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Fishery Decline: Mechanisms and Predictions [and Discussion]

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Fishery decline: mechanisms and predictions

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The hypothesis that surface water acidification is responsible for fisheries loss depends on demonstration that fishery status is determined by acidity and related chemistry of lakes and rivers. The effect of acidity is shown to be moderated by the benefit of calcium and the adverse effect of aluminium: this is why no simple acid 'threshold' or 'acceptable pH' can be set for any species. The sensitivity to both acidity and aluminium toxicity varies with age in a complex way.

Few data sets provide concurrent information on both water quality and fishery status, and a consistent picture does not emerge, possibly due to inadequate data, to natural differences between locations, but possibly because acidification alone may not be the cause at all locations.

Critical pH-levels are not known for many species, and reputed thresholds for effects vary as much as 400-fold for H^+ toxicity. Some instances occur where fish are found in relatively acid waters, and where fish losses have occurred at levels of pH not judged toxic in the laboratory. Both laboratory data and field observations have shortcomings which limit the test of the hypothesis that acidification has led to loss of fisheries.

The extent to which other environmental variables may affect fish populations in acid oligotrophic waters is quite uncertain. Unsuitable stream conditions associated with afforestation and unstable hydrological régimes may limit the benefit to be gained from remedial measures.

1. Introduction

A decline of fisheries – both lost populations and fewer species – is reported for acid lakes and streams in southern Scandinavia, and in north eastern America and Canada. Acidity of the water is a common factor, but other conditions, and the initiation and rate of fishery changes, vary between these locations. Aside from physical and biological considerations, water quality is certainly an important factor influencing fishery status of a water body. Acidity of sufficient concentration and exposure over sufficient time will kill fish, and at lower concentration may possibly have sub-lethal effects significant to the long-term maintenance of a population. Yet inconsistencies in the observations suggest that there may not be a simple direct relation between fishery status and lake–river pH, or at least that other factors remain important. A more detailed analysis of conditions in fishless lakes, and knowledge of the mechanisms of damage is needed, both to improve our understanding and to develop effective remedial action.

Determinants of a fishery include hydrological characteristics, lake–stream morphometry, habitat complexity (e.g. connectedness), incidence of disease, temperature régime, water quality, food supply and toxic pollution. Characteristically (but not invariably) acid lakes and streams drain moorland or forested upland catchments with thin, poor, soils and unreactive bedrock. Such waters are often hydrologically variable so that water level and flow, sediment load, temperature and chemical quality are typically unstable. Physical conditions may limit suitable spawning habitat, or natural access, and so may restrict fish survival, reproduction or recruitment. Water quality is not independent of these physical conditions; drainage–run-off interaction with soils may have been slight, and the water generally low in total dissolved solids and conductivity, with low alkalinity and low calcium. The degree to which water quality *per se*, rather than physical or biological factors, determines fishery status in the acid surface waters of sensitive regions is difficult to assess: information on physical conditions and year-round water quality is often lacking, and recent changes, for example of land use or fisheries management, may have occurred. Conditions influencing water quality are usually interdependent.

The strength of a fish population is determined by the balance between recruitment and loss. Biological factors enhance or reduce recruitment or mortality, in the case of 'density dependent' functions like fecundity, fry survival and growth, responding in such a way as to maintain the stability of the population: the compensatory response which allows exploitation at a certain level while sustaining yield (MacFadden 1977). Compensation seems not to be evident in acid waters, possibly because populations are so small.

The evidence that 'acidification' of lakes and rivers has damaged fisheries includes observations that:

(i) acid lakes and streams in northeastern North America and northern Europe lack fish;

(ii) where historic records are available, a loss of fish is concurrent with increased acidity;

(iii) in some instances, particular species have been lost, with impoverishment of the fish community;

(iv) within a species, missing year classes suggest that reproduction or recruitment is the cause of population decline; however,

(v) the growth of individuals in the field is not impaired.

In this review, the results of laboratory exposure to acid conditions will be used to judge how far physiological and reproductive responses to ambient water quality can account for the fishery status of acid lakes and whether future fishery status could be predicted for any predetermined water quality. Consideration will also be given to the effects of some other dependent, or independent, factors.

2. Physiological effects of acid exposure

(*a*) *Acute tests*

Short-term laboratory bioassay in which a limited number of fish species is exposed to a range of acid concentrations has been used to determine survival times or a lethal concentration.† Much of the early work was reviewed and assessed by the European Inland Fisheries Advisory Commission (EIFAC) in 1969, and again in 1979 (Alabaster & Lloyd 1980). Work on North American species has been reviewed recently by Wood & MacDonald (1982). A qualitative but progressive response to increasing acid exposure can be documented for some N American and European freshwater species (table 1); in general significant effects begin to be manifest at pH < 5.0, unless some additional component of water quality (free CO_2; high Fe; low Ca, Na, Cl; low temperature) also reduces survival.

Many early tests were poorly designed and executed: for example static, not through flow, exposure; water quality poorly controlled or inadequately monitored; and the origins of test fish uncertain. Perhaps more important, the test media were often not specified in terms of the

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† Generally expressed as ET_{50} (time at which half the population will die) or LC_{50} (concentration, i.e. pH at which half the population has died).

source or chemistry of the make-up water. Although acid surface waters are invariably 'soft', low conductivity waters, and infrequently of pH less than 4, many laboratory exposures were made in inappropriately hard waters acidified to much lower pH levels, in some cases resulting in CO_2 toxicity or other chemical effects confounding those of acidity *per se*. Aside from the common salmonids (*Salmo* spp., *Salvelinus fontinalis*) and a few other species (*Catostomus commersoni*, *Rutilus rutilus*), the acid tolerance of many species is untested; there is a particular need for information on North American species characteristic of acid oligotrophic lakes and streams.

Table 1. Summary of the effects of acid pH values on fish

(Alabaster & Lloyd 1980)

range	effect
3.0–3.5	Unlikely that any fish can survive for more than a few hours in this range although some plants and invertebrates can be found at pH-values lower than this.
3.5–4.0	This range is lethal to salmonids. There is evidence that roach, tench, perch and pike can survive in this range, presumably after a period of acclimation to slightly higher, non-lethal levels, but the lower end of this range may still be lethal for roach.
4.0–4.5	Likely to be harmful to salmonids, tench, bream, roach, goldfish and common carp which have not previously been acclimated to low pH-values, although the resistance to this pH range increases with the size and age of the fish. Fish can become acclimated to these levels, but of perch, bream, roach and pike, only the last named may be able to breed.
4.5–5.0	Likely to be harmful to the eggs and fry of salmonids, and to adults, particularly in soft water containing low concentrations of calcium, sodium and chlorides. Can be harmful to common carp.
5.0–6.0	Unlikely to be harmful to any species unless either the concentration of free carbon dioxide is greater than 20 mg l^{-1} or the water contains iron salts which are freshly precipitated as ferric hydroxide, the precise toxicity of which is not known. The lower end of this range may be harmful to non-acclimated salmonids if the calcium, sodium and chloride concentrations, or the temperature of the water are low, and may be detrimental to roach reproduction.
6.0–6.5	Unlikely to be harmful to fish unless free carbon dioxide is present in excess of 100 mg l^{-1}.
6.5–9.0	Harmless to fish, although the toxicity of other poisons may be affected by changes within this range.

Allowing for variations in response of about ±0.5 pH for different species, or strains, or of different life stages, a typical LC_{50} for adult exposure of salmonids is pH 4.0 to 4.5, and for juveniles about 4.5 (Howells 1983) (table 2). The North American white sucker (*C. commersoni*) and the yellow perch (*Perca flavescens*) are more tolerant (Wood & McDonald 1982; Rahel 1983), and the minnow (*Pimephales promelas*) somewhat more sensitive (Wood & McDonald 1982).

Acute exposures generally refer to tests over some days (to about 10). They indicate immediate response to changed conditions, without benefit of physiological adaptation or behavioural avoidance. They provide only limited insight into the response to sustained conditions or the variable conditions observed in the field. They may, however, possibly be considered representative of acid episodes and indicative of field mortality (Jensen 1974), although none of the tests simulate the extent and timing of naturally variable and reversible acid conditions, such as are observed during snow melt, or after heavy rain events.

TABLE 2. ESTIMATED SENSITIVITY TO pH OF SOME FISH SPECIES AND LOWEST FIELD pH

	acute pH exposure		long term pH	
species	adult LC_{50}	juvenile LC_{50}	lowest observed in field	comments
Salmo salar	—	eggs 4.0–4.5 alevins 4.0–4.3 fry 4.0–4.5	4.6	critical pH for egg hatch 3.3 (hard water), 5–5.5 (soft water)
Salmo gairdnerii	1 + fish, 3.4–4.5	fry 4.0–4.5	4.7	generally acknowledged to be the most sensitive salmonid
Salmo trutta	1 + fish, 4.6	eggs 4.5 alevins 4.5	3.9	critical pH for egg hatch–development, 4.5
Salvelinus fontinalis	1 + fish, 3.5	fry 3.5	3.5	variation between strains
Catostomus commersoni	4.1	eggs 4.5	4.7	critical pH for egg hatch 4.5: large mortality below, 100% survival above, population loss thought due to reproduction failure
Rutilus rutilus	4.15	eggs 6 (est.)	4.2	critical pH for egg hatch 5.5

(*b*) *Physiological responses to acute exposure*

Essential physiological functions involved in oxygen uptake and transport, ionic regulation, and acid-base balance in blood may be affected by acid exposure.

Exposure to acid can lead to blood acidosis, but there is insignificant change at pH < 4; the magnitude of blood pH depression on exposure to pH greater than 4.0 is matched or exceeded by that induced by exercise, and is well within the tolerance of the fish (Wood & McDonald 1982). Similarly, fish exposed to pH values (4.0 to 6.0) pertinent to most field conditions show little effect on oxygen uptake or transport (Wood & McDonald 1982; Carrick 1981). While oxygen consumption falls off below pH 4.0, this could be a consequence rather than a cause of dying. Observed changes in haematology are variable and inconsistent.

Ion regulation of blood and body tissues is affected by acid exposure. Homeostatic control of salt balance in freshwater fish is predominantly a function of the gills, with little role for the kidneys (Wood & McDonald 1982). For several salmonid species, blood sodium and chloride are depleted by exposure to pH of 4.5 or less (Packer & Dunson 1970; Leivestad & Muniz 1976; McWilliams & Potts 1978). Sodium and chloride diffuse along the concentration gradient across the gill, more rapidly at lower pH and lower calcium (Eddy 1975; McWilliams & Potts 1978). The active uptake of sodium which normally makes good this diffusion loss may also be inhibited in acid conditions. An increased positive electropotential across the gill membrane in acid or low calcium media contributes to the developing imbalance of blood salts (McWilliams & Potts 1978, McWilliams 1982). Calcium is thus critical in maintaining the impermeability of the gill membrane and a negative transepithelial potential. Furthermore, time-dependent acclimation can moderate these responses (McWilliams 1980*a*, *b*) (figure 1).

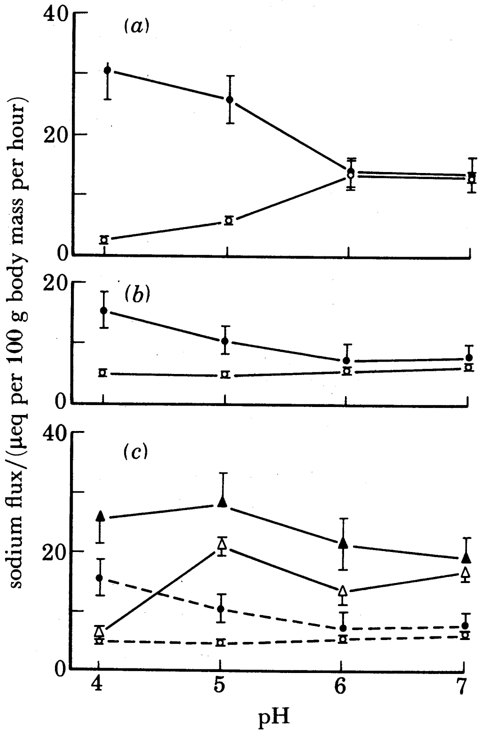

FIGURE 1. Sodium fluxes in brown trout exposed to acid media, (*a*) without previous acclimation to acid conditions, (*b*) with 6 weeks prior exposure to pH 6 medium, (*c*) in two strains of trout from acid, low calcium, water (△, ▲ Loch Grannoch trout; ○, ● Cumbrian hatchery trout). (Source McWilliams & Potts 1978; McWilliams 1980*a*, *b*, 1982.) Open symbols are influx measurements, closed are efflux.

Progressive blood and tissue loss of sodium reduces whole body salt content, with a terminal reduction at 60–70% of normal for rainbow trout (*Salmo gairdnerii*) fingerlings (Wood & McDonald 1982). However, differences in whole body salt content of fish from acid and alkaline lakes are small relative to the differences in ambient water, and the literature is conflicting (Rahel 1983). Some species, at least, are able to maintain body electrolytes within a narrow range even in acid waters.

Lee *et al.* (1983) found evidence of metabolic stress at pH < 4.8 in *S. gairdnerii* and deduced a 'zone of reproductive stress' at pH 6.5 to 5.5. *C. commersoni* taken from pH 7.2 and pH 5.2 lakes, however, did not exhibit significant differences in blood composition and energy metabolism, confirming earlier failure (Lockhart & Lutz 1977) to find a change in cortisol in white suckers from acid lakes.

The role of calcium is seen as crucial; body electrolyte loss is slower in hard than in soft water (Wood & McDonald 1982), and calcium is essential in limiting gill diffusion loss (McWilliams 1982); it is possibly important also in maintaining normal reproductive function (see below). The presence of a minimal concentration (approximately 50 μeq $\mathrm{l}^{-1} \equiv 1$ mg l^{-1}) prolongs survival in acid exposures and allows successful development of brown trout eggs and fry even at pH 4.5 (Brown 1983*a*, *b*; Brown & Lynam 1981) (figure 2).

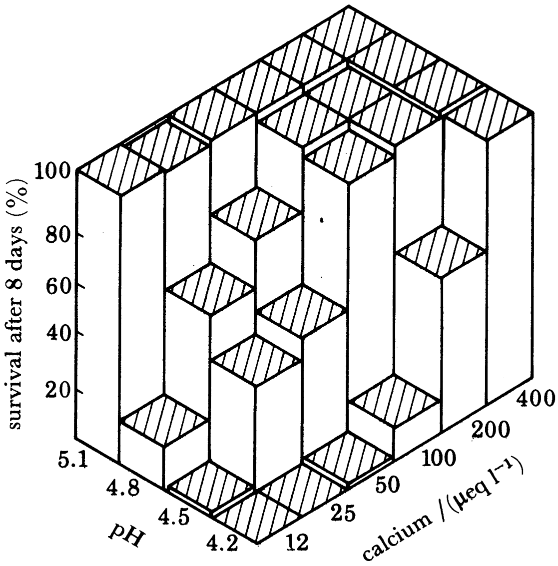

FIGURE 2. The survival of freshly fertilized eggs and fry of brown trout after 8 days exposure to a range of pH and calicum concentration. (Source: Brown & Lynam 1981.)

While laboratory tests show that transfer to acid media will affect ion regulation before mortality, clearly calcium exerts an important moderating effect, so that tolerable water conditions have to be defined at least in terms of these two variables. Since the physiological response is reversible to a degree, and since there is evidence of acclimation, the cause of fishery loss in the field must depend on the extent to which over time, the affected waters have become more acid without concurrent increase in calcium, or whether, in short term acid episodes, calcium concentrations fall below the essential minimum.

(*c*) *Field observations*

Longer term laboratory tests are virtually non-existent and to understand the effects of sustained acid exposure we are dependent on observations of the presence–absence of a species in lakes and streams of a range of acidity, or the sequence of fish loss in acidifying lakes, or other observed effects such as recruitment failure, attributable to acid conditions. The observations reported are not always consistent. Twelve North American species characteristic of oligotrophic lakes tested against a progressively declining pH are consistent with the field records of these species in Wisconsin lakes (Rahel & Magnusson 1983). In some instances, however, a species may be unexpectedly present or absent from acid waters of a particular pH level. For example, in Sweden, char (*Salvelinus alpinus*), roach (*R. rutilus*), perch (*P. fluviatilis*) and pike (*Esox lucius*) have been lost from lakes of pH 4.5–5.5 (Dickson *et al.* 1975; Almer *et al.* 1974, 1978). However, also in Sweden, minnow (*Phoxinus phoxinus*) and roach are judged the most sensitive species, and pike, perch and eels (*Anguilla anguilla*) tolerant. In Canada, yellow perch (*P. flavescens*) and burbot (*Lota lota*) were first to be lost from Lumsden Lake (1960, pH 6.8), and after 10 years (1970, pH 5.3–5.7) only chub (*Couesius plumbeus*) remained (Beamish & Harvey 1972) yet perch is thought to be tolerant, and chub sensitive. The abundance, age structure and occurrence of the white sucker (*Catostomus commersoni*) are profoundly affected in many acid lakes (Harvey 1982) yet physiological responses are not evident until pH is below 4.0 (Wood & McDonald 1982). In Adirondack lakes, brook trout, white sucker and bullheads (*Ictalurus nebulosus*) were lost from 16 high altitude lakes of pH less than 4.5 (Schofield 1976): again species of no great physiological sensitivity (Wood & McDonald 1982). In southern Norway fishless lakes are predominantly those of lowest calcium concentration (figure 3) but include a forty-fold range of acidity.

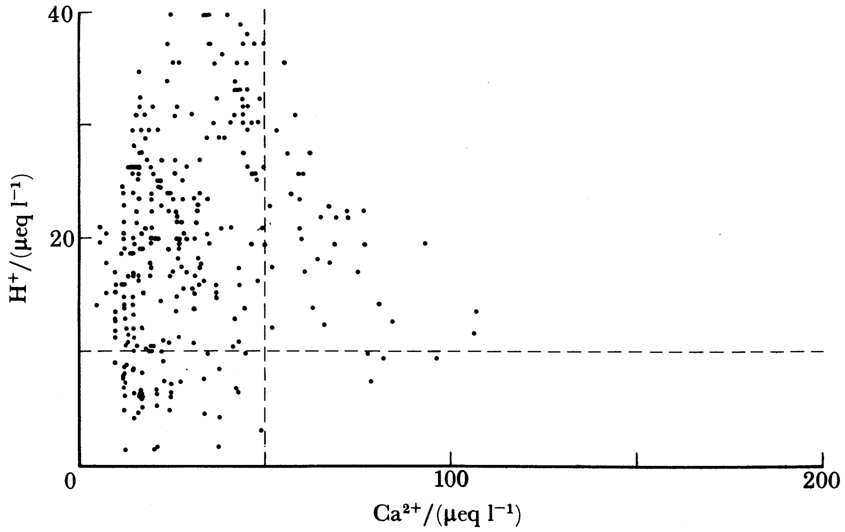

FIGURE 3. Distribution of fishless lakes in Sorlandet, S Norway in relation to acidity and calcium concentrations. (Source: data of Wright & Snekvik 1979; Chester 1983.)

Some anomalous observations must reflect the influence of factors other than acidity, or even of water quality. In addition, the continuing presence of a species in the field may indicate physiological or behavioural adaptation. Natural selection of genetic based tolerance is evident for brown trout (*Salmo trutta*) (Gjedrem 1976; Gjedrem 1980), brook trout (*Salvelinus fontinalis*) (Swarts *et al.* 1978; Robinson *et al.* 1976) and for yellow perch (*Perca flavescens*) (Rahel 1983).

(*d*) *Other water quality factors*

Some other associated water quality component could be important, either associated with, or independent of pH. 'Acidified' waters are characteristically oligotrophic and of low productivity. Although their acidification is attributed to excessive atmospheric sulphur loading (Dillon *et al.* 1979; Dickson 1980) sulphate concentrations and acidity in the lakes are not closely related, even where lakes and streams drain an area of relatively uniform geology (Brown & Sadler 1981). Nor is fishery status in S Norway lakes related to sulphate concentration, often seen as a surrogate of atmospheric acid deposition (Chester 1982). While sulphate does not affect fishery status, in stratified lakes fish losses during winter deoxygenation could possibly be associated with hydrogen sulphide (H_2S) which has a low threshold for toxicity to fry (2–20 $\mu g\ l^{-1}$) and is 99% undissociated at pH 5 (E.P.A. 1973).

Acid waters are reported of low alkalinity and may also have elevated aluminium or other metal concentrations. Alkalinity has been shown to influence the standing crop of fish, although it is less significant in trout lakes than in productive warm water lakes or reservoirs (Carlander 1955). Elevated aluminium concentrations in acid waters are sometimes in excess of 1 mg l^{-1} but fisheries do not always reflect the reported levels of pH, calcium and aluminium (table 3). Aluminium concentration reflects seasonal changes and flows, with high values coincident with increased acidity during spates (Driscoll *et al.* 1980), where concentrations of about 200 μg l^{-1} (total) or more at pH 5 (Cronan & Schofield 1979; Schofield & Trojnar 1980; Muniz & Leivestad 1979) are toxic to brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*). Some other species have been affected at still higher concentrations (cisco, *Coregonus albula*, and pumpkinseed, *Lepomis gibbosis*) (Grahn 1980; Harvey & Lee 1982).

TABLE 3. COMPARISON OF WATER QUALITY WITH OBSERVED FISHERY STATUS

(Assumptions are that pH–Ca–Al determines fishery status, and that mean data for lake sets are representative of individual lakes.)

lake set (*n*)	pH	Ca^{2+}	SO_4^{2-}	Al^{3+}	Ca/H	fishless observed (%)	fish or community
Adirondacks (217)	4.95	102	134 (by diffce)	22.8	8.5	51	mixed species
S Norway (616)	4.75	36	71	18.1	2	37	brown trout
Sudbury, Ont. (208)	5.4	272	250	(5.5)	68	28	mixed species
C Sweden (32)	5.35	271	242	8	60	22	char
N & C Sweden (101)	7.0	355	210	—	355	0 (?)	mixed species
Galloway, Scot. (57)	4.95	74	111	14	6.2	5	salmonids
N Norway (47)	5.1	52	59	5	6.2	0	salmonids
Whitefish I.R. Ont. (35)	6.5	282	368	—	282	0 (?)	mixed species
ELA, N.W. Ont. (102)	6.5	95	76	—	95	0 (?)	mixed species

Source: concentrations microequivalents per litre given in Wright (1983), corrected for sea salts. Aluminium (total) assumed to be Al^{3+}, 1 mg $l^{-1} \equiv 111$ μeq l^{-1}.

These findings are consistent with bioassay at pH 4.4 to 5.4 (Schofield & Trojnar 1980; Brown 1981; Baker & Schofield 1980; Rosseland & Skogheim 1982). As pH is lowered, toxicity is reduced (Brown 1977, 1981; Schofield & Trojnar 1980), although if calcium is below *ca.* 50 μeq l^{-1}, lower aluminium concentrations (under 100 μg l^{-1}) are toxic to fry at pH 4.5 (Dalziel & Brown 1983) (figure 4). This complex picture no doubt reflects the chemistry of aluminium: not all the measured 'total' aluminium is available, and only Al^{3+} hydroxy compounds are thought to be toxic; toxicity is significantly moderated by calcium but also by chelating substances such as citrate (Baker & Schofield 1980), and humic materials (Baker 1982). The effect at pH > 5 may be due to gross precipitation of hydroxides at the gill membrane, restricting normal respiratory exchange, while lower toxic concentrations at lower pH could result from a physiological impairment of gill membrane function. The former mechanism affects larger fish, while newly hatched fry are more sensitive to the latter (Dalziel & Brown 1983).

In addition to aluminium, some acid waters have been shown to have elevated iron, manganese, copper, nickel, and lead. These potentially toxic metals are generally rendered more available and more toxic in acid waters with low calcium concentrations. In some lakes, e.g. La Cloche lakes within 50 km of Sudbury, observed concentrations exceed those considered tolerable for fish.

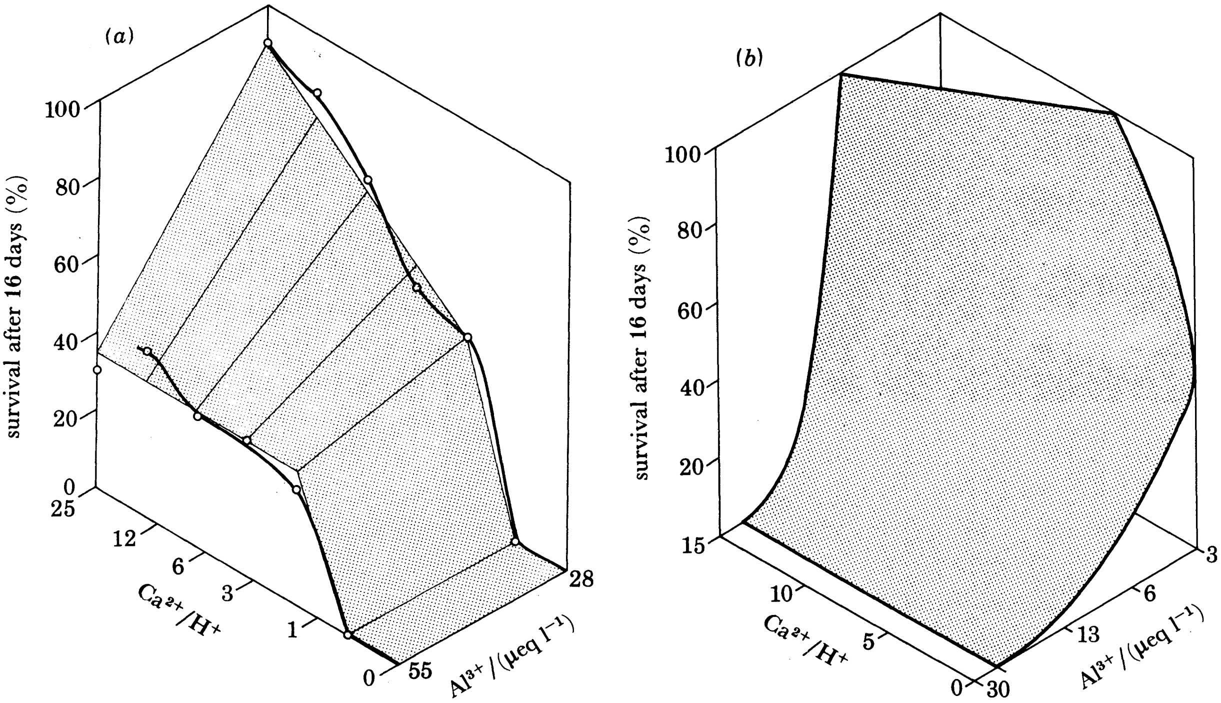

FIGURE 4. Approximate response planes for survival of brown trout fry exposed to a range of pH (4.5–5.4), calcium (1.2–100 μeq l^{-1}) (*a*) higher and (*b*) lower aluminium concentrations. (Source: data of Brown 1983*a*; Dalziel & Brown 1983.)

While aluminium, iron and manganese are largely derived from soils, the others are thought to reach surface waters via atmospheric emissions, from local point sources or from mobile sources.

(*e*) *Historic trends*

If the observed change in fishery status, e.g. in southern Norway, is a response to changed water quality attributable in turn to increased acid deposition, we could reasonably expect that change to involve acidity, calcium and aluminium levels. For brown trout a decrease in pH at least to less than 5, coupled with calcium of less than 2 mg l^{-1} and an aluminium increase to more than 200 μg l^{-1} is required. There is only limited historic evidence of changes in acidity. In S Norway for example: from pH 6 (1940s) to pH ≈ 4.8 (1970s) in 6 lakes (I.E.R.E. 1981) and from pH 5.19 (1965) to pH 4.9 (1979) in 10 rivers (Henriksen *et al.* 1981). This change, attributed to increased acid deposition, would be expected to *increase* calcium and magnesium in run off. The factor of increase indicated by synoptic data may have been 1.4 (Henriksen 1982) or 1.55 (Christopherson 1982, personal communication) of the (sulphate) change, suggesting that calcium concentrations in the past may have been insufficient for fish in even more lakes than at present. It is not known to what extent mobilization of aluminium depends on atmospheric input of sulphur or acidity.

3. Long term effects: reproduction, recruitment and growth

(a) *Effects on reproduction*

It is generally considered that losses of fish populations from acid waters are a result of reproductive failure. Evidence comes from only a few field and laboratory studies on a few species, some inappropriate to northern oligotrophic waters. Several species present in Sudbury, Ontario, lakes are reported to have impaired reproduction (Beamish & Harvey 1972; Beamish *et al.* 1975), in some cases consistent with histological findings of abnormal gonads in fish from lakes of pH 4.5 (Beamish 1974). Experimental studies on four species (Ruby *et al.* 1977, 1978; Craig & Baksi 1977; Mount 1973) show reduction of spermatogenesis and egg production on transfer from pH 6.8 to 6. Similar gonad abnormalities in the minnow are reported in a lake acidified from pH 6.8 to pH 5.8 (Schindler & Turner 1982). These observations of reproductive impairment seem surprising for so slight a change in acidity alone, together with a lack of evidence that significant blood changes occur with exposure to pH change of this magnitude. Anomalous calcium metabolism could possibly provide an explanation: white suckers (*Catostomus commersoni*) in an acid lake were reported to have lower serum calcium (Lockhart & Lutz 1977), although no evidence of bone demineralization. A field experiment with brook trout (*Salvelinus fontinalis*) exposed over a year to limed (pH 6.0 to 6.5) and natural brook water (pH 4.4 to 5.3, Ca 22–66 μeq l^{-1}) showed that fish in limed water had a higher serum calcium (Muniz & Leivestad 1979), but experimental shortcomings make the difference between limed and natural groups insignificant (Howells 1983).

(b) *Effects on recruitment*

There is more substantial evidence from both field and laboratory studies that egg hatch, fry survival, and subsequent recruitment of young fish to the population can be adversely affected by acid conditions during the early life history (Peterson *et al.* 1982). The time, mode and location of spawning is clearly important in relation to autumnal or spring acid events: while North American lake trout, white fish, lake herring and perch spawn between September and December in the lake water column, most salmonids spawn from November through to January in stream gravel beds. On the other hand, chub, smelt and rainbow trout are spring spawners. The known discontinuity in water conditions provides an additional complexity: with acid snow melt water overlying older lake water in spring, and conditions in salmonid redds influenced to an unknown but variable extent by upwelling ground water. Few direct observations are reported on the success of egg hatch in the field in relation to water quality (Leivestad *et al.* 1976; Harriman & Morrison 1982) and little detail of water quality during the developmental period is given. Conditions associated with episodic acidity are also characterized by rapid and variable flows, and sediment and gravel disturbance (Milner *et al.* 1981) which are detrimental to successful egg development and hatch of fry.

Increased mortality of eggs and fry attributable to acid toxicity could affect the size of the adult population, even though density dependent compensation may reduce a population's sensitivity because of decreased competition and predation, or because of increased fecundity. From a Leslie matrix model of brook trout (*Salvelinus fontinalis*) populations, Jensen (1974) argued, while assuming constant birth and death rates, that even 5–25% increased mortality of O+ groups would reduce yield, while 50% additional mortality would lead to extinction.

A similar model that used bioassay results to derive mortality of brown trout (*Salmo trutta*) in acid, low calcium media over the first year (Sadler 1983) was, however, unable to explain the fishery status of southern Norwegian lakes, possibly because cumulated mortality in successive years could significantly reduce recruitment in this slow growing population (at least 4 years to reach maturity). Analysis of perch (*Perca fluviatilis*) populations in Windermere, U.K., over 40 years suggests a more complex picture (Craig 1982): major fluctuations of this species were observed and attributed to biological and physical influences, and water chemistry changed only slightly over this long period of observation.

Acid lakes are generally thought to have miniscule fish populations (Harvey 1982) but even within the acid lakes of Ontario, numbers may be higher in some acid lakes, e.g. Crosson Lake (pH 5.3) *ca.* 2500 ha^{-1} than in neutral Harp and Plastic lakes *ca.* 200 ha^{-1} (Harvey 1982, table 1).

The sensitivity of fry to acid conditions, and the coincidence of seasonal acid events with fish egg hatch in the spring has led to the view that population decline of many species has occurred by this mechanism. Unfortunately direct evidence is almost entirely lacking. Fish kills observed and reported are of larger fish, and water chemistry is measured after the event. While acid and other pollutants can accumulate in the winter's snow pack, to be concentrated by fractionation and released during the spring thaw (Johannesson & Henrisken 1978), chemical and isotopic analysis of stream water at snowmelt shows that ground water is present (Johannessen *et al.* 1980), contributing 70–90% of flow when soil is not frozen (Rodhe 1981).

Seasonal episodes can cause temporary toxic conditions in streams, or in the epilimnion of lakes where snow melt water, being of lower density, overlies the main body of lake water. The extent and duration of such episodes depend on a number of conditions, of which snow depth, snow acidity, soil interaction, and accompanying rain, all play some part. The variable nature of episodes and their associated chemistry is scarcely reported, however. Whether fry and juvenile fish die from acid or other toxic exposure over the brief initial period of snow melt or from the longer sustained low calcium, but less acid, conditions that follow as the bulk of snow pack is melted, is not known.

Observations of anomalous age structure of some fish species in acid waters has been presented as evidence of such episodic events. Abnormal age class composition has been reported for pike (*Esox lucius*), white sucker (*Catostomus commersoni*), yellow perch (*Perca flavescens*) and rock bass (*Amblopites rupestris*) in acid lakes (Harvey 1982). There is, however, considerable variation in observed response with European perch (*Perca fluviatilis*) exhibiting a complete range of age classes in two Norwegian lakes (pH 4.80 and 4.95) but few fish and missing younger age classes in a less acid lake (pH 5.19) (Rosseland *et al.* 1980). Clearly other factors can affect recruitment, including temperature (Shuter *et al.* 1980), other toxic agents, and physical conditions (Schlosser 1982).

While exposure to critically acid or low calcium conditions during snow melt, or to other episodic conditions (such as raised aluminium (Schofield & Trojnar 1980)) affects recruitment and so population strength, lack of precise information on water quality during episodes makes it difficult to judge the extent to which this is responsible for fishery decline, or whether particular water bodies or particular species will be most at risk.

Liming to raise both pH and calcium concentration could be expected to improve fish survival and recruitment, or to allow restocking; fishery recovery is not always achieved however. Liming the somewhat acid Fulufäll Lakes in central Sweden brought about only short-lived improvement to char (*Salvelinus alpinus*) and grayling (*Thymallus thymallus*), while trout (*Salmo trutta*) were not much improved; restocking was unsuccessful (Lindstrom & Andersson 1981). In other Swedish lakes raised to pH 6, a better recovery of perch and char is reported (Bengtsson *et al.* 1980), and restocking of brown trout and brook trout in four southwestern lakes ($\mathrm{pH} < 5$) was successful after liming brought the pH to about 7 (Hültberg & Andersson 1982) although growth was weak. It seems that liming can be successful, at least in some surface waters.

(*c*) *Effects on growth*

Growth of fish is known to be variable, and reflects climatic and habitat conditions including food supply and water quality, as well as genetic factors; growth is better in hard, alkaline waters (Frost & Brown 1967), and in a stable temperature régime (Edwards *et al.* 1979). Carlander (1955) demonstrated that growth in lakes of 200 mg l^{-1} alkalinity was twice that of fish in lakes of low (under 5 mg l^{-1}) alkalinity. It is also accepted that production in oligotrophic temperate lakes is related to the 'morpho-edaphic index' (Ryder 1965) which reflects lake size and nutrient status. Recent analysis of water quality and fish biomass and yield in similar lakes (Hanson & Leggett 1982) has suggested that total phosphorus and macrobenthos–mean lake depth are the best predictors of both yield and biomass, regardless of the number of species present.

Fish in acid lakes have commonly better size for age than in less acid waters (Almer *et al.* 1974, 1978; Ryan & Harvey 1977, 1980) although white suckers (*Catostomus commersoni*) in George Lake, Sudbury, Ontario, exhibited reduced growth (Harvey 1980; Beamish *et al.* 1975). In southern Norway, brown trout (*Salmo trutta*) from acid lakes although not obviously larger, are reported to have fuller stomachs and better condition than those from less acid waters (Rosseland *et al.* 1980). These field observations are at variance with some laboratory studies and with the expected higher energy cost of living in acid waters. Growth in laboratory conditions of rainbow trout (*S. gairdnerii*), brown trout (*S. trutta*) char (*S. alpinus*), and brook trout (*S. fontinalis*) was reduced in acid conditions ($\mathrm{pH} < 5.5$) (Edwards & Hjeldenes 1977; Menendez 1976; Muniz & Leivestad 1979). Mount (1973) kept minnows (*Pimephales promelas*) in hard acid water over 13 months and showed reduced growth; however, excessive free $\mathrm{CO_2}$ may have been present. While bearing in mind the beneficial effects on growth of calcium and a steady temperature régime, test media should be controlled for these two variables. In only one study (Jacobsen 1977) were test fish fed a controlled diet, and kept in the same calcium concentrations; these fish (*S. trutta*) showed no differences in growth over a 48 day exposure to pH 6.26 and pH 5.

The age at which fish reach maturity, and their fecundity, is dependent on size, so that growth may have important effects on population strength and recruitment.

4. Other influences on populations

The literature on fisheries abounds in references to influences other than water quality or acidity which may affect population size or structure. Only some considered pertinent to the acidification hypothesis will be mentioned here: they could include potentially polluting industrial and agricultural activities in affected areas, winter kill in shallow stratified lakes, disease, and fisheries management.

(*a*) *Community analysis*

Evidence that many factors independent of acidity or associated water quality are important comes from analysis of mixed community lakes. Rahel & Magnusson (1983) have shown that for 138 Wisconsin lakes, interactions between species and biogeographic factors, rather than recent acidification, are probably responsible there for species absences. A frequency analysis of fish communities found in the acidified La Cloche lakes (Beamish 1974; Harvey 1975, 1982) provides some new insight (Henderson 1984). The habitat of a fish can be considered as a niche space defined by environmental variables that act as constraints. In any lake, the species complement includes species for which the environmental variables lie within the species constraint values. If these can be identified, we can predict the species likely to occur by examining the constraining variables for any lake or stream. This approach allows rigorous examination of factors that result in the observed fishery status, as well as a critical examination of historial records by checking for the past occurrence of expected species which are no longer present.

Table 4. Limiting environmental variables for common species in lakes of La Cloch region, Canada

(Source: Henderson 1983)

fish species	environmental requirements	limitation
Pumpkinseed	Ca > 4 mg l^{-1}	calcium
Yellow perch	Ca > 4 mg l^{-1}	
Northern pike	Ca > 5 mg l^{-1}, lake size 100 ha	lake morphometry
Brown bullhead	Ca > 5 mg l^{-1}, lake size 50 ha	acidity
Rock bass	pH > 4.6, lake size 80 ha	
White sucker	pH > 4.8, inlet–outlet stream	
Smallmouth bass	pH > 5.0, inlet–outlet stream	
Bluegill	inlet–outlet stream	
Bluntnose minnow	pH > 5.8	acidity
Johnnie darter	pH > 5.9	
Iowa darter	pH > 5.8	
Largemouth bass	difficult to state; lake size 190 ha but introduced to smaller lakes? Ca > 10 mg l^{-1}?	lake size
Walleye	pH > 5.2, lake size 190 ha	
Lake herring	not possible to define: possibly linked with lake size or depth	

Within the La Cloche data set, the niche space of common species can be defined by only 1 or 2 variables (table 4). This leads to a good match between observed and predicted species diversity (figure 5) in agreement with the analysis of species diversity against pH given by Harvey (1975, 1982). However, only three species (minnow and darters) appear to be constrained by acidity alone, and three (white sucker, rock bass and smallmouth bass) by acidity and lake morphology. Several species are identified as being constrained by calcium concentrations, consistent with laboratory studies on salmonid species. Predators (pike, bullhead, largemouth bass) are constrained by lake size, needed to supply adequate prey. An interesting implication is that acidification of large lakes (over 190 ha) to pH values between 4.6 and 5.2 may not be as destructive as a similar pH change in a small lake or pond. This analysis is also at variance with the historical record of species loss from Lake Lumsden, since some, such as burbot, would not be expected, even in the preacidification conditions.

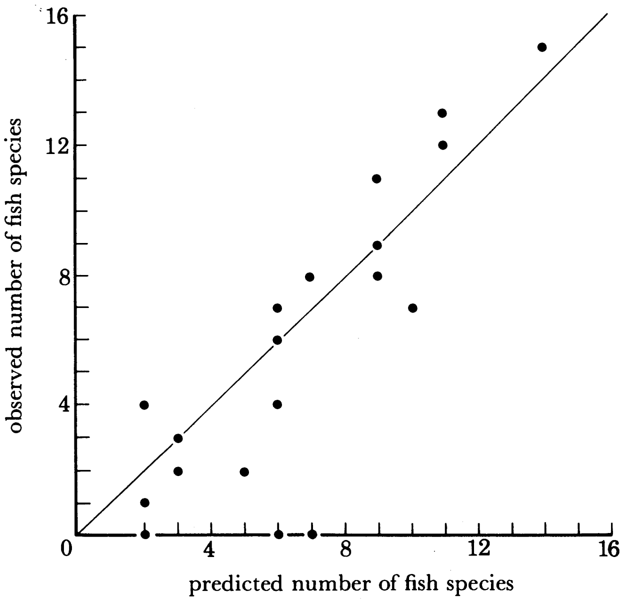

FIGURE 5. Comparison of observed with predicted number of fish species in La Cloche, Ontario, lakes. (Source: data of Beamish & Harvey 1972; Harvey 1982; Henderson 1984.)

Application of this approach to Swedish waters demonstrates that mixed species fish communities there are determined by similar environmental constraints (Henderson 1984).

(*b*) *Disease*

Disease can clearly bring about large changes in adult populations, from which recovery may be low or negligible. The loss (98%) of perch from Windermere in 1976 due to disease has not yet been made good from the present low level of population (Craig 1982). In contrast the low populations of 1950s, a consequence of heavy exploitation, did recover within 5–10 years. This long observation of a population is not matched elsewhere although there are some records of disease of trout (Dahl 1927) in the affected area of southern Norway presumably before acidification. The Atlantic salmon, known to have suffered a substantial decline in 1967–1968 from ulcerative dermal necrosis (u.d.n.) and since then from other disease agents, is considered more at risk from unsuitable river management and uncontrolled exploitation than any other factor (LeBlanc 1980).

(*c*) *Land use management*

There is historic and present evidence that streams draining afforested catchments are sometimes less than tolerable for salmonids (Huet 1951; Smith 1980; Harriman & Morrison 1982; J. H. Stoner *et al.* 1984). The reasons for change in fishery status associated with particular land use cannot be considered here in detail. However, the possibility exists that a change in catchment conditions affecting cation exchange or H^+ release associated with biomass changes is consistent with field observations (Rosenqvist 1981). In the higher altitude lakes of S Norway, a change on average in retention of only 12 meq m^{-2} a^{-1} in calcium, or release of 12 meq m^{-2} a^{-1} in H^+, would be sufficient to lead to water quality changes and associated effects on fisheries (Chester 1983).

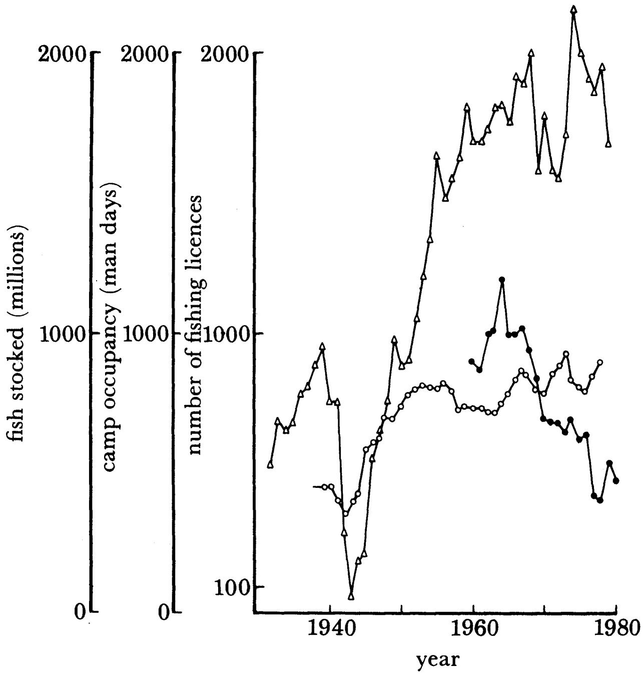

FIGURE 6. Relation between fish stocked and recreational fishery pressure in Adirondack N.Y. lakes, from 1940 to 1980, (fish stocked ●—●; camp occupancy △—△; fishing licences ○—○). (Source: data of Retszch *et al.* 1982.)

Increased input of acidity from the atmosphere, changes in biomass generated acidity, loss of calcium and greater release of aluminium as well as less stable hydrological conditions associated with forestry would all provide a less acceptable water quality for fisheries. The removal of riparian vegetation and stabilizing of stream flows has been shown to be beneficial to trophic structure, reproduction and growth of fish in a headwater stream (Schlosser 1982).

(*d*) *Fisheries management*

Few of the lakes and streams in acidified regions can be considered unaltered by man, even though formal management of the fishery is not practised. The extent to which unrecorded introductions of species or strains have been made, or their subsequent effects on the native community of species, will never be clear. In at least one instance, however, there is a detailed stocking history covering decades. In the Adirondack Lakes, New York, fishery problems were identified as early as 1860 and steps taken to introduce and maintain desired species by provision of stock from hatcheries. The growth of hatcheries and their production increased to a peak about 1960; since that time it has fallen sharply while exploitation has been steady or even increasing (Retszch *et al.* 1982) (figure 6). There is indication that some upland rivers of S Norway were restocked with trout about 1930 (Sunde 1936).

Clearly, the fishery status of affected lakes has to be considered in the light of such management practices; fishery changes in Adirondack lakes cannot be attributed to changes in acidity alone and are confounded by major alterations in stocking practice (Pfeiffer & Festa 1980). The extent to which other acid lakes might be affected by changes in stocking has not been reported.

5. Summary

Water quality and fisheries

The hypothesis that surface water acidification is responsible for loss of fisheries in affected waters depends on demonstration that fishery status is determined by the acidity and related chemistry of the lakes and rivers. While acute laboratory tests, which involve transfer of fish from circumneutral media to more acid test media, result in mortality, the effect of acidity on fish is moderated by the presence of sufficient calcium; further, aluminium is potentially toxic and its effect in turn is moderated by calcium or chelating agents. This interaction explains why no simple acid 'threshold' or 'acceptable pH' can be set for the survival of any species. A dose–response function for acidity must include terms to accommodate the benefit of calcium and the detriment of aluminium. Since sensitivity to both acidity and aluminium toxicity varies with age in a complex way, such a function must be derived for different life stages.

A difficulty in demonstrating an association in the field between acidity and fisheries is that few data sets provide concurrent information on both water quality and fishery status, and for those available, a consistent picture may not emerge, possibly because of inadequacies of data (e.g. single water samples), or natural differences between data sets (e.g. different water chemistry and different fish communities) but possibly because a single explanation, i.e. acidification, is inappropriate for all affected locations.

Estimates of critical pH values for any species are limited by inadequate data, and by differences of up to 400 fold in the reputed thresholds for pH effects. Site specific differences in water quality or other conditions may explain why viable populations of some species are found in relatively acid waters, and why fish losses have sometimes occurred at levels of pH not judged toxic from laboratory studies.

The shortcomings of laboratory bioassay (lack of experimental control, poor specification of test conditions, too few species and life stages) and of field data, especially during episodes, limit tests of the hypothesis that acidification has led to loss of fisheries.

Other factors

Acid lakes often retain fish populations, albeit small and lacking in species diversity. Physical, chemical and biological factors are all important influences. The extent to which other environmental variables may affect fish populations in acid oligotrophic waters is quite uncertain on present evidence. Unsuitable stream conditions associated with afforestation, and with unstable hydrological régimes, may limit any benefit to be gained from remedial measures designed to improve water quality.

This paper is published by permission of the Central Electricity Generating Board. I should like to thank colleagues and others for their helpful comments.

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Discussion

N. Christophersen (*Institute for Informatics, Oslo University, Oslo, Norway*). In Dr Howells's list of options for measures that could be taken to improve freshwater chemistry, no mention was made of reductions in emissions of sulphur and nitrogen compounds. I should like her comments on this point.

Gwyneth D. Howells. Since the relationships of sulphur and nitrogen emissions, rain chemistry and surface water are so uncertain, there can be no assurance that reductions would have the desired effect. What level of reduction is needed to provide tolerable levels of pH, calcium and aluminium? Present knowledge demonstrates that a change of land use and control of variable hydrology could improve water quality, and restocking with more tolerant species of strains could re-establish fisheries at least in some lakes. Together with liming, these are practical measures available in the short term.