

Freshwater acidification: its effects on species and communities of freshwater microbes, plants and animals

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Synopsis

Acidification in geologically-sensitive areas subject to appreciable acidic deposition has affected the activities of microbes, plants and animals in poorly-buffered freshwater ecosystems in Europe and N. America. Biota can be influenced directly by changes in water quality during both short acidic episodes and longer-term sustained periods of acidification: they are affected indirectly by alterations to the balance of acid-sensitive and acid-tolerant species at different trophic levels sometimes leading to a lessening of grazing pressures. Together the chemical and biological alterations result in adverse effects on some biogeochemical processes including the increased mobilisation and leaching of biologically active elements such as mercury, copper and zinc. Many field observations have now been corroborated by field (whole-lake) and laboratory experiments.

Decomposition of organic matter, attributable to microbes, has been found to be affected adversely at some locations. Conspicuously, acidification favours the prolific growth of filamentous algae particularly species of *Mougeotia*: it also shifts the balance of diatoms, minimising the occurrence of circumneutral species and favouring that of acidophilous and acidobiontic types. Because of their 'resistant' siliceous skeletons, it has been possible to trace the historical progression of acidification by examining the remains of diatoms in sediment accumulations. While their species diversity is significantly decreased, the biomass and productivity of dinoflagellates and chrysophytes are only slightly affected.

Like that of phytoplankton (dinoflagellates, chrysophytes and some diatoms), the species diversity of zooplankton is significantly decreased by acidification which has variable effects on the biomass and productivity of the group as a whole: the loss of daphnids is particularly conspicuous. Of the benthic macroinvertebrates, snails, crayfish, clams and freshwater shrimps (amphipods) have been found to be acid-sensitive whereas dragonflies and water boatmen (corixids) increase, particularly where populations of predatory fish have decreased.

Acidification has been responsible for the loss of fish from significant parts of Norway and Sweden: losses, partial or complete, have also been documented in geologically-sensitive areas of the U.K. and other parts of Europe, also Canada and the U.S.A. Eels seem to be the least sensitive to acidic conditions, followed by pike, trout, minnow and roach — the latter being the most sensitive. Prior to being eliminated, populations of fish become unbalanced because of recruitment failure and the mean age, and sometimes size, of the survivors increases. Accumulations of manganese and mercury have been detected in fish taken from acidified freshwaters. Short-term events (episodes) of extreme acidity and/or large concentrations of water-soluble aluminium have led to major fish kills.

The development of embryonic and larval stages of amphibians, including the common frog, toad and natterjack toad, is acid-sensitive. The distribution of fish-eating birds may be influenced by the effects of acidification on the performance of their prey. That of the dipper, a riverine bird, as well as its breeding success, has been restricted where acidification has decreased the availability of its macroinvertebrate prey. Deleterious effects on fish-eating mammals of reduced supplies of prey, sometimes with accumulations of mercury and cadmium and attributable directly and indirectly to acidification, have not, as yet, been confirmed.

Introduction

It is now known that major acidic, or acidifying, ions in acidic deposition have resulted in regional freshwater acidification in geologically sensitive areas including, among others, parts of Scandinavia, central and eastern Europe, the United Kingdom, Precambrian Canada and the U.S.A. (Wright *et al.* 1980; Wright 1983). Acidification is chemically characterised by losses of acid-neutralising capacity

(ANC) (Henriksen 1980) decreases in pH and increases in concentrations of sulphate, nitrate and ammonium; concentrations of aqueous aluminium (Driscoll *et al.* 1980), Mn, Zn and other metals (Dickson 1975; Hutchinson & Sprague 1986) are also known to increase in forms that are 'available' and accumulate in biota while also being directly toxic (Campbell & Stokes 1985). Hultberg (1977) found mercury in acid-stressed aquatic food chains. These chemical changes may be permanent or chronic (long-term acidification) in severely impacted areas, whereas in less affected areas they are more likely to be episodic, short-term and reversible, appearing predominantly during periods of rapid discharge, for instance during snowmelt and heavy rains.

Acidification has profound consequences for individual plants and animals and for communities and ecosystems. They have been documented in at least two continents for more than two decades (Anon. 1972; Overrein *et al.* 1980; Martin 1986).

Our knowledge has been derived from laboratory and field bioassays, mesocosm experiments, whole-system manipulations and repeated field surveys (monitoring). Each of these approaches has its advantages and disadvantages. In laboratory bioassays with one test-species in closely controlled chemical conditions cause and effect relationships may be straightforward. On the other hand, results from field surveys and deductions made from long-term monitoring need greater understanding, recognising that in these instances organisms are exposed to variable and often poorly defined acid stresses which freely roaming organisms may escape, at least temporarily. In these circumstances cause and effect relationships can only be conjectured, remembering that many biologically important factors may be confounded (in a statistical sense) or are unknown. The risks of misinterpreting field observations are self-evident, but on the other hand, laboratory bioassays are often poor replicates of the 'real world', so precluding opportunities of extrapolation. Compensatory processes and community interactions that can greatly modify responses in the field are virtual impossibilities in controlled conditions. Whole-lake manipulation experiments, in which freshwater chemistry is adjusted by the direct addition of acid or lime, test the responses of assemblages of species (communities) while at the same time impacting biogeochemical processes (Ravera 1986). Nonetheless, they are still not ideal because acidification is effected in shorter periods than usual and circumvents the important influence of the terrestrial elements of test-catchments. In a sense, the terrestrial elements of catchments associated with experimentally-acidified lakes become, at least partly, uncoupled. Nonetheless, experimental acidifications have been extremely useful in advancing understanding of many aspects of freshwater acidification (Schindler *et al.* 1985). Ideally, a combination of approaches is needed.

This paper draws on data from the different approaches but it is necessary to recognise differences in species assemblages in sensitive oligotrophic systems both within, and between, regions (Økland & Økland 1986). Additionally, there may be local differences in the composition of acidic deposition with lakes downwind of major local emission source/s being more likely to be impacted by rain with heavy metals such as Cu, Zn and Ni than are lakes upwind or in remote regions (Nriagu & Pacyna 1988). However, because of the presence of ecological analogues and the widespread occurrence of many of the species, it is acceptable to draw generalised conclusions about the biological effects of changed freshwater chemistry with the emergence of a relatively clear-cut picture if the principle of 'universality' is accepted.

It is now clear that many of the effects on aquatic organisms are directly attributed

to shifts in acid-base chemistry, including increased concentrations of hydrogen ions (pH), also cations such as inorganic (ionic) monomeric Al and heavy metals: weak acid anions may also be implicated. In contrast, the strong acid anions SO_4^{2-} and Cl^- do relatively little direct damage to freshwater organisms, whereas nitrate (NO_3^-) and ammonium (NH_4^+) may cause effects indirectly, NO_3^- by the generation of acid neutralising capacity (ANC) and NH_4^+ through the production of H^+ and/or the provision of nutrients for primary producers (Schindler 1988). Additionally, secondary changes have been recorded, for instance phosphorus retention and limitation as a result of its precipitation by aluminium (Jansson *et al.* 1986). This may decrease primary productivity of lakes and streams: on the other hand, the greater clarity of acid lakes may permit production to occur at greater depths (Dillon *et al.* 1984). Even more importantly, the thermal regimes of acidified lakes may be altered with consequences for vertical mixing and the availability (decreased) of dissolved substances. Coldwater species such as the lake trout (*Salvelinus namaycush*) could also be additionally affected because some lakes are warmer to greater depths than before.

Changes in freshwater biota associated with acidification

Many trophic levels can be identified within lakes. The effects of acidification on each of them will be discussed in turn.

Communities of microbes

Bacteria, protozoans and fungi are found throughout freshwater systems. They process organic compounds and in doing so regenerate supplies of some nutrients essential for other biota. At the same time they serve as food (prey) for bottom-dwelling animals (benthos), zooplankton and even for some kinds of phytoplankton. Evidence from early acidification experiments suggested a shift away from bacteria to fungi (Bick & Drews 1973; Traaen 1980) with associated reduced rates of decomposition but, more recently, conflicting evidence has been presented (McKinley & Vestal 1982; Chamier 1987). Fewer bacteria, bacterioplankton, were found by Rao & Dukta (1983) in acidic, low pH, lakes than in more nearly neutral lakes, but others were unable to demonstrate appreciable changes (Traaen 1980; Boylen *et al.* 1983). Francis *et al.* (1984) found that microbes were most abundant in waters with large amounts of humic material. Thus, if acidification were to decrease concentrations of dissolved organic matter (DOC) (Marmorek *et al.* 1988), populations of bacterioplankton would be expected to be decreased. But, even more important than a consideration of microbial abundance is the fate of key processes such as decomposition and nutrient cycling and their implications for the productivity of acidified lakes (Odum 1985).

Accumulations of leaves, twigs, etc. (allochthonous matter) from terrestrial vegetation, observed in some acid lakes, are also taken as indicators of decreased decomposition (Grahm *et al.* 1974). The breakdown of leaf litter is the result of leaching, invasion by microbes, also the activities of invertebrate detritus-eaters (Andersson 1985; Stenson & Eriksson 1989). Decreased litter decomposition has usually (but not always) been shown experimentally and in the field when litter was exposed to acid conditions in streams and the littoral zones of lakes (Minshall & Minshall 1978; Friberg *et al.* 1980). Conversely, since liming leads to recovery of

microbial communities the rates of decomposition of accumulated organic material increased when lime was added (Scheider *et al.* 1975; Hultberg & Andersson 1982).

Periphyton

Periphyton are photosynthetic micro-algae, for instance diatoms, growing on a variety of submerged substrates and more conspicuous filamentous green algae. Filamentous green algae often become abundant in acidified freshwaters (Grahn *et al.* 1974; Stevenson *et al.* 1985). Occurrences of this sort arouse considerable interest as they hinder public use for a variety of recreational purposes, for example fishing and bathing. Mass occurrences of filamentous algae can be experimentally induced (Hendrey 1976; Schindler & Turner 1982). Acidified systems also have fewer species of periphyton (Grahn *et al.* 1974; Stokes 1981), a decrease associated with the loss of habitat suitable for epiphytic species when the enhanced growth of acid-tolerant filamentous species (*Mougeotia*, *Zygogonium* and *Spirogyra*) forms a blanket covering of filaments. In the Experimental Lakes Area (ELA), Canada, 30–50% of the epiphyte-habitat of Lake 223 was 'occupied' by *Mougeotia* (Turner *et al.* 1987) and because of the prolific growth of this alga it is not surprising that many studies have detected increased algal biomass per unit area with increasing acidity (Mulholland *et al.* 1986; Howell 1988). The increase, however, is not solely pH-related; reduced grazing by invertebrates also plays a part (Howell 1988) and probably other factors – phosphorus limitations, changes in water transparency and thermal regimes, reduced grazing because of the loss of acid-sensitive grazers including macro-crustaceans, crayfish, amphipods and even herbivorous fishes such as minnows. It has been shown that the growth of periphyton in acidic lakes is probably carbon-limited (Williams & Turpin 1987; Stokes *et al.* 1989), and therefore the apparently most acid-tolerant species are also likely to be those that can utilise CO₂, the dominant dissolved inorganic carbon (DIC) source in acid lakes.

Liming (Lazarek 1986), the termination of experimental acidifications (Griffiths 1987; D. W. Schindler personal communication) and reductions in industrial emissions (Gunn & Keller 1990; J. M. Gunn personal communication) have led to the 'retreat' of filamentous algae as water quality and biota revert to their earlier, more pristine condition.

Diatoms, which are less conspicuous than filamentous alga, are of special significance because their persistent siliceous scales, preserved in lake sediments, have enabled diatom communities in the past to be recognised. Because the occurrence of different assemblages of species is closely correlated to lake acidity, it has been possible to infer the pH-histories over centuries of lakes, so enabling changes in water quality and in particular, acidity, to be charted with considerable precision (Battarbee 1984; Battarbee *et al.* 1990). (See Fig. 1.)

Phytoplankton

With their ability to photosynthesise, microscopic freshwater algae are of major importance in aquatic systems, being both sources of food for many herbivorous animals and key players/components in the cycling of nutrients and other elements. Communities of phytoplankton are reasonably simple to study and, possibly as a result, species composition and estimates of production and biomass have been determined in many lakes spanning a range of pHs in Europe and North America (Almer *et al.* 1978; Siegrid *et al.* 1989a,b). Additionally, mesocosm experiments

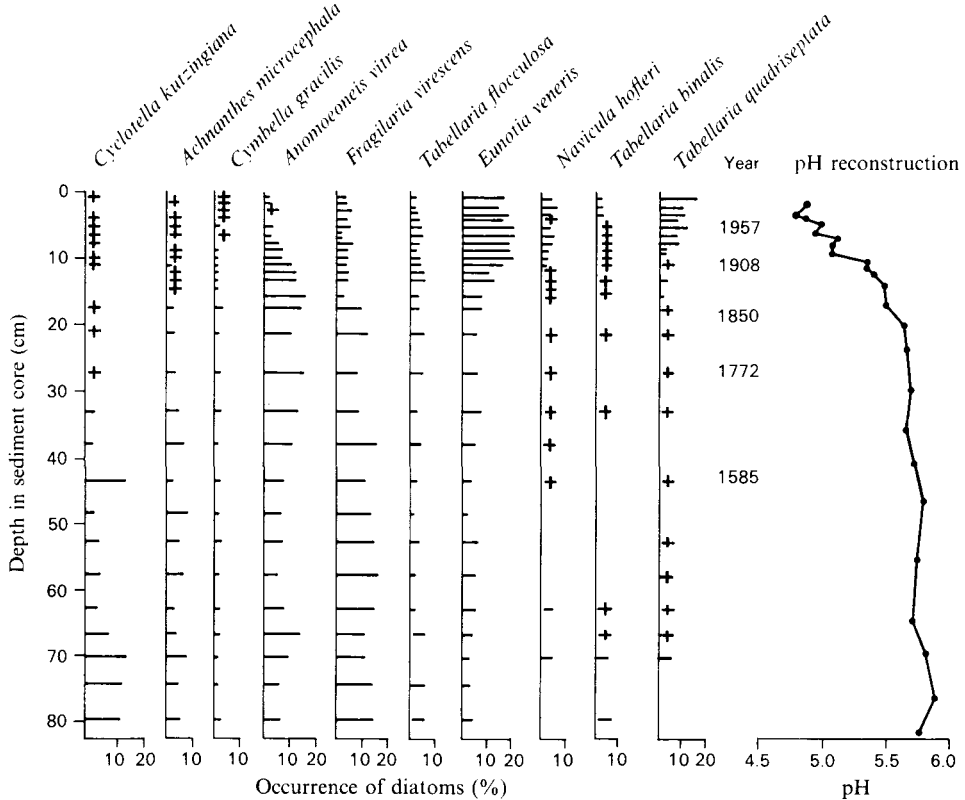


Figure 1. Historical changes in assemblages of circumneutral, acidophilous and acidobiontic diatoms found at different depths in the sediments of Round Loch of Glenhead, SW Scotland. (Layers of sediment dated using ^{210}Pb : pHs inferred using Index B (see Battarbee 1984).) (Circum-neutral, *A. microcephala*, *C. gracilis*, *A. vitrea* and *F. virescens*; Acidophilous, *T. flocculosa* and *E. veneris*; Acidobiontic, *N. hofleri*, *T. binalis* and *T. quadrisepata*.)

have been made in semi-field or 'field' conditions (Yan and Stokes 1978) including whole-lake experiments (Findlay and Kasian 1986). From the evidence that has accumulated, it is clear that increasing acidity alters the nature of phytoplankton communities (Fig. 2). Acidic water contains fewer species, and typically the dominant species change. Numbers of species decline from 30–80 in circumneutral (oligo-trophic) lakes to 10–20 species in acidic lakes, with Almer *et al.* (1974, 1978) reporting only three species in lakes of pH 4.0. In acidic conditions the species-poor assemblages of acid-tolerant phytoplankton include dinoflagellates (e.g. *Peridinium inconspicuum*), which may account for 30–50% of the biomass, also yellow green algae, the *Chrysophytes* (Stokes 1986). The shift in dominance is poorly understood. In addition to the 'emergence' of species with acid-tolerance *per se*, it has been suggested that they are less competitive than acid-sensitive species in less acid conditions (Havens & DeCosta 1987). Their ability to dominate in strongly acid conditions may also be attributable to their possibly protective morphology (armoured plates, siliceous casings and/or gelatinous sheets) (Schindler *et al.* 1985), but this is not to overlook the advantages that some have with acid- and aluminium-tolerant phosphate metabolism (Jansson *et al.* 1986; Smith 1990).

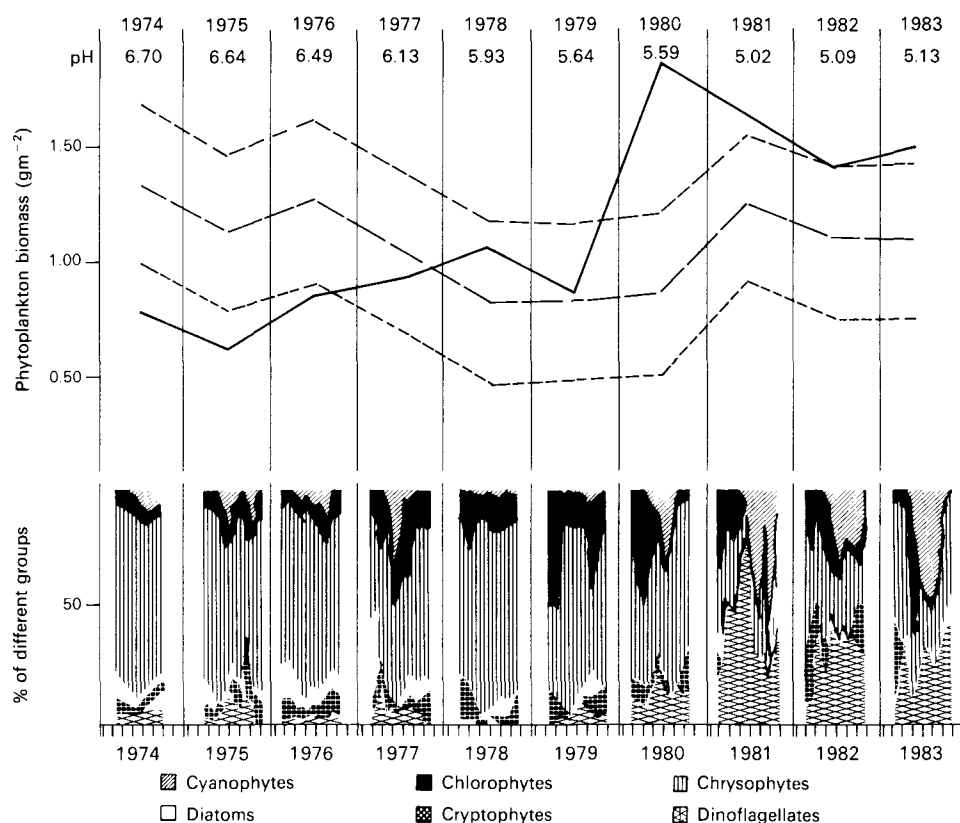


Figure 2. Effects of acidifying experimental lake L223 (—) with sulphuric acid on the biomass of epilimnetic (surface) phytoplankton and on the relative abundance of different groups of algae contributing to the epilimnetic biomass. (---, ---, --- refer to three unacidified control lakes in the same part of Canada as L223 — see Findlay & Kasian 1986.)

Changes in phytoplankton communities have implications for biota at higher trophic levels, the effects on zooplankton being immediate (Findlay & Kasian 1986). The aesthetic and health impacts of some acidobiontic species, when dominant, are also a matter of concern, notably *Gymnostomum semens*, which affects bathing (Cronberg *et al.* 1988) and *Crysochromulina brevivorita* that produces odour-causing blooms (Nicholls *et al.* 1982).

At present, it is not possible to make unqualified generalisations about effects of acidity on biomass and the primary productivity of phytoplankton. Most of the evidence from synoptic surveys suggests that there is less biomass in acid lakes (Siegfried *et al.* 1989a) but experiments acidifying neutral waters or neutralising acidic waters suggest that changes, if they exist, indicate slight increases (Yan & Stokes 1978; Schindler *et al.* 1985). In regard to primary productivity, most studies, including synoptic surveys (Almer *et al.* 1978; Dillon *et al.* 1979) and experiments (Findlay & Kasian 1986) indicate small increases, possibly reflecting improved light climates to greater depths in acid lakes with, concomitantly, the occurrence of acid tolerant species. Among the latter, large dinoflagellates seem particularly abundant, possibly because they are not readily consumed by filter-feeding zooplankton (Dillon *et al.*

1984). Acidification has, therefore, the potential to reduce the transfer of energy to the next level of the aquatic food chain for instance to zooplankton.

Macrophytes

For a variety of organisms, large algae, mosses and liverworts and higher (vascular) plants provide food and habitat (shelter, breeding and nursery grounds) – alterations to macrophyte could therefore have wideranging effects. The evidence from North America is somewhat contradictory: some reports associate decreasing numbers of macrophyte species with increasing acidity and pH-related factors (Roberts 1984; Jackson & Charles 1988), whereas in other studies this association has not been discernible (Roberts 1984; Yan *et al.* 1985). Some macrophyte species are definitely pH-sensitive but the effects may be attributable to the limited availability of Ca in acid-sensitive oligotrophic lakes. From Sweden and the Netherlands, increasing acidity is associated with a formidable expansion of *Sphagnum* spp. (Grahm 1986) and to a lesser extent *Juncus bulbosus* which restrict *Lobelia dortmanna* and *Littorella uniflora*, which tend to dominate circumneutral (pH 6.5) lakes (Roelfs 1983). Potentially the expansion of *Sphagnum* spp., by the production of dense uniform mats of tissue unsuitable for other organisms, is likely to interfere with sediment/water processes (Dillon *et al.* 1984). *Sphagnum* spp. exchange metabolically produced H^+ ions with nutrient and metal ions (Clymo 1984; Peverly 1984). Thus, they may (a) act as sinks for metals and (b) locally acidify their own micro-environments.

As yet, generalisations should not be made of the effects of acidity on the productivity and biomass of macrophyte communities, but indirect evidence, linked with improved transparency to greater depths, suggests that they may be increased (Wile *et al.* 1985). The most acid-tolerant macrophytes are able to utilise CO_2 , rather than bicarbonate, as their carbon source (Roelfs 1984). Recent evidence from the Netherlands strongly suggests that the conversion of NH_4 to NO_3 may favour the growth of acid-tolerant macrophytes while neutralisation, with the addition of lime, leads to the retreat of acidophilic macrophytes (Hultberg & Andersson 1982) and recolonisation by acid sensitive species because of increased acid neutralising capacity (ANC) and greater amounts of bicarbonate (Erikson *et al.* 1983).

Zooplankton

Some members of this group graze on phytoplankton while others are predators within their own communities. They can be directly affected by toxic conditions and indirectly by changes in the activities of primary producers at a lower trophic level, and of predators above including larger invertebrates, fish and higher vertebrates, for example, waterfowl. The prime roles of zooplankton are (a) the conveyance of energy through the food chain and (b) the recycling of elements. As with phytoplankton, the species diversity of zooplankton decreases with increasing acidity, particularly below pH 5.5–5.0 (Harvey *et al.* 1981), as has been found in extensive field surveys (Almer *et al.* 1974; Hobæk & Raddum 1980; Carter *et al.* 1986; Tessier & Horowitz 1988) and whole-lake experiments (Malley *et al.* 1982). In a study done in Norway, the mean number of species decreased from 16 to 7 as pH changed from 5.5–6.0 to below pH 5.0 (Hobæk & Raddum 1980). In Lake 223, ELA (Experimental Lakes Area), Canada, three of the original crustacean species of zooplankton and the opossum shrimp, *Mysis relicta*, disappeared between 1976 and 1981 as pH

lowered from pH 6.7 to 5.0–5.1, while the abundance of other species increased (Malley *et al.* 1982).

Many acid-sensitive species of *Daphnia* are not found in acidic lakes (Almer *et al.* 1974; Hobæk & Raddum 1980; Nilssen 1980; Carter *et al.* 1986). In Lake 223 *Daphnia galeata mendotae* disappeared at pH 5.5–5.0, but reappeared when the pH rose to 5.6; a critical pH of around 5.1 was found for this species in laboratory experiments (Malley & Chang 1986). Even in acidic lakes, numbers of zooplankton were sometimes unexpectedly small while in others the decreases were less than expected. Nonetheless, decreases in biomass generally follow those of diversity as acidity increased. To an extent the variation, which should be expected, highlights the difficulties of comparing lakes, which chemically may have reached the same level of acidification, but which initially had different numbers of sensitive species and/or a different balance of trophic levels. Some recent analyses of rotifers have indicated that the nutritional status of freshwater ecosystems maybe more closely related to biomass than pH *per se* (MacIsaac *et al.* 1987; Siegrid *et al.* 1989b).

The disappearance of sensitive zooplankton, such as Daphnids, is relatively easy to explain because they seem to be directly affected by ambient water quality. Death of Daphnids by acid stress is linked with a number of physiological phenomena including depression of oxygen uptake (Alibone & Fair 1981) and failure of osmoregulation (Potts & Fryer 1979) as shown by a net loss of body-ions such as sodium (Na) and chloride (Cl). These ions are probably lost via a mechanism similar to that operating in chloride cells found in the gills of fish. Results of bioassays with toxic aqueous Al have provided variable results. Some species are very sensitive (Havens & DeCosta 1987) while others are not (Havas & Likens 1985): some are Al-sensitive but not pH sensitive. The biomass of zooplankton in lakes in the vicinity of major sources of pollutants, with large concentrations of heavy metals Ni and Cu, has, without doubt decreased (Yan & Strus 1980). In these instances, it may be inferred justifiably, that the metals, rather than acidity, were having deleterious effects on the communities of zooplankton. Numerous bioassays with several zooplankton species have shown that the effects of acidity, in these bioassays, are comparable to the effects in field conditions: these tests have enabled the relative sensitivities of many species to be evaluated (Price & Swift 1985; Malley & Chang 1986). Field evidence suggests that the disappearance of *Cyclops scutifer* at pH < 5.0, noted by Tessier & Horowitz (1988), is probably a result of recruitment failure rather than direct toxicity. Arvola and co-workers (1986) found that adult *Cyclops scutifer* can occur in intensely acid water (pH 4.0–3.5), but that its eggsacs did not develop. Impairment of reproduction by *Daphia pulex* seems to be associated with delayed maturation of adults (Walton *et al.* 1982).

The results of surveys in Europe showing that the proportion of large-bodied zooplankton increased with increasing acidity suggest that acidity results in reduced predation by fish and more intense grazing of small zooplankton by the largest zooplankton (Stenson & Eriksson 1989). However, in North America, it seems that smaller-bodied forms gain in dominance possibly because of the more intense predation of large-bodied species by fish, and/or ducks that hunt by visual cues (Dillon *et al.* 1984). Whatever the reason(s) for the difference, it is clear that the emergence of impoverished acid and/or metal-tolerant communities ensures a minimal level of recruitment and survival of zooplankton in acidic conditions. Experiments done to examine recovery after neutralising acidity, as with the addition of lime, have shown

that recovery occurs but slowly (Hultberg & Andersson 1982) — it is, however, presumed that recovery might be accelerated by the addition of phosphorous (Yan & LaFrance 1984). In the lakes near Sudbury, Canada, the reversal of acidification has seen recolonisation by acid-sensitive zooplankton such as *Epischura lacustris* (Gunn & Keller 1990).

Benthic macroinvertebrates

Molluscs (snails, clams and smaller mussels), crustaceans (shrimps, scuds and crayfish) and many groups of aquatic insects (mayflies, stoneflies, caddis flies, etc.) break down organic material, regenerate nutrients and serve as a food source for many fish and bird species. Changes in their populations are relatively easy to assess as generation times are short. Many of them are acid sensitive and as a result have proved to be useful indicators for tracking the progress of acidification (Engblom & Lingdell 1984; Økland & Økland 1986).

The loss of benthic macroinvertebrates has been noted in synoptic surveys made in Europe and North America, the acid-tolerance of different species, sometimes with extensive distributions being inferred from the acquired records of presence. Some species of mayflies, amphipods (freshwater shrimps), crayfish, snails and clams are very sensitive to acid conditions (Økland & Økland 1986).

Several studies have shown that populations of mayflies consistently decreased with increasing acidity, their absence being noted when acidity increased beyond critical pH values (Harriman & Morrison 1982; Matthias 1983) (Table 1): for example, pH 6 for species of *Baetis* (Raddum & Fjellheim 1984), pH 5.5 for *Ephemerella* spp. (Fiance 1978). As usual there are exceptions. Thus, some species of *Leptophlebia* persist at pH 4.5–5.0 (Mackay & Kersey 1985). In a Norwegian study, it was found that 60% of mayfly species were lost when acidity reached pH 5.5, but less than 30% of stonefly species (Raddum & Fjellheim 1984). (See Fig. 3.)

The responses of amphipods are similar to those of mayflies. *Hyaella azteca* in North America (Stephenson & Mackie 1986) and *Gammarus lacustris* in Scandinavia are either absent or very rarely found at pH 6.0, while the isopod, *Asellus* (the freshwater louse) is more robust and is found at greater acidities (Økland & Økland 1986). Crayfish, such as *Orconectes virilis* and *O. rusticus* and *O. propinquus*, are missing from North American lakes with pH < 5.6 (Berrill *et al.* 1985), but the

Table 1. Ranges of animals found in neighbouring streams towards the head of the River Forth, Scotland. One stream, Corrie Burn, was circumneutral whereas the other (Kelty Burn) was acid, so reflecting different types of bedrock (Morrison 1989).

Taxa	Corrie Burn (circumneutral)	Kelty Burn (acidic)
Worms (Oligochaeta)	5	2
Snail (<i>Ancylus fluviatilis</i> Muller)	1	0
Shrimp (<i>Gammarus pulex</i> L.)	1	0
Mayflies (Ephemeroptera)	5	1
Stoneflies (Plecoptera)	9	8
Caddis (Trichoptera)	3	4
Fly larvae (Diptera)	3	3
Beetles (Coleoptera)	6	3
Fish (<i>Salmo trutta</i> L.)	1	0

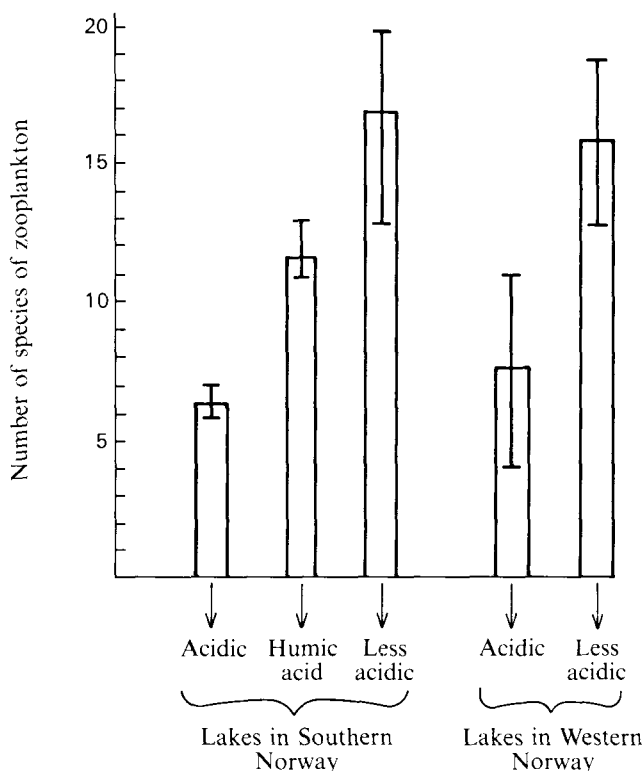


Figure 3. Association between acidity and numbers of species of zooplankton, including Crustacea, Rotatoria and Chaoborus larvae, in lakes in southern and western Norway (Raddum *et al.* 1980).

Scandinavian species, *Potamobius (Astacus) astacus* – a very sensitive species – is rarely found below pH 6.0 (Munthe Kaas Lund 1969). Molluscs, including snails and small mussels (Sphaeriidae), are similarly sensitive. Regional surveys have indicated clearly that numbers of species decrease with increasing acidity (Økland & Økland 1986). In Norway, snails, including species widespread and common in oligotrophic lakes, were usually absent when acidity went beyond pH 5.2 while mussels disappeared at pH 4.7. Comparable effects have been noted in U.S.A. (Singer 1984), Canada (Roff & Kwiatkowski 1977) and the U.K. (Sutcliffe & Carrick 1973). However, these results need to be carefully interpreted because molluscs and crayfish require Ca to build their calcareous scales (Hunter 1964) and carapaces (Malley 1980). Thus a shortage of calcium may be the prime determinant of the occurrence of molluscs, always recognising that concentrations of calcium, pH and other environmental factors are often strongly correlated (Økland 1983). By careful analysis of his regional data Økland (1990) showed that the decline in numbers of mollusc species with decreasing pH is real even when the effects of calcium have been taken into account.

Some of the pH tolerances inferred from field observations are now supported by the results of laboratory tests and whole-lake acidification experiments. In experiments done with Lake 223 the community of benthic macroinvertebrates decreased significantly when acidity was increased from pH 6.7 to 5.0–5.1 (Schindler 1988).

The opossum shrimp, *Mysis relicta* was eliminated at pH 6.0–5.8 (Nero & Schindler 1983) while *Orconoeetes virilis*, the crayfish whose recruitment was decreased at pH 5.6 was eliminated at pH 5.0 (Davies 1989). France (1984) suggested that this crayfish decline was possibly attributable to the greater sensitivity of juveniles (France 1984) plus losses of pouched eggs from females and parasitism (France 1987). *Hexagenia*, a common genus of mayflies, disappeared from Lake 223 at pH 5.1 (Schindler *et al.* 1985).

The larval stages of many insects inhabiting running water actively migrate and/or are dispersed passively downstream by drift. The short-term addition of acids and/or aluminium to streamwater has resulted in increased drift of sensitive mayfly species, the more tolerant showing little or no response (Hall *et al.* 1980; Ormerod *et al.* 1987). The response of the acid-sensitive mayflies may be behavioural or it may be an expression of induced lethal, or sublethal, damage. Whatever the reason the net result is the same, namely decreased insect emergence. Acidic episodes in headwater streams may therefore cause depopulation and the impoverishment of communities even in the early phases of long-term acidification as supported by observations made on streams in Ontario, Canada sampled in 1937–42 and again in 1984–85 (Hall & Ide 1987). Changes of this sort have been discerned in headwaters, currently subjected to acidic episodes while at sites downstream not subject to episodic acidification populations remained unchanged. Similar effects on insects have been recorded in Scandinavia (Engblom & Lingdell 1984) and Germany (Mathias 1983) while data from the past indicate that species of snails and mussels were lost in Sweden over a 30-year period as lakes were acidified (Mossberg 1979).

Together these observations from surveys indicate consistent negative correlations between pH and (i) species richness, and (ii) diversity of benthic macroinvertebrates, the loss of sensitive species sometimes being partially offset at moderate acidities by more acid-tolerant forms. Mackay & Kersey (1985) found five genera of mayflies in streams between pH 5.3 and 6.7 but only one, *Leptophlebia*, in streams with pH varying between 4.8 and 4.3. For all groups of benthic macroinvertebrates numbers of genera decreased from 25 to 8, a decrease of two-thirds.

In addition to species richness the biomass of benthic invertebrates decreased with increased acidity (Økland & Økland 1986), but the interpretation of this effect is complicated by temporal variations in water quality in different habitats (Raddum 1980). Surface dwellers, living in the littoral zone, are exposed to episodic events more than sediment, or burrowing, macroinvertebrates that inhabit the deeper parts of lakes (LaZerte 1984).

Macroinvertebrates are affected by chemical and ecological factors. Hydrogen-ion toxicity certainly plays a part and it may explain some of the field effects (Engblom and Lingdell 1984). Crayfish decline and loss in Lake 223 has been substantiated in controlled laboratory exposures (Malley 1980) that have confirmed that acidity affects eggs and juvenile stages, with the moulting stages being particularly sensitive (Davies 1989). The same is true of field and laboratory observations of *Gammarus* (Engblom & Lingdell 1984) and *Hyaella* (France & Stokes 1987). Recruitment failure and reduced growth have been observed in mayflies, *Ephemerella funeralis* (Fiance 1978), and snails, *Amnicola* spp. (Rooke & Mackie 1984); it seems, therefore, that these phenomena are commonplace in the elimination of sensitive species.

Acid toxicity among invertebrates is attributable to distinctive physiological effects affecting, for instance, ion and osmoregulatory processes (Vangenechten *et al.* 1989).

They commonly appear at low pH with the stress responses including net losses of NaCl from some groups of animals (Potts & Fryer 1979; Havas & Likens 1985). In other instances including some crustaceans (Malley 1980; Appelberg 1985) and probably molluscs (Mackie 1987) Ca uptake fails. In addition to concentrations of H^+ ions there is evidence that inorganic aqueous aluminium is implicated. Its toxicity to some waterfleas has been substantiated (Havas & Likens 1985) also to blackfly larvae (Herrmann 1987) at pH 5. In the latter instance, the effect is mitigated by the presence of humus. Respiratory effects, both increases and decreases, have been noted. While Al seems toxic in its own right, its presence has sometimes decreased H^+ toxicity: and some macroinvertebrate species have high degrees of Al tolerance (Herrmann 1990; Howells *et al.* 1990). As yet there are not convincing explanations of all of these different responses – more investigations are warranted.

As already mentioned, macroinvertebrates are affected by ecological, as well as chemical, influences of acidification. Among secondary ecological effects is the possibility that the reduced growth rates of acid stressed populations of macro-invertebrates (Fiance 1978) may in part reflect the consequence of a food source of inferior quality. By decreasing microbial decomposition of allochthonous matter, species able to utilise coarse detritus should be favoured – shredders more so than scrapers that feed on microalgae and other micro-organisms living on decaying organic material (Stenson & Eriksson 1989). Shifts in shredder/scrapper guilds have been observed (Townsend *et al.* 1983). Larger predators, e.g. dragonflies and corixids, are known to appear in large numbers in acid lakes in part as a result of the elimination or predatory fish (Eriksson *et al.* 1980). This change in top predators to acid-tolerant forms is likely to affect the nature of predation pressures. Mesocosm experiments and others, excluding brown trout from acidic streams in southern England, have clearly shown that acidification favours acid-tolerant predators including the caddisfly, *Plechnochnechia conspersa* (Schofield *et al.* 1988). Observations made (a) of experiments testing the effects of lime (Raddum *et al.* 1986); and (b) of lakes that are chemically recovering after decreasing industrial emission of sulphur pollutants, suggest that macroinvertebrate communities benefit as lakes deacidify (Gunn & Keller 1990). However, Hultberg & Andersson (1982) and Nyberg *et al.* (1986) have suggested that the magnitude of the recovery and/or reinvasion by acid-sensitive macroinvertebrates may have been masked, in some instances by the introduction, or recovery of, fish. An opportunity to investigate these interrelations, which need more exploration, has been lost by restocking with fish at the same time as ameliorating acidity by the addition of lime.

Freshwater fish

Ecological effects of acidification on fish populations have been noted from two sources – historical data and field surveys (Jensen & Snekvik 1972; Watt *et al.* 1983; Baker & Schofield 1985; Harriman *et al.* 1987). These observations have been supported by (a) field measurements of acid-stress on natural fish stocks (Leivestad & Muniz 1976; Lacroix & Townsend 1987) and (b) laboratory (Baker & Schofield 1982) and whole-lake experiments (Mills *et al.* 1987). The elimination of fish from thousands of lakes in sensitive areas of Scandinavia (Muniz 1984), elsewhere in Europe and in North America (Dillon *et al.* 1984) subject to appreciable acidic deposition, dramatically demonstrates a consequence of regional acidification. It has affected commercial and recreational fisheries and perhaps even more seriously

eliminated genetically unique populations. Several large-scale liming programmes have been initiated to conserve, and protect, fish stocks and/or restore those that have been lost (Nyberg 1984).

Fish are among the top predators in many aquatic ecosystems: they also suffer predation by birds and mammals including man. They occupy a variety of niches: some are herbivorous, some prey on macroinvertebrates while others such as pike (*Esox lucius*) and the lake trout (*Salvelinus namaycush*) are partly or wholly piscivorous. Some feed and breed in freshwater lakes and streams: others, like the Atlantic salmon (*Salmo salar*), spawn in freshwater but move to marine environments, often the high seas, to feed whereas a third group including eels (*Anquilla* spp.), feed in freshwaters and move to marine habitats to spawn. Changes in populations of freshwater fish have wide-ranging influences, not only on freshwater, but also marine, ecosystems. Freshwater fish are found in streams, ponds and lakes which, when oligotrophic, have dilute waters sensitive to acidification. There are numerous recorded examples of the loss of individual species from, and changes in species composition of, fish communities in acid-stressed freshwaters, for example, their gradual disappearance with concomitant acidification, during the 1950s and 60s from seemingly pristine clear lakes in the LaCloche Mountains in Ontario, Canada (Beamish & Harvey 1972; Beamish *et al.* 1975; Harvey & Lee 1980). For example, in 1950 there were eight species of fish in Lumsden Lake. Yellow perch (*Perca flavescens*) and burbot (*Lota lota*) have not been recorded since 1960 and between 1960 and 1965 the sport fishery failed. The lake trout (*Salvelinus namaycush*) and slimy sculpin (*Cottus cognatus*) were lost by 1967 while in 1968 the white sucker (*Catostomus commersoni*) suddenly became rare. In 1969 the lake herring (*Coregonus arteedi*), trout-perch (*Percopsis omiscomaycus*) and white sucker (*C. commersoni*) were caught for the last time while lake chub (*Couesius plumbeus*) finally succumbed in 1970. Evidence from a survey made of many lakes in the LaCloche Mountains confirmed the link between the absence/presence of fish species and water chemistry (pH). There was a gradual decline in numbers of fish species with increasing acidity (Harvey & Lee 1982; Matuszek & Beggs 1988), starting immediately below pH 6 with the loss of sensitive cyprinid minnows. Similar observations have been made of lakes in the Adirondack Mts where lake trout is often absent when waters are more acid than pH 5.4 and brook trout when acidity passed pH 5.1 (Schofield & Driscoll 1987). In Scandinavia the sequence of disappearances – minnows, roach and finally pike and eels (consistently the most tolerant species) – is similar (Almer *et al.* 1974). (Table 2)

Table 2. Relative tolerance of fish to acid conditions based on a survey of 50 lakes in Sweden (Almer *et al.* 1974).

	Latin binomial	Common name
Most sensitive	<i>Leuciscus rutilus</i>	Roach
	<i>Phoxinus phoxinus</i>	Minnow
	<i>Salvelinus alpinus</i>	Arctic char
	<i>Salmo trutta</i>	Trout
	<i>Coregonus albula</i>	European Cisco
	<i>Perca fluviatilis</i>	Perch
	<i>Esox lucius</i>	Pike
Least sensitive	<i>Anguilla vulgaris</i>	Eel

These losses of fish species are reflected in decreasing densities and biomasses (Beamish 1970; Hultberg & Stenson 1970) and hence productivities and yields (Beggs *et al.* 1985; Harriman *et al.* 1987). Prior to extinction, some fish species may temporarily respond to decreased predation and competition (for food) by increased growth and with larger length/weight ratios (Almer 1972; Harvey 1982). However, when recruitment is totally inhibited extinction is inevitable (Mills *et al.* 1987). The rate of this extinction depends on the degree of acid-stress, the life history and the longevity of different species and their acid-tolerance. Acid-sensitive species with short life cycles such as minnows have disappeared more rapidly than lake trout, which lives for 20–30 years or more.

The Atlantic salmon, which spends 2–4 years in freshwater and relatively few years at sea, is particularly acid-sensitive (Leivestad *et al.* 1976) (Fig. 4). Its decline in acidified rivers of southernmost Norway probably started, in some instances, prior to the First World War but took a further 50–60 years before being finally eliminated – records of catches were rarely made from these rivers after 1970 (Muniz 1981). The progressive decline was possibly slowed in some locations by ‘pockets’ of less sensitive water. These observations in the field are now supported by the results of laboratory tests (Peterson *et al.* 1980; Fivelstad & Leivestad 1984) and bioassays made on-site (Lacroix & Townsend 1987). As a result of the whole-lake acidification of Lake 223, the reproduction of fathead minnows ceased at pH 5.9, shiny sculpin at 5.6–5.9, lake trout at 5.6, pearl dace at 5.1 and white sucker at pH

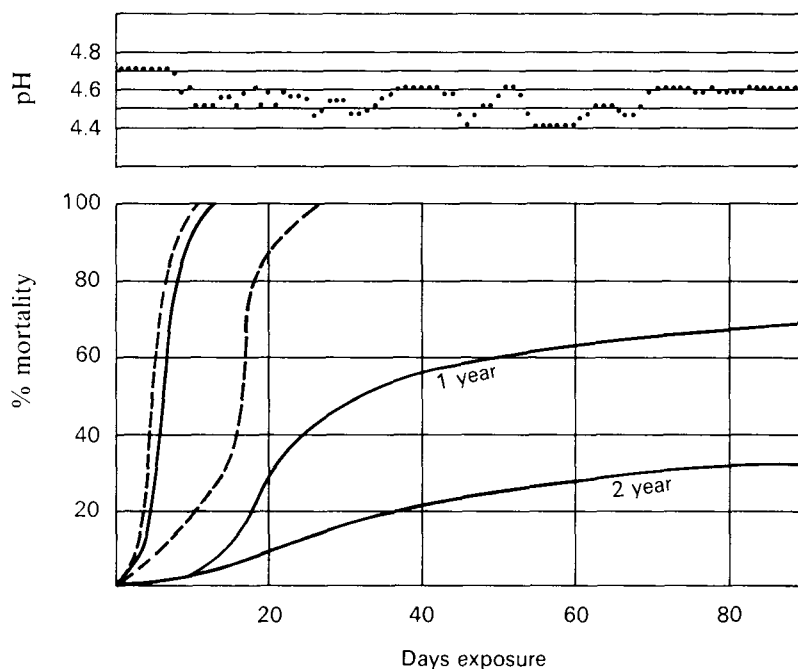


Figure 4. Cumulative mortalities of first-year rainbow trout (*Salmo gairdneri*), brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) when exposed to water from an acid brook. Additionally, two-years-old brook trout were included (Leivestad *et al.* 1976). (From left to right ———, *S. gairdneri*; — *S. salar*; ——— *S. trutta*; — 1 and 2 year *S. fontinalis*.)

5.0–5.1 (Mills *et al.* 1987). It is clear that pH or pH-related factors are crucial including aqueous aluminium and sometimes Ca (Muniz & Leivestad 1980; Baker & Schofield 1982). The sometimes artificial nature of some of these assays does not preclude the involvement of other factors.

With greater sophistication, experimental studies have shown that different life-stages – egg, sac fry, emergent fry, juveniles and adult fish – have different sensitivities to acid-stresses, the most sensitive being the younger stages, particularly newly hatched or ‘swim-up’ fry just starting to feed (Baker & Schofield 1985). Not surprisingly, therefore, many acid-stressed populations are dominated by older fish and lack young fish as a result of partial, or total, recruitment failure (Harvey 1982).

These acidification effects can be experimentally reversed by redirecting water quality away from acidity to circumneutrality by liming (Nyberg 1984) or decreasing emissions responsible for acidification (Gunn & Keller 1990). Liming effectively gives rise to bicarbonate alkalinity with the precipitation and formation of less toxic forms of aqueous aluminium (Driscoll *et al.* 1989). The reproduction of surviving acid-stressed fish populations resumes and new year classes are recruited so helping to re-establish a more normal balance of year classes (Nyberg *et al.* 1986). If, however, recruitment failure persists too long, the surviving population, on ageing, rapidly declines and becomes eliminated (Hultberg & Stenson 1970). When mortality primarily affects adults and spawners but without eliminating spawning and recruitment the average ages of surviving populations decrease. While these smaller and younger populations may survive for decades they are likely to be eventually eliminated (Rosseland *et al.* 1980; Ryan & Harvey 1980; Bravington *et al.* 1990). It is therefore possible that the regional effects of acidification on fish have been seriously underestimated. In terms of survival a species is likely to be influenced by its preferences of spawning site. Stream spawners, because of the risks of episodic acidic events of low pH, are likely to be more at risk than lake spawners that experience less variable and thus probably more favourable environments for spawning and nursing young fish (Andersen *et al.* 1984; Gunn 1989).

The importance of freshwater chemistry for controlling fish status is not challenged. Regional surveys, particularly in areas of North America (Matuszek & Beggs 1988) and Scandinavia (Wright & Snekvik 1977), have identified pH and inorganic monomeric aluminium and, in some instances, Ca as the most important determinants of fish survival (Muniz & Walløe 1990). In the absence of complete analyses of water quality, pH is often used as a surrogate variable. It has been regarded as of value because of close correlations with other acid–base variables, e.g. aqueous aluminium, specific conductivity and base cations. However, some of these correlations can be spurious and remote from causality (Muniz & Walløe 1990). Angling records of progressively acidified rivers in southernmost Norway have been paralleled by records obtained in Nova Scotia, Canada, where salmon declines have been reported (Watt *et al.* 1983). In rivers of Nova Scotia, however, concentrations of labile toxic aluminium are smaller than in Norway, and this being so, the effects are primarily attributed to low pH during episodic events affecting the younger riverine stages of salmon (LaCroix & Townsend 1987). However, as in Norway, more neutral rivers within the region seem not to be affected.

Absence/presence data for brown trout from many Norwegian lakes show that numbers of lakes that have populations of fish decrease with increasing acidity (Sevaldrud *et al.* 1980; Henriksen *et al.* 1989). Other analyses have also identified

pH, concentrations of inorganic aluminium (and altitude) as significant determinants of the status of brown trout in southern Norway (Muniz & Walløe 1990). Perhaps surprisingly Ca was not found to protect against the toxic effects of aluminium. In contrast, preliminary results indicate that the survival of perch (*Perca fluviatilis*) is much more dependent on large ionic concentrations (including Ca).

It has only been possible in a few instances to link changes in fish status with protracted (longterm) historic records of pH, in some instances deduced from palaeo-ecological reconstructions. Where this information has been available, in North America, extinctions have been limited to lakes which had become more acidic than 5.5 (Haines & Baker 1986). Data from Loch Fleet, Scotland, are of particular interest because indirect "assessments" of pH are available: they were derived from palaeo-ecological studies of diatoms in the lake sediments (Battarbee *et al.* 1985). They suggest that Loch Fleet began to acidify *ca.* 1960: catches of trout declined from the mid-1950s (Harriman *et al.* 1987). By 1978–79 Loch Fleet had a mean pH of 4.3: it was devoid of trout in 1984, if not sooner, when fish status was surveyed. Assays with eggs, fry and juveniles of trout indicated that the water in 1984 was toxic to brown trout (Turnpenny *et al.* 1988).

There are similar examples recorded in Maine and the Adirondack Mountains (Haines & Baker 1986). Interestingly, previously perturbed fish communities in lakes in the vicinity of large emission point sources of SO₂ in Canada are now recovering (Gunn & Keller 1990) as emissions are decreased and water quality improves (Keller *et al.* 1986). The concomitant lessening of acidity and improved water quality has been reflected in greater reproduction by surviving lake trout, and problems encountered when restocking brook trout have now been overcome. Similarly, populations of white sucker have recommenced reproduction while immigrant populations have been able to establish themselves (Gunn & Keller 1990).

As mentioned earlier, fish populations in decline in acid-stressed lakes often encounter less competition for food and as a result the growth of surviving individuals improves (Almer *et al.* 1978). Conversely, the loss of prey (food), can be reflected in poor growth (Beamish 1974) and poor condition particularly among piscivorous species such as pike and lake trout. Lake trout, in Lake 223, became emaciated when their preferred food, minnows, disappeared (as a result of acidity) (Mills *et al.* 1987): Hultberg & Stenson (1970) found a small and old population of slow-growing pike in an acid Swedish lake where they had apparently been forced to survive on invertebrates. If metabolic stress from acidic pHs and large concentrations of aluminium were outwardly reflected in reduced rates of feeding (Lemly & Smith 1987), these reduced rates would go a long way to explaining reduced growth (Muniz & Leivestad 1976). However, changes of growth rate have not always been observed (Rosseland *et al.* 1980) so suggesting other mechanisms of sublethal stress (Rosseland 1980). Physiological disruption of ion and/or osmoregulation in the gills of fish is a major aspect of the toxicity of acidic solutions with large concentrations of aqueous aluminium (Leivestad *et al.* 1976; McWilliams & Potts 1978; Wood & McDonald 1987). This primary effect leads to the loss of body salts and secondary internal effects on water and ion balances within, and between, different internal tissues and structures. While low pH (high acidity) seems primarily to evoke ion regulatory effects, at least at realistic pHs and concentrations of Ca, aluminium evokes respiratory stress (Wood & McDonald 1987). Aluminium or Al bound to mucus precipitates onto the surfaces of gills and affects diffusion processes across gill lamellae (Ultsch

& Gros 1979). Changes in gill structure have also been documented (Leino *et al.* 1987; Evans *et al.* 1988) as have changes in the enzyme systems of the specialised chloride cells involved in the active uptake of salt in gill epithelia (Staurnes *et al.* 1984). There is also evidence suggesting that acid/aluminium stress may decrease Ca uptake by fish (Reader *et al.* 1988) with smaller amounts of Ca in bones (Fraser & Harvey 1982). The report made in 1975 by Beamish *et al.* of the apparent inability of female fish to produce viable eggs, also of lowered serum calcium concentrations (Lockhart & Lutz 1977), would suggest that Ca depletion may be a significant factor in fish decline. However, this is not supported by recent experiments where brook trout exposed to pH/Al stress produced viable eggs despite lowered concentrations of plasma Ca (Mount *et al.* 1989). Notwithstanding, there is evidence to show that some, at least, of these physiological effects are reversible, with the prospect of recovery (Leivestad & Muniz 1976). Fivelstad & Leivestad (1984) and Booth *et al.* (1988) have been able to go some way in explaining sensitivity differences between species in terms of their physiology.

Concentrations of Mn, Zn, Hg and others are, like those of Al, often increased in acidic lakes (Dickson 1975; Hutchinson & Sprague 1986). In acidified lakes in Canada the concentrations of Mn in the vertebral centra of white suckers were increased by a factor of x5 while those of Ca were decreased (Bendell-Young & Harvey 1986). Elsewhere, the mercury content of fish in acidifying lakes was much larger than in fish in control lakes (Håkanson 1980; Sloan & Schofield 1983; Suns *et al.* 1987), a difference probably reflecting the larger concentrations of soluble Hg in acid lakes (Almer *et al.* 1978) where the formation, and uptake, of methyl mercury is enhanced (Fagerstrøm & Järnelöv 1972). McMurty *et al.* (1989) found that concentrations of organic mercury accumulated in fish were correlated with H^+ ion concentration and the organic content (DOC) of lake water. Similarly Suns *et al.* (1987) found a relationship between pH and lead (Pb) in fish. Anderson & Borg (1988) did the same for cadmium (Cd) despite Campbell & Stokes (1985) indicating that its accumulation in fish should decrease in waters more acid than pH 5. While there are indications that accumulations of Zn and Cu, like those of Al, are toxic (Hutchinson & Sprague 1986) much more needs to be known of their influences on fish, also their predators including man.

Amphibians

Surveys have shown that some widespread species are conspicuous by their absence from acidic (low pH) and/or 'high aluminium' ponds (Albers & Proutry 1987; Glooschenko *et al.* 1988). Many species are of concern because their habitats for reproduction, temporary pools and shallow waters, are vulnerable to acidification (Pough 1976; Pough & Wilson 1977; Clark & Euler 1982), a hazard exacerbated because spawning usually occurs in early spring when pulses of acidic/aluminium 'contaminated' waters particularly toxic to embryonic stages, are commonly experienced (Freda 1986). These episodes can kill (Gascon & Bider 1985). The complete loss of the frog, *Rana temporaria* (Fig. 5), and reproduction failure in the toad, *Bufo bufo*, have been reported in Sweden (Hagstrøm 1977) with similar occurrences also being noted in the Netherlands where these animals usually avoid fens more acidic than pH 4.5 (Strijbosch 1979). In the United Kingdom, Beebee *et al.* (1990) have documented the decline of the natterjack toad, *Bufo calamita*, which used to breed in ponds, in Woolmer Forest, that are now too acid to allow the development of

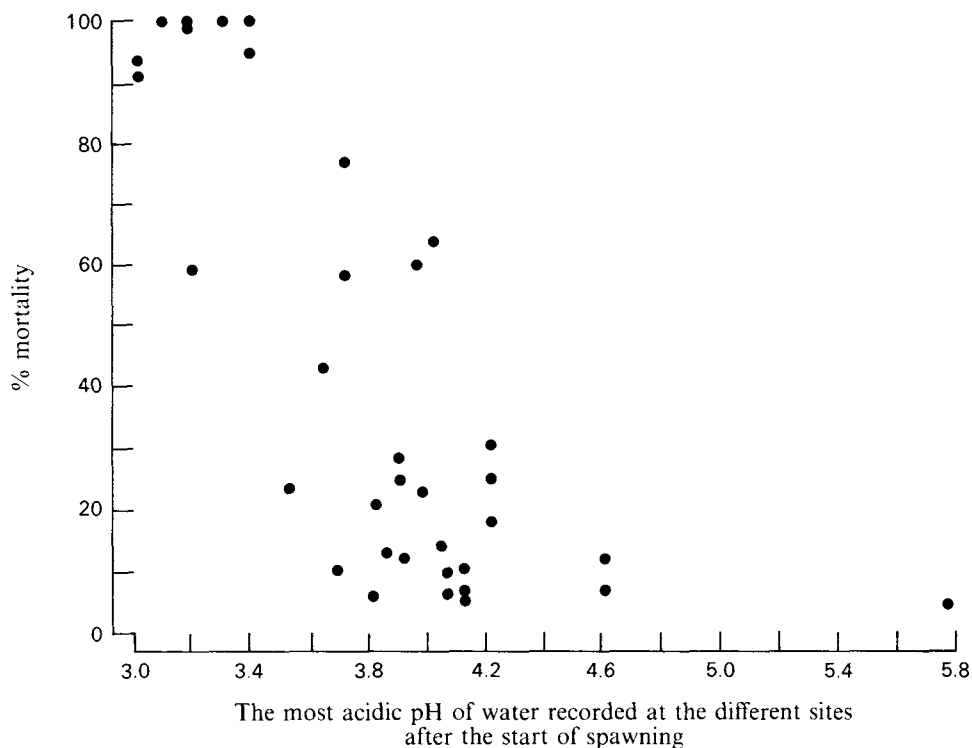


Figure 5. Relation between the mortality of embryos developing within spawn clumps of *Rana temporaria*, the common frog, and the most acidic pH recorded in breeding ponds in the Cairnmore of Fleet, Scotland (Cummins & Ross 1986).

embryonic and larval stages. Evidence of diatoms, macrophytes, and deposits of heavy metals and soot particles in sediments indicates that the decline of amphibians is associated with the acidification of ponds recently attributable, in some measure, to acidic deposition.

Even small increases in the acidity of naturally acidic ponds, rich in organic matter, may jeopardise many species (Freda 1986). Ranges of toxicity tests and physiological studies are currently being explored in the hope of attributing causes to events in the field (Freda & McDonald 1989); it is known that amphibians are affected but details of damage mechanisms still need to be completed.

Waterfowl

Although Nyholm's (1982) study of fly catchers (*Ficedula hypoleuca*) suggests that Al enrichment in bones, suspected of interfering with normal Ca-metabolism, is attributable to acidification the evidence of direct toxic effects, attributable to acidification, on the performance of birds is not substantiated. However, waterfowl may be adversely and indirectly affected by the loss of prey. For example, if small fish, a preferred food of mergansers and loons, are scarce or absent, the distribution of mergansers and loons can be restricted (McNichol *et al.* 1987). Many acid-sensitive macroinvertebrates are eliminated from waters that can still support populations of fish. In these instances, predatory fish and birds may compete with each other and

become impoverished (DesGranges & Hunter 1987; McAuley & Longcore 1988). On the other hand, waterfowl may thrive if predatory fish are absent (Hunter *et al.* 1986). The greater clarity of acidifying lakes may also favour predatory birds which hunt using visual cues (Eriksson 1984). However, the elimination of crustaceans and insect larvae may decrease the size and quality, in terms of Ca concentration, of the surviving food resource (Blancher & McNicol 1988).

The effects of impoverished sources of food for insectivorous birds were highlighted by Ormerod and co-workers (1986; 1989) and Ormerod & Tyler (1987) working in Wales: they have related significant effects on the performance of the dipper (*Cinclus cinclus*) to the loss of sensitive prey, mayflies and caddis fly larvae, from acidified streams near their breeding sites. Dippers usually select locations with abundant invertebrates. Studies over time have shown that populations of dipper along the River Ifron decreased as acidity increased between 1960 and 1984: there was a change of pH of 1.7. units (Ormerod & Tyler 1987).

In general, the evidence indicates that some species of birds, that breed alongside lakes and streams, have smaller clutches, and thinner eggshells: breed later with fewer second clutches while their young grow less rapidly and suffer more mortality, when lakes and streams are acidified (Hansen 1987) (Table 3).

Mammals

Because of the paucity of in-depth studies, it is not possible to assess if the loss of fish, associated with acidification has had, or is likely to have, an effect on the distribution of otters and mink (Bevanger & Albu 1986). The possibility of accumulations of elements such as mercury also needs to be kept under review (Wiener 1987).

Table 3. Performance of dippers *Cinclus cinclus* exploiting acidic (pH < 6) and circumneutral (pH > 6) streams in Upland Wales during 1985 and 1986: acidic streams were typically at higher altitudes than the circumneutral streams (Ormerod *et al.* 1991).

	Nature of streams		Statistical probability of differences between acidic and circumneutral streams
	Circumneutral	Acidic	
Laying dates (day 1 = 1st Jan)			
1985	88.5	104.7	0.001
1986	98.8	125.2	0.001
Clutch size			
1985	4.9	4.1	0.001
1986	4.8	4.0	0.001
Brood size			
1985	4.2	3.4	0.03
1986	4.2	3.8	NS
Second clutches (%)			
1985	23.2	Nil	—
1986	201	Nil	—

N.B. Using regression, pH explained significantly more of the variance in laying date than altitude.

Discussion

From observations made predominantly in northern Europe, Canada and the U.S.A. a number of generalisations can be made.

- (a) Assemblages of freshwater microbes, plants and animals alter when streams, rivers and lakes (lochs), dependent upon geologically sensitive bedrock, are acidified by inputs of acidic deposition.
- (b) All diatoms, invertebrates, fish, etc. are not equally acid-tolerant/sensitive.
- (c) While the species composition of diatom assemblages, also those of invertebrates, may be radically altered, acidification tends to have a relatively small effect on their biomass – there is a degree of compensation.
- (d) Unlike its effect on diatoms, the degree of acidification experienced in the field is, in many instances, sufficient to eliminate crustacea (snails and crayfish), amphibians and fish.
- (e) Some of the changes to assemblages of plants and animals are directly attributable to the effects of acidification on water quality (pH, concentrations of aluminium and transparency) whereas others are brought about indirectly. For example phytoplankton biomass, albeit of different species, may be greater in acidified lakes than in 'pristine' lakes because acidity decreases the performance of herbivores with consequent lessening of grazing pressures: the decline of the dipper, a riverine bird, is strongly associated with the disappearance of its sensitive prey, including mayflies and caddis fly larvae.

In summary, the reasons for change often need to be sought in relation to indirect effects on organisms at different trophic levels in addition to direct toxicity which, itself, is known to vary appreciably in its impact, for example, newly hatched fish are more sensitive than adults.

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