4 to 0 and average time-catch abundance decreases from 13.7 to 0 individuals collected per half-hour.

In Finnish lakes, Aho[2] noted that the distribution of snails was determined mainly by chemical factors when total hardness was low (< 1° dH = 7.1 mg Ca/l). In Norway, ten environmental factors were registered by J. Økland[111] in 403 low-calcium lakes (< 1° dH ≈ 5.2 mg Ca/l+1.2 mg Mg/l). Using stepwise multiple regression analyses with the number of snail species as well as total time-catch abundance as dependent variables, the most important factors turned out to be 1) total hardness, 2) type of macrovegetation in the water, and 3) pH. Including lakes with total hardness > 1° dH in the analyses, the importance of pH for explaining variations in the data was negligible. This serves to illustrate that effects of pH are only evident when calcium content (and/or total hardness) is low.

In Norway, J. Økland[110, 111] noted that 9 of the 11 most common snail species increased their tolerance to low pH with increasing calcium concentration. In data presented by Økland and Kuiper[118] the same tendency is evident for the most widely distributed small mussels (Sphaeriidae). Amelioration of acid stress by increasing levels of calcium is shown schematically in figure 20.

Small mussels (Sphaeriidae) are generally more tolerant to low pH than most snails. This phenomenon is observed in Canada[23, 77], Norway[68, 107, 110, 117, 127] and Sweden[101, 103]. Three theories are offered for explaining this phenomenon. 1) Raddum[127] and Collins et al.[23] noted that many small mussels burrow in the sediments (*infauna*) and may therefore benefit from the acid-neutralizing capacity of the sediments. 2) Rooke and Mackie[136] mentioned that young mussels are protected within the shell of the adult until they are released as miniature replicas. This would seem to be an advantage as compared with most snails which lay eggs, sometimes one at the time and not well protected from the surrounding water. 3) Mackie and Flippance[84] showed that the mussel *Musculium securis* was able to utilize calcium from food sources, and suggested that small mussels are able to thrive in low-calcium lakes because they are not as dependant upon dissolved calcium in the water as perhaps other molluscs are. A physiological influence of low pH on calcium uptake would then be diminished.

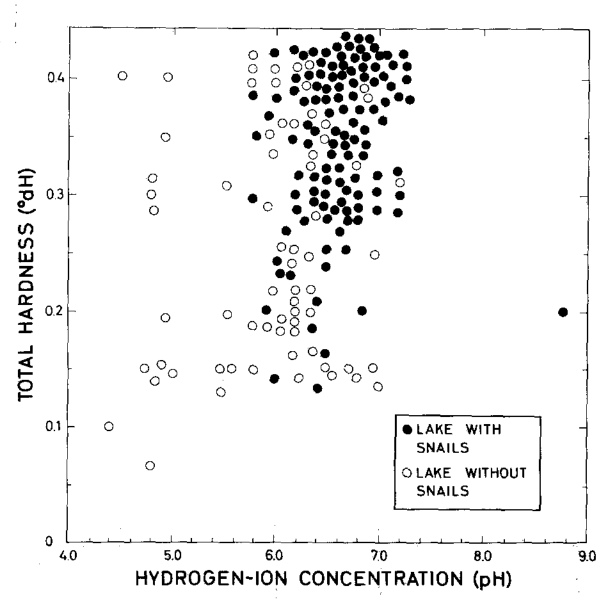

Figure 10. Presence/absence of snails in low total hardness lakes of southeastern Norway with given pH and total hardness (summer surface values). A total hardness of 0.4° dH corresponds to ca. 2.2 mg Ca/l+0.4 mg Mg/l. Within one and the same level of total hardness (horizontal levels) lakes without snails tend to be more acidic than those harbouring snails. Modified from J. Økland[110]. With permission from the SNSF-project.

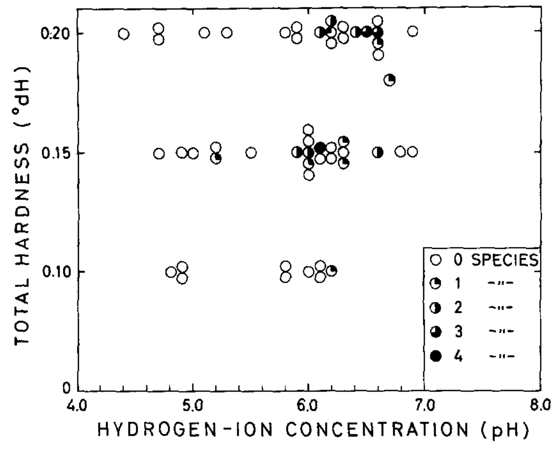

Figure 11. Summer surface values of pH and total hardness in lakes with given number of small mussels (Sphaeriidae) in Norway. Within one and the same level of total hardness (e.g. 0.2° dH ≈ 1.2 mg Ca/l+0.2 mg Mg/l) the number of species tend to decrease with decreasing pH. From Økland and Kuiper[118]. With permission from the SNSF-project.

Studies correlating molluscan faunas with alkalinity[1,2,85] generally find a poorer fauna with decreasing alkalinity. This is interesting since acidification – defined as loss of alkalinity – would imply a change to a poorer fauna. Biological effects of acidification are evident only for waters of relatively low alkalinity (< 100 μeq/l) and correlations mentioned above may be due to 1) correlation between alkalinity and calcium, water of low alkalinity generally having a low calcium concentration[4,59,77], 2) correlation between alkalinity and pH, water of low alkalinity tending to have low pH[77,80,85], and 3) an effect of alkalinity per se, low alkalinity implying low concentrations of carbonate and bicarbonate. Molluscs use the latter ions for the construction of $CaCO_3$-shells, and acidification deprives them of a necessary resource. As discussed by Rooke and Mackie[134] molluscs may, however, also form carbonates from metabolic carbon dioxide. The poor molluscan fauna in lakes of low alkalinity is therefore associated with low pH values, a low concentration of calcium, and possibly partly also reflects the low concentration of bicarbonate and carbonate.

The large naked external and/or internal body surfaces over which water passes freely in active molluscs contribute to explaining their high sensitivity to the chemical environment. Acid stress is not well understood from a physiological point of view. As reviewed by Havas[52], high acidity is often associated with corrosion of the older parts of the shell, and some molluscs draw from the $CaCO_3$-reservoir of the shell to compensate for internal acidosis; this resulting in erosion of the shell inside. Mackie and Flippance[83] showed that many species of small mussels responded to low alkalinity by forming short heavy shells, which presumably offer more protection against corrosion by H^+ ions than do long thin shells. In acid water poor in calcium some species reduce the $CaCO_3$-part of the shell; this becomes soft and flexible[21,118,142]. There is much infraspecific (interpopulation) variation and some species from the softest waters[137] do not have the lightest shells in terms of calcium. Some molluscs extract 80% of their shell calcium directly from the water and 20% indirectly through their food[154], and a small mussel *(Musculium securis)* was found to obtain a major fraction of its calcium from leaf litter[84] (cf. remarks above). There was clear evidence for decreasing uptake of calcium with decreasing pH in experiments with crayfish. Similar experiments with molluscs are lacking. For molluscs the need for calcium in shell building is evident while the need for carbonate is less clear, since it may be formed from carbon dioxide. For snails and mussels acid stress involving a high concentration of small mobile H^+ ions probably interferes with calcium metabolism, acid/base balance and mechanisms influencing ion balance in general (osmoregulation).

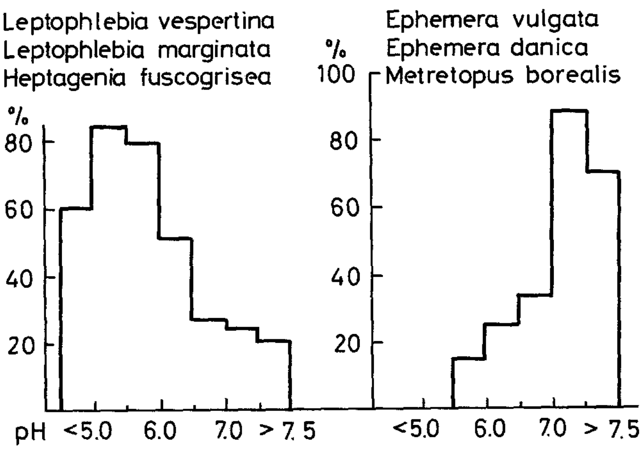

Figure 12. Based on data from 600 small streams in Sweden occurrence of two species complexes of mayflies (Ephemeroptera) is shown. Acid-sensitive species are shown to the right, acid-tolerant species to the left. Absence of the latter group in less acid and alkaline waters is probably due to competitive exclusion from other species. Data from P.-E. Lingdell, in Johansson and Nyberg[75] (modified). With permission from Institute of Freshwater Research, Drottningholm.

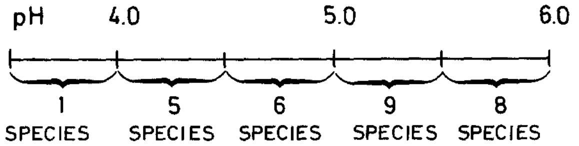

Figure 13. Number of mayfly species (Ephemeroptera) with more than 50% mortality when tested in the given pH intervals. Data from Engblom and Lingdell[30]. With permission from Institute of Freshwater Research, Drottningholm.

Mayflies (Ephemeroptera) and midges (Chironomidae)

Acidification in the Swedish lake Västra Skälsjön caused a drop in pH from 6.3 in 1943 to 5.2–5.3 in 1973. Mossberg[101] noted that the large mayfly *Ephemera vulgata* and several species of midges, e.g. *Heterotrissocladius määri,* disappeared. In Lake Örvattnet (Sweden) Grahn and Hultberg[45] noted that *E. vulgata* was no longer present in 1972–1973 at pH 4.9. This lake had a pH of 6.5 in 1937 and in 1968 *E. vulgata* occurred at pH 5.8. In the Swedish lake Gårdsjön pH dropped from 6.0 in 1960 to 4.5 in 1980. Henrikson et al.[60] and Henrikson and Oscarson[63] studied chironomid head capsules preserved in the lake sediments and noted a decrease in total chironomid density as well as changes in the composition of the fauna going from deeper to more recent layers in the sediments. Time-trend studies in Swedish mountain areas by Engblom and Lingdell[32] indicated that the lake Torrön area

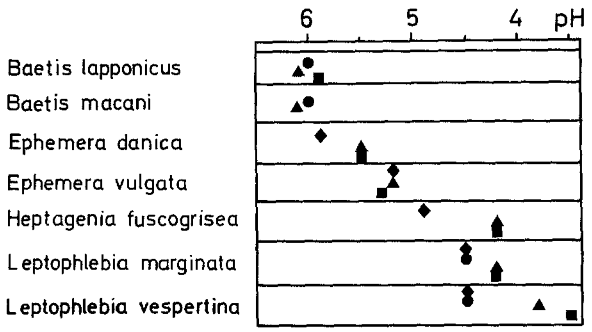

Figure 14. Comparison of lower pH tolerance limits for a selection of species of mayflies (Ephemeroptera). Diamonds: from Otto and Svensson[121]. Dots: from Raddum and Fjellheim[128]. Triangles: empirical data, and squares: experimental data, from Engblom and Lingdell[32]. Modified from[32]. With permission from Institute of Freshwater Research, Drottningholm.

had undergone drastic changes, the most sensitive mayfly species having disappeared from 1971 to 1983. In the Fulufjäll nature reserve further south the fauna was dominated by acid-tolerant species both in 1973 and in 1983 while a northern area (Vindelfjäll nature reserve) showed no change from the 1960s to 1983, sensitive species still being present. These findings are in agreement with the general tendency of decreasing effects of acid precipitation going from south to north in Sweden[4, 149].

As reviewed by Matthias[88] there is a general tendency for a decreasing number of species of mayflies to be found with decreasing pH, in many countries. Some 3500 sites were studied by Engblom and Lingdell[30–32] in streams all over Sweden. The lower pH limit as observed in the field corresponded fairly well with pH sensitivity found in experiments. Some species were extremely sensitive, with a lower pH limit around 6.0 *(Baetis lapponicus, B. macani)*; others were extremely tolerant, *Leptophlebia vespertina* enduring pH values below 4.0. Figure 12 shows on the right an acid sensitive species complex, on the left an acid tolerant complex, and figure 13 the number of species influenced in given intervals of pH. Including data from some 300 streams in South Sweden studied by Otto and Svensson[121] and from 135 localities in Norway investigated by Raddum and Fjellheim[128], figure 14 compares pH sensitivity found in field surveys and laboratory experiments for selected species.

Survival rates in acidified stream water for mayfly larvae of the genus *Baetis* at different pHs are shown in figure 3. In other experiments Matthias[88] showed that mortality rates were the same for fed and unfed larvae, concluding that the absence of *Baetis* from acid German streams was due to a direct effect of low pH. For *B. rhodani*, experiments by Minshall and Minshall[100] in England also pointed to a direct chemical effect of low pH. Raddum[126] noted decreased mortality for larvae of *B. rhodani* in experiments at pH 4.5–4.7 when total salinity increased.

In 34 Norwegian lakes Raddum[125, 127] found a reduced number of species of chironomids and a reduced abundance at low pH. Studying five lakes in more detail, Raddum and Saether[130] observed the lowest mean abundance of chironomids in lakes situated in regions with the longest history of acidification, independent of lake water pH, although the number of species decreased with decreasing pH.

With decreasing pH the chironomid group Tanytarsini is usually reduced in numbers and biomass. Bell[12] noted experimentally that *Tanytarsus dissimilis* could not complete its life cycle below pH 5.5.

Many chironomid species are extremely tolerant to low pH. Therefore these midges make up a substantial part of the bottom fauna in acid waters[26, 77, 79, 82, 101, 103, 153, 156]. In Sweden Mossberg[101] and Mossberg and Nyberg[103] noted that the genus *Chironomus* increases in importance in acid lakes and in Canada Havas and Hutchinson[53] collected *C. riparius* in acid ponds of pH 2.8.

Other insects

For stoneflies (Plecoptera) and caddisflies (Trichoptera) most field studies reveal a decreasing number of species with decreasing pH. This has been documented in Norway by Hendrey and Wright[56], Raddum[125] and Raddum and Fjellheim[128], in Sweden by Harmanen[50] and Otto and Svensson[121] and in West Germany by Matthias[87, 88].

Other groups of insects are extremely tolerant to low pH or contain a substantial proportion of tolerant species. In naturally acid lakes in Canada Kerekes et al.[78] noted the presence of beetles (Coleoptera) and the alderfly *Sialis* (Megaloptera) at pH 3.6; the following groups occurred at pH 4.0: damselflies (Zygoptera) of the Odonata group, backswimmers (Notonectidae) and water boatmen (Corixidae) of the group of true bugs (Hemiptera), and the phantom midge *Chaoborus* (Chaoboridae). One or more of these groups were also present in waters of pH 5 or lower in other places in Canada[77, 79, 133], as well as in Belgium[106, 155], Norway[107], Scotland[21], Sweden[45, 46, 72, 101, 103, 156] and the USA[145]. Black flies (Simuliidae) are also pH tolerant; Knox and Davidson[79] noted their presence at pH 4.8 in Canada, and Burns et al.[21] described populations at pH 5.0 in Scotland.

Insects: fish predation, and physiology

In acidified lakes low pH tolerant insects sometimes increase in abundance due to reduced fish predation. This was first noted in Sweden by Grahn and Hultberg[45] when beetles (Coleoptera), water boatmen (Corixidae) and damselflies (Agrionidae) increased in numbers and also tended to move into the free water masses. Similar observations including those of increasing populations of backswimmers (Notonectidae), water striders (Gerridae) and phantom midges *Chaoborus* spp. are documented by other Swedish workers[36, 46, 61, 62, 64, 103], and these observations are corroborated by observations from Norway[107, 125], Canada[77], and the USA[145].

In Norway Raddum[127] noted increased mean individual weight of mayflies (Ephemeroptera), caddisflies (Trichoptera) and midges (Chironomidae) in acid lakes with low fish predation. In English rivers Hildrew et al.[66] found a decline in large-bodied species with increasing pH and increasing fish predation. In Canada, Dermott[27] observed an increased biomass of benthic animals in lakes with lower pH as a result of an increase in large littoral species normally susceptible to fish predation. In a situation of acidification benthic invertebrates are therefore not affected only by more or less direct chemical changes in the environment, but also through indirect effects related to changes in fish populations.

Studies on mortality rates for insect larvae held at different pH levels by e.g. Bell and Nebeker[14], Raddum[125, 126], Raddum and Steigen[131], and Matthias[88] reveal large differences between individual species. In the period of emergence, when aquatic insects change to aerial adults, Bell[13] noted particular sensitivity for several species of dragonflies, stoneflies, caddisflies and mayflies. Raddum and Steigen[131] noted a reduced energy content in insect larvae when held or collected from sites with low pH. They referred this observation to the need for more energy 1) to maintain ion balance under acid stress and/or 2) for increased activity for escaping unfavourable conditions and/or searching for food.

Havas and Hutchinson[54] reported decreased internal levels of Na and Cl in larvae of the midge *Orthocladius consobrinus* when kept under acid stress. This impairment

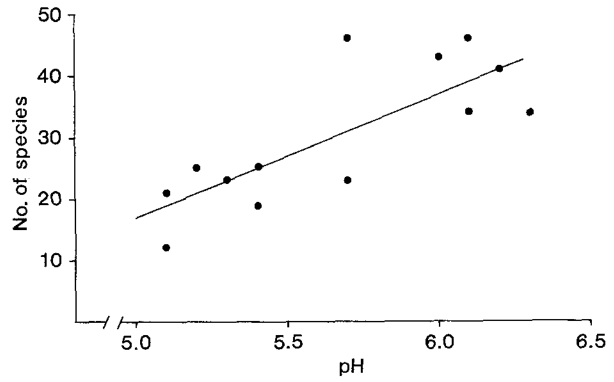

Figure 15. In 13 Swedish streams the number of species of benthic invertebrates increased significantly with increasing pH ($r = 0.78$, $p < 0.01$). pH values are averages from May, August and October. From Otto and Svensson[121]. With permission from E. Schweizerbart'sche Verlagsbuchhandlung.

in ion balance illustrates a general principle probably holding true for a large proportion of low pH sensitive invertebrates. Insects tolerant to low pH may maintain a stable haemolymph NaCl balance at low pH, as shown by Vangenechten and Vanderborght[155] for the water boatman *Corixa punctata* which occurs in waters down to pH 3.5–4.2. Jernelöv et al.[74] showed that a strain of the midge *Chironomus riparius* collected in ponds of pH 2.8 in Canada had an elevated content of haemoglobin as compared with a population from circumneutral water in Sweden; this buffered the haemolymph. Published records indicate no toxic effect of aluminum for insects tolerant to low pH[25, 55, 158]. Comments on new unpublished results are given in a final section on physiological effects of high H^+ concentration.

Worms (Oligochaeta), flatworms (Turbellaria), leeches (Hirudinea) and mites (Hydracarina)

Aquatic worms (Oligochaeta) decreased significantly in acidified lakes in Florida, as shown by Crisman et al.[26], while the proportion of chironomids increased. In Norway Raddum[127] noted a decline in those lakes which were most heavily influenced by acid precipitation as measured by excess sulphate and not by low pH. Also from Sweden there are indications of a reduced biomass in acidified lakes[101, 156]. There is considerable variation as to pH tolerance among species and groups[77]. Presence of oligochaetes has been noted down to pH 4.0 in Canada[78] and 4.1 in Scotland[51].

For leeches (Hirudinea), flatworms (Turbellaria) and mites (Hydracarina) there are data from Belgium[106], Canada[23, 77, 78, 133], Norway[107, 128], Scotland[21, 51], Sweden[45, 46, 101, 103, 121, 156], and West Germany[87–89]. Leeches occur mainly above pH 5.5 in Norway but have been found down to pH 4.2 in Sweden[121]. Flatworms are known down to pH 4.0 in Canada[78], and mites down to pH 4.2 in Scotland[51]. These predatory groups usually represent only a minor fraction of the total benthic biomass in lakes and streams.

pH and benthic fauna

Effects of acidification on benthic animals in running water can be inferred by comparing streams of different acidity or sites within the same stream. Decreasing pH is usually associated with decreasing numbers of species and number of individuals. This generalization appears from studies in England by Sutcliffe and Carrick[147] and Townsend et al.[152], in Sweden by Friberg et al.[42] and Otto and Svensson[121] (cf. fig. 15), and in the USA by Arnold et al.[11]. In streams investigated by Mackay and Kersey[82] in Canada, midges (Chironomidae) outnumbered the non-dipterous orders by an order of magnitude. The total number of benthic invertebrates was not reduced in the most acid streams due to a large number of newly-hatched tiny larvae of low pH tolerant chironomid species.

An impoverished benthic community in acid streams is partly of physiological nature due to increased H^+ concentration as discussed previously for crustaceans, molluscs and insects. Increased concentration of toxic metals may also be of importance. Additional effects are those associated with a reduced food supply, as discussed by e.g. Arnold et al.[11], Otto and Svensson[121], Hildrew et al.[67], Townsend and Hildrew[151], and Winterbourn et al.[157]. The

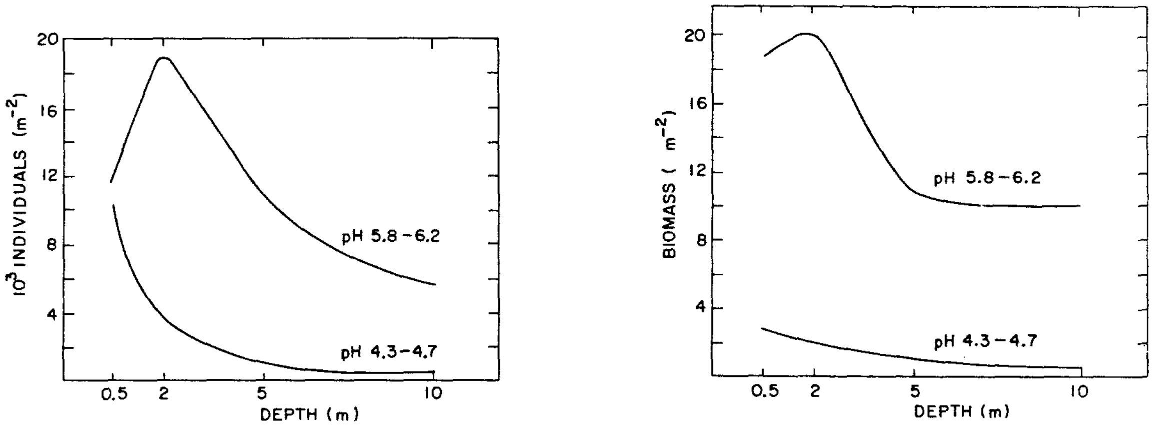

Figure 16. For two groups of Norwegian lakes with different acidity (pH 5.8–6.2, n = 5, and pH 4.3–4.7, n = 3) are shown number of individuals of benthic invertebrates and biomass in different depth regions. From Raddum[125]. With permission from Brookhaven National Laboratory.

food effect is related to differences in quality and quantity of organic material present in streams of different pH. Acid sites have a higher proportion of leaves and other coarse particulate organic matter and a higher proportion of those invertebrates (shredders) which make use of this type of food. Less acid sites have a higher proportion of fine particulate organic matter of better quality (more microorganisms) and those animals (collectors, filterers) consuming this type of food. Less acid sites also have a large proportion of invertebrates of the grazer/scraper type consuming attached algae and the organic layer associated with the substratum, these food resources seemingly being more abundant in less acid streams.

Effects of acidification on benthic animals in lakes may be inferred by comparing lakes of different acidity. For two groups of Norwegian lakes figure 16 shows that lakes of pH ca. 4.5 have lower numbers of individuals of benthic invertebrate species, and lower biomass as compared with lakes of pH ca. 6.0. Research regarding the number of species, and the results for crustaceans, snails and mussels studied in some 1000 Norwegian lakes reveal a thinning out of species and groups in acid waters (fig. 17). Selecting only those species which were widespread and also important in the diet of fish, figure 18 presents a drastic decline in species number with decreasing pH. These results are in agreement with the general tendency previously documented for crustaceans, molluscs and several groups of insects: acid lakes generally have fewer species and a lower biomass of benthic invertebrates. This conclusion is mainly founded on European studies. In several American lakes of different pH levels total benthic fauna was not diminished in those of low pH. This was noted in Canada by Hendrey et al.[57], Collins et al.[23], Dermott[27], Kelso et al.[77] and in the USA by Crisman et al.[26] and Singer[145]. Four principles/theories are offered to explain this phenomenon; the first two have already been mentioned.

1) A decrease in low pH sensitive species and biomass is to some extent compensated by an increase in low pH tolerant insects especially vulnerable to fish predation, since fish populations generally decrease or vanish completely in acid lakes. 2) Acid lakes often have a relatively higher proportion of species living in the sediments *(infauna)*, somewhat insulated from pH conditions in the water column (as compared with species belonging to the *epifauna* inhabiting surfaces or swimming). 3) Collins et al.[23] suggested that a lower concentration of aluminum in acid American lakes as compared with European lakes might be significant. 4) In North America large river systems running north-south facilitated the survival of the freshwater fauna during the ice ages; this gave a much higher number of species as compared with Europe (and especially Scandinavia), and provided a longer history of adaptation to extreme environments for the species concerned. American species or strains of amphipods, crayfish, benthic water fleas (Cladocera) and midges enduring environments of lower pH than that experienced for

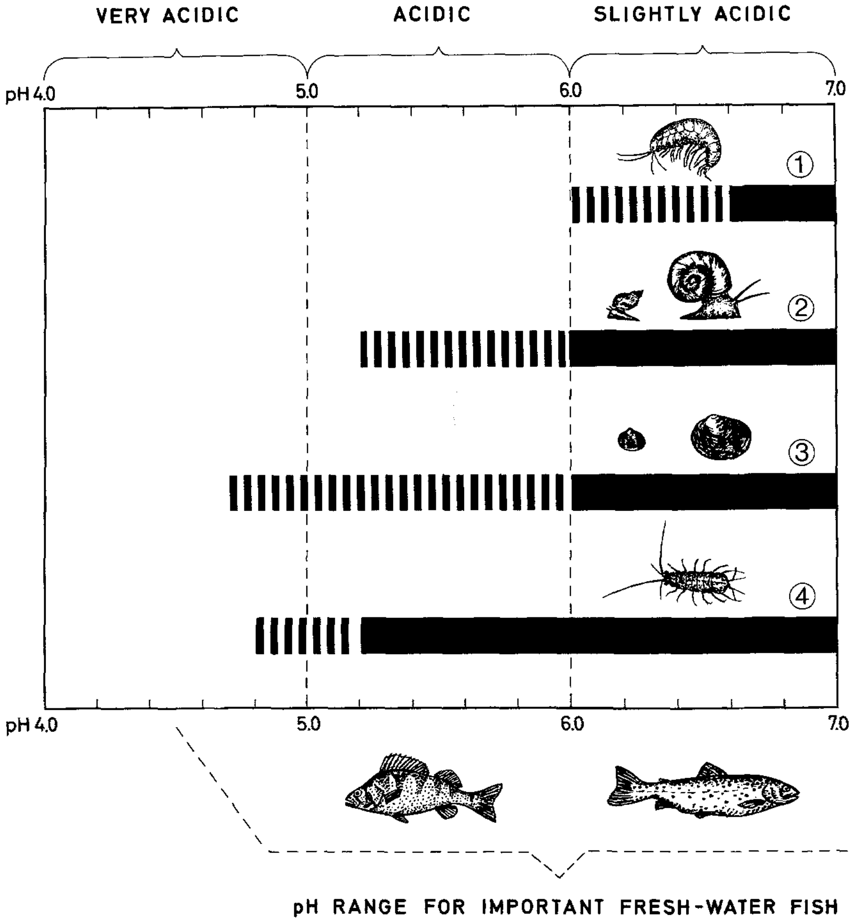

Figure 17. The pH range of lakes with four groups of bottom animals important as fish-food in Norway. At the bottom of the figure the distribution of freshwater fish according to pH range is indicated. In the slightly acidic sub-range (to the right) all groups are present. Few species penetrate into the very acid range (to the left). Data from ca. 1000 lakes, pH representing summer surface values.
1) The freshwater 'shrimp' *Gammarus lacustris* (the most important food organism for trout in Norway) is not present below pH 6.0. In lakes with pH 6.0–6.5 *G. lacustris* occurs only in mountain areas. In lakes with pH ≥ 6.6 the species also occurs in lowland districts.
2) Freshwater snails (Gastropoda) – as a group are not present below pH 5.2. In lakes with pH 5.2–6.0 only a few species occur.
3) Small mussels (Sphaeriidae) – as a group are not present below pH 4.7. In lakes with pH 4.7–6.0 only a few species occur.
4) The freshwater louse *Asellus aquaticus* is not present below pH 4.8. In lakes with pH 4.8–5.2 the species is infrequent. Modified from Økland and Økland[113]. With permission from the SNSF-project.

related species or strains in Europe/Scandinavia have already been mentioned.

Artificial acidification, and liming of lakes and streams

The lake acidification experiment described by Schindler and Turner[140] has been mentioned with regard to effects on crustaceans. Other experiments pertaining to effects on benthic fauna will be briefly summarized below. More information on artificial acidification is presented in the review by Ravera[132]. For natural streams in the USA acidified to pH 4.0, both Herricks and Cairns[65] and Hall et al.[49] showed increasing downstream drift of insect larvae with a concomitant decrease in the density of bottom animals. Mayflies (Ephemeroptera) were particularly affected, Fiance[40] also noting reduced growth of *Ephemerella funeralis*. Increased drift was also induced when Hall et al.[48] added aluminum to a stream; this caused a drop in pH from 6.4 to 5.0.

Using outdoor experimental channels, Zischke et al.[159] studied the effects of acidification to pH 6.0 and 5.0 on a wide variety of benthic invertebrates in the USA, concluding that the crustacean *Hyalella azeca* and the snail *Physa gyrina* were most sensitive; chironomids, the crustacean *Crangonyx,* and flatworms (Turbellaria) had intermediate tolerance; and damselflies (Odonata), isopods (Crustacea) and leeches (Hirudinea) were most tolerant. In the channels used by Burton et al.[22] the snail *Physa heterostropha* was eliminiated at pH 4.0, the crustacean *Asellus intermedius* was markedly reduced in numbers, and the caddisfly *Lepidostoma liba* (Trichoptera) was not affected. In artificial channels in Canada Allard and Moreau[3] noted increased mortality and drift of invertebrates following acidification to pH 4.0; addition of aluminum had no significant effect as compared with the addition of acid alone.

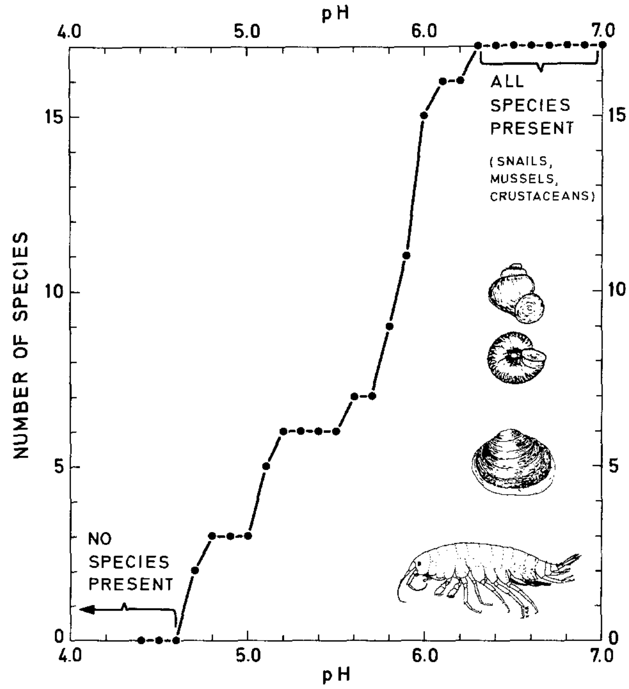

Figure 18. The pH tolerance limit for 17 widespread species of benthic fish-food organisms in Norway (snails, mussels, crustaceans). As conditions become more acid, a rapid drop in species number occurs about pH 6.0. None of the species occurred in lakes with pH below 4.7. Since the curve represents marginal habitats, it is an optimistic version. Same material as in the previous figure. Modified from Økland and Økland[113]. With permission from the SNSF-project.

Spreading of lime in acidified waters has been performed in order to increase the pH level and thereby restore the environment for fish. Effects of liming on benthic animals have been studied in Canada[138], Norway[20, 129] and Sweden[16, 34, 71, 123]. Littoral species sensitive to low pH usually increase in abundance and new species become established. Total biomass may increase or show no change, but it often decreases, especially in the profundal zone of lakes. This decrease has been connected to precipitation of aluminum complexes in the surface layer of the sediments; this perhaps influences the physical structure of the surface layer, since the toxic effects of such complexes remain to be proved for the species concerned.

Physiological effects of high H^+ concentration

The physiological response of aquatic animals to low pH is reviewed by Havas[52] who summarized the major mechanisms in a conceptional framework shown in figure 19. There are at least four physiological functions altered at low pH, i.e. 1) calcium regulation, 2) sodium regulation, 3) respiration, and 4) acid/base balance. These mechanisms are interrelated and appear to be affected at different H^+ concentrations.

Examples of how crustaceans, molluscs and insects react physiologically at low pH are given on previous pages. *Calcium regulation* is especially important to crustaceans and molluscs. For crustaceans there is clear evidence for a weakened calcium uptake at low pH. *Sodium regulation* is important to most aquatic animals because of its relation to general ion balance and osmoregulation. Some insects which tolerate low pH are particularly well adapted in this respect. *Respiration* or O_2/CO_2 regulation is not well understood for benthic invertebrates in fresh water. *Acid/base balance* is closely related to other physiological processes and may, if affected, lead to secondary effects for sodium and calcium regulation as well as for respiration. Data from field surveys and experiments presented previously reveal increased tolerance of low pH for several species of crustaceans, molluscs and insects when external calcium or total salinity increases. This is in agreement with findings for fish discussed by McWilliams[93] of calcium modifying gill permeability to Na^+, Cl^-, and H^+ ions at low pH. The phenomenon of pH tolerance modified by other factors – in this case calcium – is shown schematically in figure 20.

Another element shown to influence aquatic organisms in acid environments is aluminum, imposing salt depletion and respiratory distress for fish, especially around pH 5 (cf. Muniz and Leivestad[104]). Data and experiments mentioned previously indicated some negative effects of elevated concentrations of aluminum on crustaceans. This has also been corroborated by work in progress by M. Havas in Toronto, Canada, and by R. C. Petersen and co-workers in Lund, Sweden. Toxicity of aluminum seems to interact with pH and humic materials and also affect some insects as shown by work in progress by J. Herrmann and K. Andersson in Lund, Sweden. Much work is still needed to understand the physiological response of benthic invertebrates to aluminum and other potentionally toxic metals.

Importance of benthic animals

Some invertebrates can be used as 'early warning' signals since they are more sensitive to acid water than many species of fish[32,98,108,112-114,124,128] (also shown in fig. 17). Data on well-being and presence/absence of such species are often more informative than chemical studies carried out a few times a year since they integrate environmental impact over time. Studies of invertebrates have recently been included in the Norwegian governmental program for supervision of acidification trends in selected watercourses.

The feeding activity of macroinvertebrates converts debris from plants and other organic material into palatable matter for use by fish, riparian mammals, waterbirds and man (crayfish). Changes in fish diet may affect fish production[113,114]. Effects on water birds are discussed by Eriksson[35], who states that ducks feeding on aquatic insects are favoured by reduced competition when fish disappear in acid lakes. Passerine birds breeding near the shores of acid lakes suffer from impaired reproductive success, probably due to exposure to aluminum through feeding on emerging insects[35]. Lack of dippers in the most acid streams in Wales, southwest Scotland and northern England has been connected with reduced populations of those insects which serve as food in less acid streams[5].

In acid lakes the zooplankton community changes towards a greater frequency of large species when fish predation is replaced by predation by benthic invertebrates moving into the free water masses[36,62,64]. This, in turn, may affect phytoplankton and primary production.

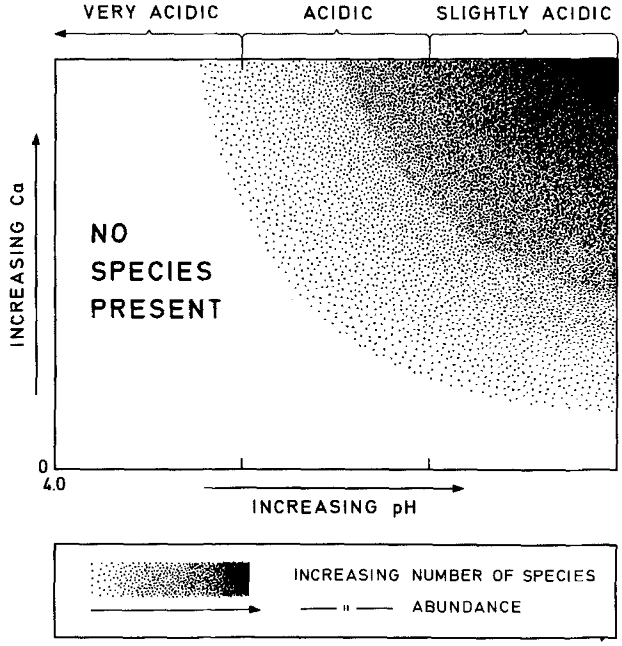

Figure 20. Schematical diagram showing the principle of reduced acid stress with increasing concentration of external calcium (lower pH values tolerated when calcium increases). Originally based on tolerance values for widespread species of snails, small mussels and crustaceans studied in ca. 1000 lakes in Norway. The same principle also holds true for certain other invertebrates and for fish. From Økland and Økland[113]. With permission from the SNSF-project.

By mechanical influence and physiological consumption of organic material, benthic invertebrates affect decomposition rates[15] and contribute to the recycling of inorganic nutrients. Changes in the benthic fauna may therefore affect total aquatic productivity.

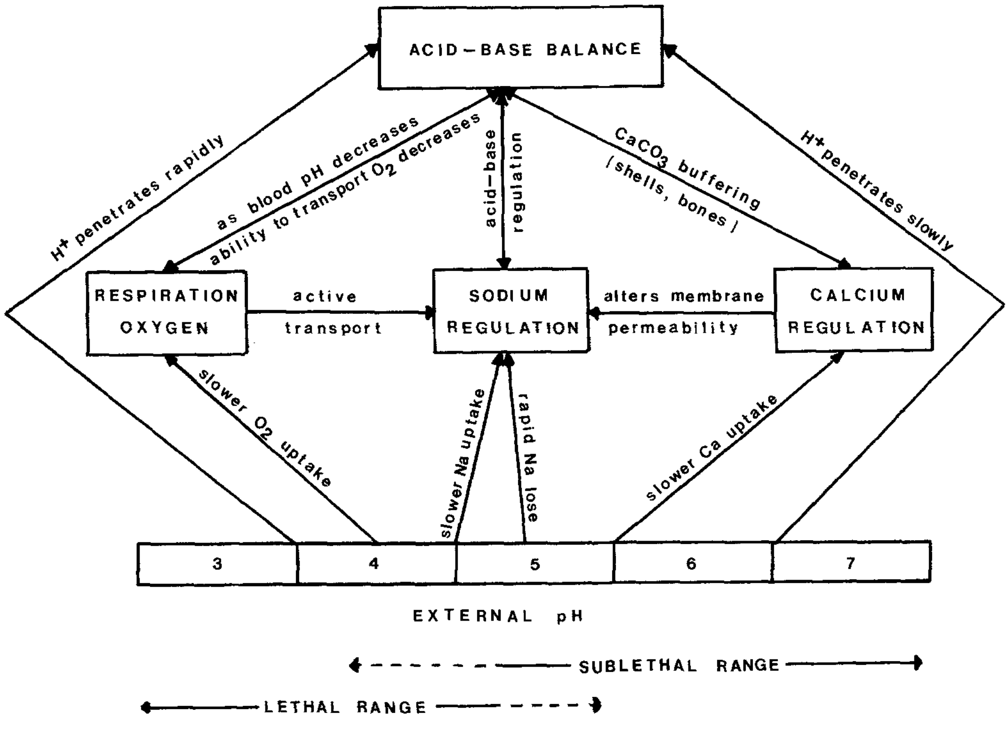

Figure 19. Major physiological responses of freshwater animals exposed to low pH. From Havas[52]. With permission from North American Benthological Society.

Conclusions

1) In certain European lakes and streams some species of crustaceans, snails, mussels and insects have disappeared in parallel with acidification of the water. For some species experimental evidence points to a direct physiological effect of high H^+ concentration (low pH values).

2) pH also serves as an index for special environmental characteristics and correlates with a number of causal factors influencing the benthic fauna. Indirect effects of decreasing pH values are:
A) Decreasing fish populations inducing an increase in the size of individuals and also in population density for several invertebrates tolerant to low pH.
B) Changes in quality and quantity of food, inducing changes in the proportion of species belonging to different feeding groups.
C) Increasing levels of toxic metals and changes in type and amount of substratum and shelter. Effects of these changes are not well elucidated.

3) There is no absolute lower pH limit for a given species since:
A) Different life cycle stages often have different tolerances to H^+ concentration.
B) The effect of low pH is modified by other factors.
C) Local populations of the same species may have different sensitivity to acid stress.
D) There is a gradual thinning out in population density towards low pH for sensitive species.

4) Comparing sites of different acidity with benthic fauna there is a general tendency towards decreasing number of species and biomass with decreasing pH, especially in Europe. Also, taking time-trend studies into account and including experimental evidence, we find that several species of crayfish and most of the other crustaceans as well as snails and mussels/clams are very sensitive to low pH. There are many sensitive species of mayflies (Ephemeroptera) and some also among midges (Chironomidae), stoneflies (Plecoptera) and caddisflies (Trichoptera). Other groups of insects are more tolerant to low pH and in the most acid sites insects dominate the benthic fauna. Four theories are offered to explain why some acid lakes in North America do not present an impoverished benthic fauna.

5) Several species with well established pH sensitivity are used for monitoring acidification. Some are more sensitive than fish and serve as early warning signals in the acidification process.

6) Benthic animals serve as food for fish and birds, affect decomposition rates of organic material and contribute to the recycling of inorganic nutrients. Changes in the benthic fauna influence the transfer of energy and elements in lakes and streams. Quantitative aspects of these processes are not well elucidated.

1 Aho, J., Ecological basis of the distribution of the littoral freshwater molluscs in the vicinity of Tampere, South Finland. Annls zool. fenn. *3* (1966) 287–322.

2 Aho, J., Freshwater snail populations and the equilibrium theory of island biogeography. II. Relative importance of chemical and spatial variables. Annls zool. fenn. *15* (1978) 155–164.

3 Allard, M., and Moreau, G., Influence d'une acidification expérimentale en milieu lotique sur la dérive des invertébrés benthiques. Verh. int. Verein. Limnol. *22* (1984) 1793–1800.

4 Almer, B., Dickson, W., Ekström, C., and Hörnström, E., Sulfur pollution and the aquatic ecosystem, in: Sulfur in the Environment, part II: Ecological Impacts, pp. 271–311. Ed. J.O. Nriagu. John Wiley & Sons, New York, Chichester, Brisbane, Toronto 1978.

5 Anonymous, Dippers inhibited by acid water. Acid News *1* (1985) 15–16.

6 Appelberg, M., The effect of low pH on *Astacus astacus* L. during moult. Pap. 2nd Scand. Meet. Freshwater Crayfish, Lammi, Finland, 1979, pp. 1–6. Enclosure 4 in: Appelberg, M.[8].

7 Appelberg, M., Response of acid stress upon the oxygen uptake in eggs of the crayfish *Astacus astacus* L., in: Freshwater Crayfish, V. Pap. 5th int. Symp. Freshwater Crayfish, Davis, California, USA, 1981, pp. 59–70. Ed. C.R. Goldman. Avi Publishing Company, Inc., West Port, Connecticut 1983.

8 Appelberg, M., Effects of acidification and liming on populations of crayfish. Summary of the project for the period 1978–1984. Institute of Limnology, Uppsala, LIU *1984:B7* (1984) 1–16 (in Swedish).

9 Appelberg, M., Changes in haemolymph ion concentrations of *Astacus astacus* L. and *Pacifastacus leniusculus* (Dana) after exposure to low pH and aluminium. Hydrobiologia *121* (1985) 19–25.

10 Appelberg, M., Early development of the crayfish *Astacus astacus* L. in acid water. Rep. Inst. Freshwat. Res., Drottningholm *61* (1984) 48–59.

11 Arnold, D.E., Bender, P.M., Hale, A.B., and Light, R.W., Studies on infertile, acidic Pennsylvania streams and their benthic communities, in: Singer, R. (ed.)[141], pp. 15–33, 1981.

12 Bell, H.L., Effects of pH on the life cycle of the midge *Tanytarsus dissimilis*. Can. Ent. *102* (1970) 636–639.

13 Bell, H.L., Effect of low pH on the survival and emergence of aquatic insects. Wat. Res. *5* (1971) 313–319.

14 Bell, H.L., and Nebeker, A.V., Preliminary studies on the tolerance of aquatic insects to low pH. J. Kans. ent. Soc. *42* (1969) 230–236.

15 Benfield, E.F., and Webster, J.R., Shredder abundance and leaf breakdown in an Appalachian Mountain stream. Freshwater Biol. *15* (1985) 113–120.

16 Bergquist, B., Studies on bottomfauna, and content of mercury in bottomfauna and sediments of the Lake Ölen, Örebro län, 1976–1980. Before and after liming. Inst. Limnology, Uppsala, LIU *1980: B9* (1980) 1–24 (in Swedish).

17 Borgstrøm, R., Brittain, J., and Lillehammer, A., Invertebrates and acid water. Review of sampling sites. SNSF-project, Oslo-Ås, Norway, *IR 21/76* (1976) 1–33 (in Norwegian with English summary).

18 Borgstrøm, R., and Hendrey, G.R., pH tolerance of the first larval stages of *Lepidurus arcticus* (Pallas) and adult *Gammarus lacustris* G.O. Sars. SNSF-project, Oslo-Ås, Norway, *IR 22/76* (1976) 1–37.

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

20 Brettum, P., and Hindar, A., Effects of liming on the biological system (in Norwegian), in: Liming of Acid Waters. Final Report, chapter 6. Ed. K. Baalsrud. Kalkingsprosjektet, Miljøverndepartementet, Oslo, Norway 1985.

21 Burns, J.C., Coy, J.S., Tervet, D.J., Harriman, R., Morrison, B.R.S., and Quine, C.P., The Loch Dee project: a study of the ecological effects of acid precipitation and forest management on an upland catchment in south-west Scotland. 1. Preliminary investigations. Fish Mgmt *15* (1984) 145–167.

22 Burton, T.M., Stanford, R.M., and Allan, J.W., The effects of acidification on stream ecosystems, in: Acid Precipitation. Effects on Ecological Systems, pp. 209–235. Ed. F.M. D'Itri. Ann Arbor Science, Ann Arbor 1982.

23 Collins, N.C., Zimmerman, A.P., and Knoechel, R., Comparisons of benthic infauna and epifauna biomasses in acidified and non-acidified Ontario lakes, in: Singer, R. (Ed.)[141], pp. 35–48, 1981.

24 Confer, J.L., and Kaaret, T., Zooplankton diversity and biomass in recently acidified lakes. Can. J. Fish. aquat. Sci. *40* (1983) 36–42.

25 Correa, M., Coler, R.A., and Yin, C.-M., Changes in oxygen consumption and nitrogen metabolism in the dragonfly *Somatochlora cingulata* exposed to aluminum in acid waters. Hydrobiologia *121* (1985) 151–156.

26 Crisman, T.L., Schulze, R.L., Brezonik, P.L., and Bloom, S.A., Acid precipitation: the biotic response in Florida lakes, in: D. Drabløs and A. Tollan (Eds)[29], pp. 296–297, 1980.

27 Dermott, R., The benthic fauna of poorly buffered lakes displaying a gradient of pH, in: Acid Rain/Fisheries. Proc., Int. Symp. on Acidic precipitation and fishery impacts in northeastern North

America, Ithaca, New York, August 2-5, 1981, p.350. Ed. R.A. Johnson. Compiled under the direction of T.A. Haines. American Fisheries Society, Bethesda, Maryland 1982. Published more extensively in Hydrobiologia *128* (1985) 31–38.

28 Dillon, R.T. Jr, and Benfield, E.F., Distribution of pulmonate snails in the New River of Virginia and North Carolina, USA: interaction between alkalinity and stream drainage area. Freshwater Biol. *12* (1982) 179–186.

29 Drabløs, D., and Tollan, A. (eds), Ecological impact of acid precipitation. Proc. int. Conf. Sandefjord, Norway, 11–14 March 1980. SNSF-Project, Oslo-Ås, Norway 1980.

30 Engblom, E., and Lingdell, P.-E., Usefulness of the bottom fauna as a pH indicator. Rep. natn. Swedish Environm. Protec. Bd. SNV *PM 1741* (1983) 1–181 (in Swedish with English summary).

31 Engblom, E., and Lingdell, P.E., Usefulness of the bottom fauna as a pH indicator. Acidification Res. Sweden *1* (1984) 7.

32 Engblom, E., and Lingdell, P.-E., The mapping of short-term acidification with the help of biological pH indicators. Rep. Inst. Freshw. Res., Drottningholm *61* (1984) 60–68.

33 Environmental Resources Limited. Acid rain. A review of the phenomenon in the EEC and Europe. A report prepared for the Commission of the European Communities, Directorate-General for Environment, Consumer Protection and Nuclear Safety. Graham & Trotman, 1983.

34 Eriksson, F., Hörnström, E., Mossberg, P., and Nyberg, P., Ecological effects of lime treatment of acidified lakes and rivers in Sweden. Hydrobiologia *101* (1983) 145–164.

35 Eriksson, M.O.G., Acidification of lakes: effects on waterbirds in Sweden. Ambio *13* (1984) 260–262.

36 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.

37 Eriksson, M.O.G., Henrikson, L., and Oscarson, H.G., Effects of acidification on freshwater molluscs in Älvsborgs län. Länsstyrelsen, Älvsborgs Län *1981: 2, part II* (1981) 1–12 (in Swedish).

38 Eriksson, M.O.G., Henrikson, L., and Oscarson, H.G., The acidification – a threat against the pearl mussel! Sveriges Natur *73* (1982) 16–19 (in Swedish).

39 Eriksson, M.O.G., Henrikson, L., and Oscarson, H.G., The pearl mussel in Sjuhäradsbygden. Sjuhäradsnatur *4* (1983) 58–63 (in Swedish).

40 Fiance, S.B., Effects of pH on the biology and distribution of *Ephemerella funeralis* (Ephemeroptera). Oikos *31* (1978) 332–339.

41 France, R.L., Response of the crayfish *Orconectes virilis* to experimental acidification of a lake with special reference to the importance of calcium, in: Freshwater Crayfish V. Papers from the Fifth Int. Symp. on Freshwater Crayfish, Davis, California, USA, 1981, pp.98–111. Ed. C.R. Goldman. Avi Publishing Company, Inc., West Port, Connecticut 1983.

42 Friberg, F., Otto, C., and Svensson, B.S., Effects of acidification on the dynamics of allochthonous leaf material and benthic invertebrate communities in running waters, in: D. Drabløs, and A. Tollan (eds)[29], pp.304–305, 1980.

43 Fürst, M., The effect of acidification on populations of *Astacus astacus* L., in: Nordiskt kräftsymposium 1977, pp.89–94. Ed. M. Fürst. Inform. Inst. Freshw. Res., Drottningholm *14*, 1978 (in Swedish with English summary).

44 Gledhill, T., Sutcliffe, D.W., and Williams, W.D., A revised key to the British species of Crustacea: Malacostraca occurring in fresh water. Scient. Publs Freshwat. biol. Ass. *32* (1976) 1–72.

45 Grahn, O., and Hultberg, H., Effects of acidification on the ecosystem of oligotrophic lakes – integrated changes in species composition and dynamics. Swedish Water and Air Pollution Research Laboratory IVL, Gothenburg. *B 192* (1974) 1–17 (in Swedish with English summary).

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

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

48 Hall, R.J., Driscoll, C.T., Likens, G.E., Pratt, J.M., Physical, chemical, and biological consequences of episodic aluminum additions to a stream. Limnol. Oceanogr. *30* (1985) 212–220.

49 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 *61* (1980) 976–989.

50 Harmanen, M., Der Einfluss saurer Gewässer auf den Bestand der Ephemeriden- und Plecopterenfauna. Gewäss. Abwäss. *66/67* (1980) 130–136.

51 Harriman, R., and Morrison, B.R.S., Ecology of streams draining forested and non-forested catchments in an area of central Scotland subject to acid precipitation. Hydrobiologia *88* (1982) 251–263.

52 Havas, M., Physiological response of aquatic animals to low pH, in: R. Singer (ed.)[141], pp.49–65, 1981.

53 Havas, M., and Hutchinson, T.C., Aquatic invertebrates from the Smoking Hills, N.W.T.: Effect of pH and metals on mortality. Can. J. Fish. aquat. Sci. *39* (1982) 890–903.

54 Havas, M., and Hutchinson, T.C., Effect of low pH on the chemical composition of aquatic invertebrates from tundra ponds at the Smoking Hills, N.W.T., Canada. Can. J. Zool. *61* (1983) 241–249.

55 Havas, M., and Likens, G.E., Toxicity of aluminum and hydrogen ions to *Daphnia catawba, Holopedium gibberum, Chaoborus punctipennis,* and *Chironomus anthracinus* from Mirror lake, New Hampshire. Can. J. Zool. *63* (1985) 1114–1119.

56 Hendrey, G.R., and Wright, R.F., Acid precipitation in Norway: effects on aquatic fauna. J. Great Lakes Res. *2*, Suppl. 1 (1976) 192–207.

57 Hendrey, G.R., Yan, N.D., and Baumgartner, K.J., Responses of freshwater plants and invertebrates to acidification, in: Proc. Int. Symp. for Inland Waters and Lake Restoration, Portland, Maine, September 8–12, 1980, pp.457–466. EPA/DECD, 1980.

58 Henriksen, A., A simple approach for identifying and measuring acidification of freshwater. Nature *278* (1979) 542–545.

59 Henriksen, A., Susceptibility of surface waters to acidification, in: Acid rain/Fisheries. Proc., Int. Symp. on Acidic precipitation and fishery impacts in northeastern North America, Ithaca, New York, August 2–5, 1981, pp.103–121. Ed. R.A. Johnson. Compiled under the direction of T.A. Haines. American Fisheries Society, Bethesda, Maryland 1982.

60 Henrikson, L., Olofsson, J.B., and Oscarson, H.G., The impact of acidification on Chironomidae (Diptera) as indicated by subfossil stratification. Hydrobiologia *86* (1982) 223–229.

61 Henrikson, L., and Oscarson, H.G., Fish predation limiting abundance and distribution of *Glaenocorisa p. propinqua.* Oikos *31* (1978) 102–105.

62 Henrikson, L., and Oscarson, H.G., Corixids (Hemiptera – Heteroptera), the new top predators in acidified lakes. Verh. Int. Verein. Limnol. *21* (1981) 1616–1620.

63 Henrikson, L., and Oscarson, H.G., History of the acidified Lake Gårdsjön: the development of chironomids. Ecol. Bull. (1985) in press.

64 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: D. Drabløs, and A. Tollan (eds)[29], p.316, 1980.

65 Herricks, E.E., and Cairns, J. Jr, The recovery of stream macrobenthos from low pH stress. Rev. Biol. *10* (1974) 1–11.

66 Hildrew, A.G., Townsend, C.R., and Francis, J., Community structure in some southern English streams: the influence of species interactions. Freshwat. Biol. *14* (1984) 297–310.

67 Hildrew, A.G., Townsend, C.R., and Francis, J., Cellulolytic decomposition in streams of contrasting pH and its relationship with invertebrate community structure. Freshwat. Biol. *14* (1984) 323–328.

68 Hinz, W., Zur Molluskenfauna verschieden stark durch saure Niederschläge verschmutzter Seen in Südnorwegen. Gewäss. Abwäss. *66/67* (1980) 7–28.

69 Hinz, W., Mollusken-Siedlungsdichten in Seen Südnorwegens. Mitt. dtsch. malak. Ges. *3*, Suppl. (1982) 39–41.

70 Hubendick, B., Die Verbreitungsverhältnisse der limnischen Gastropoden in Südschweden. Zool. Bidr. Upps. *24* (1947) 419–559.

71 Hultberg, H., and Andersson, I.B., Liming of acidified lakes: induced long-term changes. Water Air Soil Pollut. *18* (1982) 311–331.

72 Hultberg, H., and Stenson, J., Effects of acidity on the fishfauna of two small lakes in Bohuslän, south-western Sweden. Fauna Flora *65* (1970) 11–20 (in Swedish with English summary).

73 Hunter, W.R., Physiological aspects of ecology in non-marine molluscs, in: Physiology of Mollusca, vol.2, pp.83–126. Eds K.M. Wilbur and C.M. Yonge. Academic Press, New York and London 1964.

74 Jernelöv, A., Nagell, B., and Svenson, A., Adaptation to an acid environment in *Chironomus riparius* (Diptera, Chironomidae) from Smoking Hills, NWT, Canada. Holarctic Ecol. *4* (1981) 116–119.

75 Johansson, K., and Nyberg, P., Acidification of surface waters in Sweden – effects and extent 1980. Inform. Inst. Freshw. Res., Drottningholm *6* (1981) 1–118 (in Swedish with English summary).

76 Jungbluth, J. H., Untersuchungen zur Verbreitung, Morphologie und Ökologie der *Margaritifera*-Populationen an den atypischen Standorten des jungtertiären Basaltes im Vogelsberg/Oberhessen (Mollusca: Bivalvia). Arch. Hydrobiol. *78* (1976) 165–212.

77 Kelso, J. R. M., Love, R. J., Lipsit, J. H., and Dermott, R., Chemical and biological status of headwater lakes in the Sault Ste. Marie district, Ontario, in: Acid Precipitation. Effects on Ecological Systems, pp. 165–207. Ed. F. M. D'Itri. Ann Arbor Science, Ann Arbor 1982.

78 Kerekes, J., Freedman, B., Howell, G., and Clifford, P., Comparison of the characteristics of an acidic eutrophic, and an acidic oligotrophic lake near Halifax, Nova Scotia. Water Poll. Res. J. Canada *19* (1984) 1–10.

79 Knox, D., and Davidson, L.-A., Investigation of macroinvertebrates from the Westfield and North River study area, Nova Scotia. Can. Tech. Rep. Fish. aquat. Sci. *1213* (1983) 11–22.

80 Linthurst, R. A. (ed.), The acidic deposition phenomenon and its effects: Critical assessment review papers. Vol. II: Effects Science. United States Environmental Protection Agency, 1984.

81 Lund, H. M.-K., Crayfish in Norway, its habitat requirements and commercial aspects. Fauna, Oslo *22* (1969) 177–188 (in Norwegian with English summary).

82 Mackay, R. J., and Kersey, K. E., A preliminary study of aquatic insect communities and leaf decomposition in acid streams near Dorset, Ontario. Hydrobiologia *122* (1985) 3–11.

83 Mackie, G. L., and Flippance, L. A., Relationships between buffering capacity of water and the size and cacium content of freshwater mollusks. Freshwat. Invert. Biol. *2* (1983) 48–55.

84 Mackie, G. L., and Flippance, L. A., Calcium sources for growth of *Musculium securis* (Bivalvia: Pisidiidae). Can. J. Zool. *61* (1983) 874–878.

85 Mackie, G. L., and Flippance, L. A., Intra- and interspecific variations in calcium content of freshwater Mollusca in relation to calcium content of the water. J. moll. Stud. *49* (1983) 204–212.

86 Malley, D. F., Decreased survival and calcium uptake by the crayfish *Orconectes virilis* in low pH. Can. J. Fish. aquat. Sci. *37* (1980) 364–372.

87 Matthias, U., Zur Problematik der Gütebeurteilung von sauren Fliessgewässern. Z. Wasser Abwasser Forsch. *16* (1983) 107–110.

88 Matthias, U., Der Einfluss der Versauerung auf die Zusammensetzung von Bergbachbiozönosen. Arch. Hydrobiol. Suppl. *65* (1983) 407–483.

89 Matthias, U., and Meinel, W., Zur anthropogenen Gewässerversauerung im Kaufunger Wald. Phillipia *5* (1982) 76–86.

90 McKillop, W. B., Distribution of aquatic gastropods across the Ordovician dolomite – Precambrian granite contact in southeastern Manitoba, Canada. Can. J. Zool *63* (1985) 278–289.

91 McKillop, W. B., and Harrison, A. D., Distribution of aquatic gastropods across an interface between the Canadian Shield and limestone formations. Can. J. Zool. *50* (1972) 1433–1445.

92 McMahon, B. R., and Morgan, D. O., Acid toxicity and physiological responses to sub-lethal acid exposure in crayfish, in: Freshwater Crayfish V. Pap. 5th int. Symp. Freshwater Crayfish, Davis, California, USA, 1981, pp. 71–85. Ed. C. R. Goldman. Avi Publishing Company, Inc., West Port, Connecticut 1983.

93 McWilliams, P. G., The effects of calcium on sodium fluxes in the brown trout, *Salmo trutta*, in neutral and acid water. J. exp. Biol. *96* (1982) 439–442.

94 Meijering, M. P. D., Die *Gammarus*-Fauna der Schlitzerländer Fliessgewässer. Arch. Hydrobiol. *68* (1971) 575–608.

95 Meijering, M. P. D., Zum Lebensformtypus *Gammarus* und dessen Indikationswert für Fliessgewässerschäden. Natur Mensch, Jahresmitt. (1982) 133–138.

96 Meijering, M. P. D., Die Verbreitung von Indikatorarten der Gattung *Gammarus* im Schlitzerland (Osthessen) in 1968 und 1982, in: Gewässerversauerung in der Bundesrepublik Deutschland. Ed. Umweltbundesamt. Materialen *1* (1984) 96–105.

97 Meijering, M. P. D., Auswirkungen saurer Niederschläge auf Bäche. Wissenschaft und Umwelt *2* (1984) 102–104.

98 Meijering, M. P. D., and Pieper, H. G., Die Indikatorbedeutung der Gattung *Gammarus* in Fliessgewässern. Decheniana-Beihefte (Bonn) *26* (1982) 111–113.

99 Meinel, W., Matthias, U., and Zimmermann, S., Ökophysiologische Untersuchungen zur Säuretoleranz von *Gammarus fossarum* (Koch). Arch. Hydrobiol. *104* (1985) 287–302.

100 Minshall, G. W., and Minshall, J. N., Further evidence on the role of chemical factors in determining the distribution of benthic invertebrates in the River Duddon. Arch. Hydrobiol. *83* (1978) 324–355.

101 Mossberg, P., Benthos of oligotrophic and acid lakes. Inform. Inst. Freshw. Res., Drottningholm *11* (1979) 1–40 (in Swedish with English summary).

102 Mossberg, P., and Nyberg, P., Effects of acidification on buttom fauna and fish in Lake Västra Skälsjön. Inform. Inst. Freshw. Res., Drottningholm *9* (1976) 1–23 (in Swedish with English summary).

103 Mossberg, P., and Nyberg, P., Bottom fauna of small acid forest lakes. Rep. Inst. Freshw. Res., Drottningholm *58* (1979) 77–87.

104 Muniz, I. P., and Leivestad, H., Acidification – effects on freshwater fish, in: D. Drabløs and A. Tollan (eds)[29], pp. 84–92, 1980.

105 National Research Council Canada. Acidification in the Canadian aquatic environment: Scientific criteria for assessing the effects of acidic deposition on aquatic ecosystems. NRCC 18475. Environmental Secretariat, Ottawa, Canada 1981.

106 Neven, B., and Beckers, B., Investigations of the benthic macro-invertebrates community in the acid bogs in the Campine region of Limburg, in: Acid Deposition and the Sulphur Cycle. Proc., Symp. Brussels 6 June, 1984, pp. 263–275. Ed. O. L. J. Vangenechten. Scope Belgium 1984.

107 Nilssen, J. P., Acidification of a small watershed in southern Norway and some characteristics of acidic aquatic environments. Int. Revue ges. Hydrobiol. *65* (1980) 177–207.

108 Økland, J., On the acidification of inland waters in Scandinavia and the importance of the hydrogen-ion concentration (pH) for fish-food organisms in Norwegian lakes. Fauna, Oslo *22* (1969) 140–147 (in Norwegian with English summary).

109 Økland, J., Total hardness, hydrogen-ion concentration (pH) and Gastropoda in Norwegian lakes, with remarks on acidification of watercourses. Fauna, Oslo *32* (1979) 96–111 (in Norwegian with English summary).

110 Økland, J., Environment and snails (Gastropoda): Studies of 1000 lakes in Norway, in: D. Drabløs and A. Tollan (eds)[29], pp. 322–323, 1980.

111 Økland, J., Factors regulating the distribution of fresh-water snails (Gastropoda) in Norway. Malacologia *24* (1983) 227–288.

112 Økland, J., and Økland, K. A., Use of fresh-water littoral fauna for environmental monitoring: Aspects related to studies of 1000 lakes in Norway, in: The Use of Ecological Variables in Environmental Monitoring, pp. 168–183. Ed. H. Hytteborn. The National Swedish Environmental Protection Board, Report SNV *PM 1151.* (1979) 1–348.

113 Økland, J., and Økland, K. A., pH level and food organisms for fish: Studies of 1000 Lakes in Norway, in: D. Drabløs and A. Tollan (eds)[29], pp. 326–327, 1980.

114 Økland, J., and Økland, K. A., Acidification threatens trout diet. Studies of 1000 lakes in Norway. Res. Norway *1980* (1981) 21–26, 56.

115 Økland, K. A., On the ecology of Sphaeriidae in a high mountain area in South Norway. Norw. J. Zool. *19* (1971) 133–143.

116 Økland, K. A., Localities with *Asellus aquaticus* (L.) and *Gammarus lacustris* G. O. Sars in Norway, and a revised system of faunistic regions. SNSF-project, Oslo-Ås, Norway, TN *49/79* (1979) 1–64.

117 Økland, K. A., Mussels and crustaceans: Studies of 1000 lakes in Norway, in: D. Drabløs and A. Tollan (eds)[29], pp. 324–325, 1980.

118 Økland, K. A., and Kuiper, J. G. J., Small mussels (Sphaeriidae) in fresh water in Norway – distribution, ecology, and relation to acidification of lakes. SNSF-project, Oslo-Ås, Norway, IR *61/80* (1980) 1–85 (in Norwegian with English summary).

119 Økland, K. A., and Kuiper, J. G. J., Distribution of small mussels (Sphaeriidae) in Norway, with notes on their ecology. Malacologia *22* (1982) 469–477.

120 Økland, K. A., and Økland, J., Factor interaction influencing the distribution of the freshwater 'shrimp' *Gammarus.* Oecologia *66* (1985) 364–367.

121 Otto, C., and Svensson, B. S., Properties of acid brown water streams in South Sweden. Arch. Hydrobiol. *99* (1983) 15–36.

122 Overrein, L. N., Seip, H. M., and Tollan, A., Acid precipitation – effects on forest and fish. Final report of the SNSF-project 1972–1980. SNSF-project, Oslo-Ås, Norway, FR *19/80* (1980) 1–175.

123 Petersen, R. C., Kullberg, A., Persson, U., and Fritzon, A., Fylleån – biological effects of liming of an acidified stream. Final report, spring 1984. Institute of Limnology, Lund 1984 (in Swedish).

124 Pieper, H.-G., and Meinel, W., Zur Prognostizierbarkeit von Waldschäden durch Indikatoren der Gattung *Gammarus* in Fliessgewässern der Mittelgebirge. Beitr. Naturk. Osthessen *19* (1983) 85–89.

125 Raddum, G., Invertebrates: quality and quantity as fish food, in: Limnological aspects of acid precipitation. Proc., Int. Workshop, Sagamore Lake Conference Center, Sept. 25–28, 1978, pp. 17–24. Ed. G. R. Hendrey. Brookhaven National Laboratory Associated Universities, Inc. 1978.

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.

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Impact of acidification on phytoplankton and zooplankton communities

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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.