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Effects of Aluminium in Acidified Aquatic Ecosystems



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P.O. Box 89, Korsvoll	Televeien 1	Rute 866	Thormøhlensgt 55	Søndre Tollbugate 3
N-0808 Oslo 8	N-4890 Grimstad	N-2312 Ottestad	N-5008 Bergen	N-9000 Tromsø
Norway	Norway	Norway	Norway	Norway
Phone (47 2) 18 51 00	Phone (47 41) 43 033	Phone (47 65) 76 752	Phone (47 5) 32 56 40	Phone (47 83) 85 280
Telefax (47 2) 18 52 00	Telefax (47 41) 44 513	Telefax (47 65) 78 653	Telefax (47 5) 32 88 33	Telefax (47 83) 80 508

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Rosseland, Bjørn Olav	NIVA	
Brandrud, Tor Erik	NIVA	
Raddum, Gunnar G.	University of Bergen	
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Abstract:
In the acidic aquatic environment, pH, aluminium and calcium are still the three most important factors to explain losses of biota. The inorganic (labile) monomeric species of aluminium acts as a toxic agent on gill-breathing animals such as fish and invertebrates, by causing loss of plasma and haemolymph ions leading to osmoregulatory failure. A series of different effects on all levels of organization within an organism are described, as well as important population responses. In contrast to the situation for invertebrates and fish, the aquatic macrophytes seems to tolerate high concentrations of aluminium. The macrophytes appear thus to be much more sensitive for other chemical factors which changes during acidification, especially the shift from bicarbonate- towards direct CO ₂ -uptake as primary source for carbon.

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Bjørn Olav Rosseland

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Bjørn Olav Rosseland¹

Tor Erik Brandrud¹

Gunnar G. Raddum²

¹ Norwegian Institute for Water Research
P.O. Box 69 Korsvoll, N-0808 Oslo, Norway

² Zoological Museum, University of Bergen
N-5007 Bergen

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FOREWORD

In April 1991, the United Nations, Economic Commission for Europe, UN-ECE, sent a request to the Norwegian Institute for Water Research, NIVA, to prepare a technical paper on the effects of acidification on the terrestrial and aquatic environment. In a letter of May 2nd 1991, NIVA proposed to prepare a two-stage technical paper concentrating on the effects of aluminium in the aquatic environment; first step by reviewing the literature up to the Glasgow 1990 Conference, and second step by integrating the papers from the Glasgow Conference Proceedings and the articles from the conference to be published in a special issue of Environmental Pollution, both being published in Autumn 1991.

On May 29th, 1991, NIVA received a contract from the UN-ECE, for the preparation of the first-step article:

"Preparation of a draft technical report on effects of acidification (approximately 25 to 30 pages) on aquatic ecosystems and biota, analysing inter alia long-term trends on:

- aluminium effects in fish
- invertebrates
- aquatic vegetation"

The draft technical paper, "Effects of aluminium in acidified aquatic ecosystems", was finished on June 23th 1991.

Due to extremely long publication period, the last issue of the journal "Environmental Pollution" containing articles from the Glasgow Conference, was received at NIVA in August 1992. This final report then include all relevant papers from the proceedings, as well as new literature from the period between these two reports.

Oslo, November 12, 1992



Bjørn Olav Rosseland
Professor, dr. philos
Head of Research Department for Environment Technology.

ABSTRACT

Aluminium (Al) when present in high concentrations, has for long been recognized as a toxic agent to aquatic freshwater organisms, i.e. downstream from industrial point sources of Al-rich process water. Today the environmental effects of aluminium are mainly a result of acidic precipitation; acidification of catchments leads to increased Al concentrations in soil solution and freshwaters. Large parts of both the aquatic and terrestrial ecosystems are affected.

In the acidic aquatic environment, pH, aluminium and calcium are still the three most important factors to explain the losses of biota. Since aluminium concentrations always increases in waters being acidified, the ecological role of H^+ and Al alone is difficult to separate. Laboratory studies where the effects of each factor can be separated, have, however, made comparison possible.

Aluminium acts as a toxic agent on gill-breathing animals such as fish and invertebrates, by causing loss of plasma and haemolymph ions leading to osmoregulatory failure. In fish, the inorganic (labile) monomeric species of aluminium reduce the activities of gill enzymes important in the active uptake of ions. Where waters of different qualities (especially acid and neutral) are mixed to form a new chemical composition, aluminium transformation processes in these mixing zones might create an increased toxicity of the water to fish. These phenomena do explain the extreme toxicity often seen in connection to episodes in nature, thus having serious implications on the ecological structure in the affected areas.

In contrast to the situation for invertebrates and fish, the aquatic macrophytes seems to tolerate high concentrations of aluminium. The macrophytes appear thus to be much more sensitive for other chemical factors which changes during acidification, especially the shift from bicarbonate- towards direct CO_2 -uptake as primary source for carbon.

In addition to the great changes occurring on biotic species and population levels in acidified areas, aluminium seems also to accumulate in freshwater invertebrates as well as in plants. Dietary organically complexed aluminium, may easily be absorbed and interfere with important metabolic processes in mammals and birds. Aluminium contaminated invertebrates and plants might thus be a link for aluminium to enter into terrestrial food chains.

INTRODUCTION

It has been known for many years that high aluminium concentrations in waters polluted by industrial sources are toxic to invertebrates and fish (Penny and Adams 1863, Weigelt *et al.* 1885, Thomas 1915, Ebeling 1928, Oshima 1931, Ellis 1937, Sanborn 1945, Pulley 1950, Murdock 1953, Wallen *et al.* 1957, Jones 1964, Dickinson Burrows 1977, Hunter *et al.* 1980, Lamb and Bailey 1981). It is the acidification caused by acid rain, however, that has caused the ecological significance of aluminium toxicity.

Acidic waters have been recognized as a problem for freshwater fisheries in certain regions of Norway since the 1920's (Dahl 1927). Forty years later a linkage between acidic waters and pH of precipitation was hypothesized (Dannevig 1959). Aluminium (Al) as a main toxic element in acidic waters was recognized nearly twenty years later (Schofield 1977, Dickson 1978, 1979). Today the three elements, H⁺ (pH), Al and Ca, are still considered to be most important for the toxicity of acid water to freshwater biota (Wood and McDonald 1987, Exley and Phillips 1988, Henriksen *et al.* 1989, Howells *et al.* 1990, Rosseland and Henriksen 1990, Rosseland *et al.* 1990, Spry and Wiener 1991, Rosseland and Staurnes 1993, Bulger *et al.* 1993).

Acidification has caused a wide range of changes in the aquatic vegetation, but none of these changes have so far been attributed to aluminium (Farmer 1990, Maessen *et al.* 1992). Both pH and aluminium, however, have been documented to have a variety of effects on invertebrates and fish. Freshwater invertebrates disappear in acidic waters as a response to low pH and aluminium (Herrmann 1987a). In addition, bioaccumulation of aluminium in invertebrate prey organisms has been suggested as a possible explanation for the impaired hatching success observed among birds (Nyholm 1981, Hussein *et al.* 1988, Rosseland *et al.* 1990). Recent experiments have demonstrated that dietary fed aluminium citrate at concentrations lower than found in invertebrates in acidified areas, can reduce eggshell thickness and cause reproduction failure in birds (Wolff and Phillips 1990). However, a recent review by Tyler and Ormerod (1992) points to the documented low serum calcium in dippers from acidified areas, caused by a low calcium diet, being the most probable explanation to reduced eggshell thickness.

The biological significance of Al-speciation and the toxicity of the monomeric labile Al-species on fish was demonstrated by Driscoll *et al.* (1982). Henriksen *et al.* (1984) demonstrated their relevance during episodic changes in water quality occurring in streams and rivers, and Rosseland *et al.* (1992) have demonstrated the increased Al-toxicity that occurs in mixing zones between acid and neutralized streamwaters.

These effects of aluminium depend not only on animal species, but also on the life history stage of the animals. In nature, the effects of aluminium alone are difficult to isolate from a variety of potentially interrelated adverse factors. Large variations in pH, Al-species distribution, calcium and other metals and ions relevant for biological response do occur especially during episodes of high waterflow, and in lakes and streams where different water qualities mixes, (Henriksen *et al.* 1984, Skogheim *et al.* 1984, Gagen and Sharpe 1987, Lacroix and Townsend 1987, Rosseland *et al.* 1992, Rosseland and Hindar 1991). The

situation is made even more complex by the fact that the organisms themselves strongly influence their chemical microenvironment near their body surface (i.e. along the gills (see Playle and Wood 1989, 1990, Exley *et al.* 1991). The basic chemistry of the external water will therefore not necessarily represent the true toxic components relevant to the fish. Our knowledge today about an exact chemical threshold level for a certain physiological response, might therefore be based on wrong assumptions.

Calcium has a fundamental biological importance for water breathing animals. The Ca^{2+} -ion is a key factor in the permeability of all membranes, including gill epithelium. In many acidified areas, the calcium concentration is so low that it is close to the concentration limit for soft water tolerant salmonid species. In such areas, one must be aware of any substance having an adverse effect on the Ca metabolism.

In the laboratory, the effects of aluminium *per se* can be studied at given levels of pH, Ca and other variables. The results from such studies will also be used below, focusing on specific responses to Al.

In many cases, a specific response is related to certain species of aluminium, i.e. the monomeric inorganic species also termed "labile Al" (LAI). In such cases, the separation technique of Driscoll (1984) with or without minor modifications (Schecher and Driscoll 1987, 1988), and the hollow fiber technique separating the inorganic monomeric Al species of different molecular size (Lydersen *et al.* 1987), has been used.

EFFECTS OF ALUMINIUM AND ACIDIFICATION ON AQUATIC MACROPHYTES

Acidification has been reported to cause a wide range of changes in the aquatic vegetation, none of which is believed to be due to toxic levels of aluminium *per se* (Farmer 1990, Maessen *et al.* 1992). However, very little is known about the critical loads of aluminium for aquatic macrophytes.

Many aquatic plants, especially the bryophytes, are able to accumulate very high levels of aluminium (and other metal ions) without showing signs of injuries (Farmer 1990, Sprenger & McIntosh 1989). Some acidophilic species such as *Sphagnum subsecundum* and the liverwort *Jungermannia vulcanicola* have been found to contain aluminium concentrations of 5-9 % of tissue dry weight (Farmer 1988, Satake *et al.* 1984). Both submerged *Sphagnum* spp. and *Jungermannia vulcanicola* show increased aluminium accumulation with increased acidification/Al-levels in the water (Denton and Oughton 1992, Satake *et al.* 1984). It is well known that the leaf surfaces of *Sphagnum* mosses have a very efficient ion exchange capacity (Clymo 1973), taking up cations such as Al^{3+} in exchange with H^+ . The submerged *Sphagnum* species may thus actively contribute to the acidification of lakes (Hendrey 1982), at the same time as some portion of the aluminium in the lake probably becomes immobilized in the slowly decomposing *Sphagnum* -rich sediment.

In ecosystems with naturally high aluminium concentrations such as the tropical rainforest, the plants cope with the potentially toxic aluminium levels in two diametrically opposite ways. Some species manage actively to prevent the aluminium to enter the plant tissue, while others accumulate the metal in a non-toxic form (Andersson 1988). The latter seems to be a

common and successful strategy also among the acid-tolerant aquatic macrophytes.

Due to the very limited knowledge of the possible effects of (very) high aluminium levels on aquatic macrophytes, it seems natural to extend the present review to also consider some general effects of acidification: What are the impacts on aquatic vegetation, and how can they be explained?

The major effects of acidification on aquatic macrophytes seem to be at the ecosystem level. Although a shift in community structure and species composition is fairly often reported, the processes involved are not well understood. The following more or less documented general effects on the vegetation may be distinguished:

Vegetation of soft water lakes and slow flowing rivers.

The species diversity decreases with increasing acidity (Rørslett 1991, Brandrud & Mjelde 1992). Elodeid (long shoot) vegetation disappears in moderately acidified lakes already at a pH < 5.5 (-5.0) (Arts 1990a, Brandrud & Mjelde 1992), while isoetid (short shoot/rosette) vegetation has been reported to disappear from acidified, shallow lakes of pH < 5.0 in certain parts of Europe, especially in the Netherlands (Farmer 1990, Arts *et al.* 1989, Roelofs 1983). However, in other acidified parts of Europe, especially southernmost Norway and North America, this latter character element of soft water lakes is intact and thriving at pH 4.4 - 4.5 (Brandrud & Mjelde 1992, Rørslett and Brettum 1990, Heitto 1990, Hunter *et al.* 1986, Catling *et al.* 1986, Roberts *et al.* 1985).

The graminid species *Juncus bulbosus* and the submerged *Sphagnum* moss species *S. auriculatum* (= *S. denticulatum*) and *S. cuspidatum* are reported to form extensive mats covering the soft bottoms of a number of acidified lakes in Northern and Western Europe (Grahn 1977, 1986, Roelofs 1983, Arts 1990b). In acidified areas of North America, however, such vegetation changes have been observed only to a very small degree (Schindler 1993). Development of dense algal mats have been reported from both continents (Grahn 1986, Schindler 1993).

Vegetation of rapid flowing rivers and streams.

According to observations from the British Isles and Norway, the majority of stone-inhabiting mosses such as the *Fontinalis* species becomes rare or disappears in moderate acidified rivers of pH < 5.5 (-5.0) (Ormerod *et al.* 1987a, Brandrud & Mjelde 1992). The aquatic mosses are replaced by the acidophilic liverworts *Nardia compressa*, *Scapania undulata* and *Marsupella emarginata* in acidified rivers and streams (Ormerod *et al.* 1987a, cf. also Satake *et al.* 1989).

Possible explanations for the vegetation changes.

The observed vegetation effects and changes seems largely to be explained by the use of different sources of inorganic carbon by the different species groups. The elodeids are all more or less dependent on HCO₃⁻ for their inorganic carbon uptake (Maberly and Spence 1983), and therefore dominate in alkaline and neutral waters with high carbonate content. They disappear when the pH is lowered to ca. 5.5, where the CO₂/HCO₃⁻ equilibrium is

shifted completely in the direction of CO₂. The lack of the "bicarbonate species" may to a large degree explain the low species diversity in acid waters, although such an explanation must be combined with others, for instance the dominance of unfavourable soft, organic, anaerobic bottoms in acidic lakes.

The acidophilic species such as *Juncus bulbosus* and submersed *Sphagnum* spp. are all characterized by a CO₂ uptake directly from the water column. These plants seem to be strongly favoured by the elevated CO₂ levels in waters undergoing acidification, especially above organic bottoms where ample CO₂ is produced by the decomposers (Roelofs *et al.* 1984, Paffen & Roelofs 1991, Grahn 1988). However, during a long term acidification process, the sediment also become acidified, which reduces the decomposition rates and the CO₂ production. The CO₂ concentration in the water column may thus be depleted to pre-acidification levels. This may explain why a marked short-term increase in abundance later can be followed by a reduction to more normal levels of these acidophilic/acid-tolerant species (Brandrud & Mjelde 1992, Roelofs pers. comm.). The often rather conflicting results and theories on macrophyte development in acidified lakes (cf. Schindler 1993) may also probably be explained by such differences/fluctuations in the inorganic carbon supply of the lakes.

The observed decrease in the isoetid vegetation in acidified lakes can hardly be explained directly by changes in carbon supply. These species are based mainly on CO₂ uptake from the sediments (Farmer 1990), and with their slow growth rate, they seem to be able to persist even at low CO₂ levels. In situ observations and laboratory experiments indicate that these species may sustain their normal growth rates at pH > 4.0 (Johansen & Brandrud 1992, Laake 1976). However, reduced vitality and finally disappearance has been observed when the isoetids have become overgrown by epiphytic algae, *Juncus* or *Sphagnum*, all of which are species able to take advantage of the high CO₂ levels in acidified waters .

EFFECTS OF ALUMINIUM ON INVERTEBRATES

Acidification has generally been accompanied by declining numbers and biomass of both planktonic and benthic invertebrates (Leivestad *et al.* 1976, Haines 1981, Hörnström *et al.* 1984, Økland and Økland 1986, Meriläinen and Hynynen 1990, Sarvala and Halsinaho 1990). However, the mechanisms by which aluminium *per se* can act as a harmful agent on these organisms are largely unknown (Herrmann 1987a).

Hörnström *et al.* (1984) and Sarvala and Halsinaho (1990), indicated that aluminium could affect the zooplankton community in acidified surface waters. On adding aluminium to an acid stream, Hall *et al.* (1985, 1987), Raddum and Fjellheim (1987) and Ormerod *et al.* (1987b) and Merrett *et al.* 1991) observed an increased drift of mayfly nymphs, chironomids and dipterid midges. Many animals related to the surface film were found dead in drift samples, presumably caused by reduction of surface tension; this was indicated by a pronounced foam production connected with elevated aluminium concentrations (Hall *et al.* 1985, Ormerod *et al.* 1987b). Al-induced mortality of stoneflies, the isopod *Asellus* and caddis larvae was reported by Burton and Allan (1986), who also demonstrated a reduced mortality whenever the organic content of the water was high. The counteracting effect of humic acids relative to Al-toxicity was also demonstrated by Petersen *et al.* (1986) on

blackfly larvae, by Sarvala and Halsinaho (1990) on crustacean zooplankton, and by Kullberg (1992) on benthic stream communities.

Raddum *et al.* (1984) noted low abundance of benthic invertebrates in the deeper part of a lake after liming. It was suggested that possible precipitation of Al-complexes in the sediments (Dickson 1983, Wright and Skogheim 1983) could be responsible for the negative development of chironomids in the profundal compared with the littoral and sublittoral zone. Effects of such AL-complexes were also thought to affect the ephememerid fauna in running water during episodes with increasing pH (Engblom and Lingdell 1983). Recent investigations of mixing zones of acid and non acid water have shown that these zones are very toxic to fish (Rosseland *et al.* 1992). Lime on sediments can create mixing zones in the microhabitat and put the suggestions mentioned above in a new perspective.

Meriläinen (1988) investigated an estuary receiving river water which in periods had elevated concentrations of monomeric inorganic aluminium. He concluded that the periods with acidic and aluminium-rich water were the main reason for the low benthic biomass and the reduced diversity in the acidic freshwater area of the estuary.

Not all invertebrate species tested have shown high sensitivity to aluminium. No additional mortality of aluminium was observed on bivalves and gastropods (Mackie 1986) or crayfish (Berrill *et al.* 1985) in acidic waters. Appelberg (1985), however, demonstrated reduced haemolymph Na^+ content in crayfish exposed to acidic aluminium-rich waters. At very low pH, high concentrations of aluminium can have an ameliorating effect, on for example mayfly nymphs (*Heptogenia sulphurea*) (Herrmann 1987a) and small planktonic crustacean (*Daphnia magna*) (Havas 1985, Havas and Likens 1985). The mechanisms involved might be the same as found for fish (see below), but in both cases the actual concentrations of aluminium are much higher than normally found in acidic waters containing these organisms.

Raddum and Steigen (1981) found that the caloric content of stoneflies and caddisflies from acidic rivers was lower than from more neutral rivers; this implies an increased energy consumption (metabolism) in acidic waters. Increased respiration was later demonstrated to be a response to aluminium, highly pronounced for the most sensitive mayfly species (Herrmann and Andersson 1986). As is the case with fish (Rosseland 1980, Leivestad *et al.* 1987)), pH alone seemed less important for the respiratory response.

Aluminium can also impair reproduction, shown on *Daphnia magna* (Beisinger and Christensen 1972).

Otto and Svensson (1983) suggested that, as in fish, aluminium affects invertebrates by disturbing osmoregulation. Malley and Chang (1985) showed a reduced Ca^{2+} uptake when exposed to aluminium-rich water. In *Daphnia magna*, aluminium reduced the Na^+ influx and to a lesser extent increased the outflux, thus impairing osmoregulation (Havas and Likens 1985). The temporal reduced outflux at low pH might explain the reported beneficial effects of aluminium at low pH. Witters *et al.* (1984) demonstrated a reduced haemolymph Na^+ content in *Corixa* exposed to high Al-concentrations, and Herrmann (1987b) found that aluminium caused a reduced Na^+ content of mayfly nymphs at low pH. Sutcliffe and Hildrew (1989) says that in mountain areas where concentrations of sodium can be well below $100 \mu\text{equiv l}^{-1}$, hydrogen and aluminium will be completely dominant. Due to

their relatively small size and high mobility, they may be transported inwards across the gills instead of sodium, potassium or calcium in invertebrates. This will disturb the normal internal equilibrium with fatal loss of vital ions from blood and tissue.

As with fish, aluminium acts on the respiratory and osmoregulatory organs of invertebrates, for example the anal papillae of the phantom midge (Havas 1986). This might explain why air-breathing invertebrates like the waterboatmen (*Corixa*) are very tolerant to acidic waters (Vangenechten *et al.* 1979, Witters *et al.* 1984).

Aluminium can accumulate in the bodies of invertebrates living in acidic waters (Hall and Likens 1981, Nyholm 1982, Herrmann 1987a). Many insects with aquatic larvae and nymph stages can leave their previous body metal pool in their excuviae on emerging (Young and Harvey 1988). The aquatic stage in their life history may therefore be the most metal-contaminated stage. The amount of contaminated aluminium and heavy metals in insect larvae as well as adults, however, is dependent on acidity and oxygen concentration of the sediments (Young and Harvey 1988).

On the other hand, examples of decreased concentration of aluminium have been observed in the food web, starting with periphyton through zooplankton to fish (King *et al.* 1992). This decrease in metal content in tissue of organisms is called biopurification and is the opposite of the more common biomagnification. In a review paper of Wren and Stephenson (1991), the conclusion is that aluminium does not biomagnify in aquatic environment and that aluminium in natural good water quality generally afford little risk of toxicity to invertebrates. However, in water with decreased pH, aluminium concentrations usually increase and coupled with reduced pH at certain levels the water will be toxic to sensitive invertebrates.

Birds such as the pied flycatcher (*Ficedula hypoleuca*), which lives on insects in or close to acidic lakes, have been reported to have high Al-concentrations in bone marrow and eggs indicating a food-chain transport (Nyholm and Myhrberg 1977, Nyholm 1981, 1982). The impairment of egg hatching of these birds have therefore been hypothesized to be caused by this bioaccumulation. Whether the impairment of egg hatching caused by reduced eggshell thickness is related to Al-accumulation or other changes in the environment, is still under debate. A recent review by Tyler and Ormerod (1992) points to that the documented low serum calcium found in dippers (*Cinclus cinclus*) from acidified upland streams in Wales, was most probably caused by a low calcium diet. This low serum calcium in female dippers then resulted in a reduced eggshell thickness and hatching success. Aluminium was not mentioned as a possible link to these disturbances.

However, in spite of some discrepancies in results, several feeding experiments have pointed to a possible role of aluminium for these environmental changes. Feeding experiments, using aluminium sulphate enriched food at Al-concentrations similar to the one found in insects from acidified areas, did not affect growth or reproduction of Ring doves *Streptopelia risoria* (Carriere *et al.* 1986). In similar dietary experiments with Japanese quail (*Coturnix coturnix japonica*), however, the eggshell thickness have been reduced (Hussein *et al.* 1988). Experiments using dietary fed aluminium citrate at concentrations lower than found in invertebrates in acidified areas, have also shown reduced eggshell thickness and caused reproduction failure in Japanese quail (Wolff and Phillips 1990). We know from experiments with mammals that aluminium interfere with the Ca regulatory system and can disturb calcium homeostasis. Al also binds to calmodulin, which is a multifunctional, Ca-dependent

protein regulating a variety of cellular reactions, including regulation of many enzymes (Ganrot 1986).

Based on the results from Sweden (Nyholm and Myhrberg 1977, Nyholm 1981, 1982), and some of the feeding experiments, the impairment of egg hatching of these birds might therefore to some extent link the environmental problems of aluminium appearing in the acidic aquatic ecosystem to the terrestrial ecosystem.

EFFECTS OF ALUMINIUM ON FISH

For a long period of time, pH (H^+) alone was considered to be toxic at the egg stage (Day and Garside 1977, 1979, 1980, Leivestad *et al.* 1976, Peterson *et al.* 1980, Shepard 1987), with an increasing influence of aluminium with age after hatch (Baker and Schofield 1980, 1982, Wood and McDonald 1982). More recently, however, it has been demonstrated that aluminium reduces both ion uptake at the eyed-egg stage and the activity of Na-K-ATPase in the embryo (Leivestad *et al.* 1987, McWilliams 1990, McWilliams and Shepard 1989, 1991, Shepard 1988, Shepard and McWilliams 1989).

Al and pH are known to interfere with whole body mineral content and skeletal calcification at the embryo and fry stage (Sayer *et al.* 1991). Recent studies on strain of brown trout having different sensitivity to acid waters (Sadler and Lynam 1989a, 1989b, Dalziel and Lynam 1991, Kroglund and Rosseland 1992, Kroglund *et al.* 1992) seem to indicate differences in calcification rate at the alevin stage (Sadler *et al.* 1990) as a possible key to understand these strain differences. In spite of a comparable total body Ca, the most resistant strains had the lowest calcification rate of finrays and skeletal. This phenomenon might thus indicate an important resistant mechanism for embryo survival before swimup, giving priority to a high plasma/serum Ca to ensure Ca homeostasis.

After hatch, the main target organ for the Al-effects is the gill where the ion and gas exchange takes place. In addition to the effects of H^+ , aluminium causes loss of plasma ions (Na^+ , Cl^-), reduced osmolarity, increased hematocrit, reduced oxygen tension and increased CO_2 pressure (hypercapnia) in the blood (Muniz and Leivestad 1980, Rosseland 1980, Rosseland and Skogheim 1982, 1984, 1987a, 1987b, Rosseland *et al.* 1986a,b, 1991, Fivelstad and Leivestad 1984, Neville 1985, Neville and Campbell 1988, Witters 1986, Jensen and Weber 1987, Ormerod *et al.* 1987c, Vangenechten *et al.* 1987, Witters *et al.* 1987, 1990, 1991, Leivestad *et al.* 1987, Wood and McDonald 1987, Booth *et al.* 1988, Vuorinen *et al.* 1992).

In acidic waters (pH 4.6 - 5.3) with low levels of calcium (0.5 - 1.5 mg Ca/l), inorganic monomeric aluminium between 25 - 75 $\mu g/l$ is toxic (Henriksen *et al.* 1984, Rosseland 1989, Rosseland *et al.* 1986a, Rosseland and Skogheim 1987, Skogheim and Rosseland 1986). The Al-induced ion loss reflects both an increased outflux and a decreased influx of ions (Dalziel *et al.* 1986, 1987, Wood and McDonald 1987, Wood *et al.* 1988, McWilliams 1990, McWilliams and Shepard 1991). The effect on influx is probably caused by a reduced activity of enzymes such as Na-K-ATPase, Mg-ATPase and carbonic anhydrase (Staurnes *et al.* 1984, Kjartansson 1984, Leivestad *et al.* 1987, Reite and Staurnes 1987, Rosseland *et al.* 1992). Aluminium acts specifically on the enzymes of the gill, as neither the ATPase systems in the pseudobranch or the kidney was affected (Kjartansson 1984). The Al-induced efflux is considered to reflect modifications on opening

of the tight junctions of the paracellular channels (Wood and McDonald 1987, Exley *et al.* 1991). The ameliorating effect of Ca on Al- and pH response (Leivestad *et al.* 1980, Brown 1982, 1983, McDonald *et al.* 1983, Shephard 1988, McWilliams 1990, McWilliams and Shephard 1991, Rosseland 1989) is probably by tightening of the junctions, thereby preventing the passive loss of ions (Wood and McDonald 1987).

Populations of perch (*Perca fluviatilis*) shows a higher tolerance to pH and aluminium in lakes with high organic content (TOC) (Henriksen *et al.* 1989, Hesthagen *et al.* 1992). The ameliorating effect on aluminium toxicity of organic substances like humic acids and citrate (Baker and Schofield 1982, Driscoll *et al.* 1980, Hulsman *et al.* 1983, Rosseland and Skogheim 1987b, Leivestad *et al.* 1987, Witters *et al.* 1990), as well as silicon (Birchall & Chappel 1989, Birchall *et al.* 1989, Exley 1989), is due to these substances ability to chelate the inorganic monomeric aluminium, thus reducing the concentration of the toxic aluminium fraction.

The explanation of how Al affects the gill, have to take into account basic chemical properties of Al, basic properties of the gill epithelium and its surface microenvironment, as well as what is known about how Al interfere with basic biochemical and physiological functions. Fish exposed to acidic Al-rich waters will accumulate aluminium on the gill surface (Schofield 1977, Schofield and Trojnar 1980, Muramoto 1981, Buerger and Soltero 1983, Pagenkoff 1983, Skogheim *et al.* 1984, Neville 1985, Karlsson-Norrgren *et al.* 1986a,b, Harvey and McArdle 1986, Witters *et al.* 1987, Wood and McDonald 1987, Jagoe *et al.* 1987, McCahon *et al.* 1987, Youson and Neville 1987, Playle and Wood 1989, 1990, Rosseland *et al.* 1992, Vuorinen *et al.* 1992). Important biochemical properties of the gill epithelium for the explanation of Al precipitation and binding, are its net negative charge, the glycoproteins and sialic acid in mucous, the phosphate groups on membrane phospholipids, carboxylate groups on the membrane proteins, and the binding structure of membrane transport proteins (McDonald 1983, Exley and Phillips 1988, Exley *et al.* 1991). Of crucial importance is also the fact that the gill boundary layer closest to the epithelium, is both chemically and physically dissimilar to water outside this layer. The chemistry of boundary layer is very much influenced by the organism itself.

The precipitation and accumulation of aluminium onto the gill is due to the negative charge of the mucus caused by sialic acid residues (McDonald 1983), and the chemical changes occurring in the gill micro habitat during respiration (Wright *et al.* 1986 Playle and Wood 1989, 1990, Exley *et al.* 1991, Rosseland and Staurnes 1993). The gill also serves as an excretion organ for ammonia (NH_4^+) (Masoni and Payan 1974). At low pH and high aluminium, the reduced blood pH (acidosis) and increased CO_2 (hypercapnia) will interfere with the formation from ammonium (NH_3) to ammonia, thus more is excreted as NH_3 . At the interface between mucus and water, the ammonium will be transformed to ammonia, changing the pH and thus enhancing precipitation of aluminium at the gill surface (Wood and McDonald 1987). In low pH waters, inorganic monomeric aluminium will occur mainly on low molecular weight forms (Lydersen 1992, Lydersen *et al.* 1990a, 1990b, 1992, Oughton *et al.* 1992, Rosseland *et al.* 1992). When pH raises, f. eks. when acid Al-rich water mixes with limed or neutral waters, low molecular inorganic forms of aluminium will be transformed to high molecular weight forms and hence precipitate (Lydersen *et al.* 1992, Oughton *et al.* 1992). In such mixing zones, rapid Al-precipitation onto fish gills, osmoregulation failure, and gill lesions have been observed, the water in the mixing zone being more toxic than the original acid water (Rosseland *et al.* 1992, Polò *et al.* 1993). The process which occur in the

gill micro environment, enforcing the precipitation of aluminium onto the gill (Playle and Wood 1989, 1990, Exley *et al.* 1991), is probably the same process (changes in molecular size of the inorganic monomeric Al) which occur in mixing zones (Rosseland *et al.* 1992). Since Al-polymerization kinetics is temperature dependent (Lydersen *et al.* 1990b, 1992), it is not surprising that Al-toxicity is reduced at low temperatures (Polèo *et al.* 1991, Polèo 1992).

In nature, the increased aluminium toxicity occurring in mixing zones is a problem connected to areas where acid groundwater enters neutral or limed lakes or rivers (Norton and Henriksen 1983), acid tributaries enters a neutral or limed river (Skogheim *et al.* 1984, Rosseland *et al.* 1992), and in hatcheries with inappropriate neutralized water with short retention time post treatment (Rosseland and Hindar 1991).

There are species and strain differences in sensitivity to low pH (Grande *et al.* 1978, Gjedrem 1980, Robinson *et al.* 1976, Swarts *et al.* 1978) and aluminium (Dalziel and Lynam 1991, Kroglund and Rosseland 1992, Kroglund *et al.* 1992, Rosseland and Skogheim 1984, 1987a, 1987b, Rosseland and Staurnes 1993, Rosseland *et al.* 1986b, 1990, 1992, Sadler and Lynam 1989a, 1989b, Sadler *et al.* 1990, Wood and McDonald 1987). These species differences are also reflected in the accumulation rate of aluminium onto the gills, as well as the whole body (wb) ion concentration, i.e. fish with the lowest wb Na (greatest loss) have the highest Al-concentration on the gill surface (Wood and McDonald 1987). Although strain differences in sensitivity have been documented for many fish species, such differences have not been observed in experiments with Atlantic salmon (Kroglund *et al.* 1990) and American bullhead (*Ictalurus nebulosus* (Le Sueur)) (Bogaerts *et al.* 1991).

Precipitated Al-complexes can irritate the gill and cause inflammation, oedema, swelling and sometimes irradiation of the secondary lamella (Schofield 1977, Schofield and Trojnar 1980, Karlsson-Norrgren *et al.* 1986a,b, Jagoe *et al.* 1987, Playle and Wood 1989, 1990, Rosseland *et al.* 1992). Also an increased number of mucus cells (Linnenbach *et al.* 1987) and chloride cells (Jagoe *et al.* 1987, Jagoe and Haines 1990) have been observed relative to Al-accumulation onto the gills. In spite of high Al-concentration on the gill these histopathological changes are not observed when the humus content in the water is high, indicating a labile Al-dependent irritation (Karlsson-Norrgren *et al.* 1986b).

What actually is the dominating or most important of these processes outside the cells; hydroxide precipitation in mucous or the binding to epithelium, could be hypothesized to be primarily a matter of reaction rates and concentrations, probably being affected by temperature, and situations such as the unstable Al chemistry of mixing zones characterized by an already ongoing Al polymerization (Rosseland *et al.* 1992).

Although increased levels of aluminium in blood plasma not have been found (Neville 1985, Wood and McDonald 1987), Al-accumulation in body tissue does occur (Hunter *et al.* 1980, Muramoto 1981, Buerger and Soltero 1983, Haines *et al.* 1987). In the field, such accumulation might reflect both a direct gill-dependent uptake and a food chain dependent uptake (Haines *et al.* 1987). It was suggested by Muramoto (1981) that aluminium could pass through the gill as metal-complexes in the presence of complexing ligands. How Al actually comes into the cells is unknown, but Exley *et al.* (1991) suggested from findings from *in vitro* experiments with phospholipid vesicles that apical bound Al alters membrane permeability to allow the intracellular accumulation of Al. Inside the cell, citrate might be an excellent ligand to Al and act as an intermediate chelator, passing Al to groups with higher

affinity. The gill activities of the enzymes carbonic acid anhydrase and Na-K-ATPase are inhibited in acid/Al-exposed salmonids (Staurnes *et al.* 1984, Rosseland *et al.* 1992). The interaction between Al and ATP (mainly the tendency for ATP to form stronger complexes with Al than with Mg) may imply that Al can affect many enzymes reactions where ATP is a substrate, and possibly causing severe disturbances of the energy metabolism of the cells (Ganrot 1986). Al also binds to calmodulin, which is a multifunctional, Ca-dependent protein that regulates a variety of cellular reactions, including regulation of many enzymes (Ganrot 1986). In mammals, Al has been shown to interfere with the Ca regulatory system and Ca homeostasis, and similar interference might be suspected in the gill epithelium cells (discussed by Excely *et al.* 1991). Al has recently been shown to inhibit the Ca^{2+} uptake over the gills of freshwater carp, *Cyprinus carpio*, Verbost *et al.* 1992. The cytosolic plasma Ca^{2+} concentration is very well regulated, and in eukariotic cell a higher concentration than 10^{-7} - 10^{-8} cause breakdown of the cellular functions (Wiercinski 1989). Myocardial cell necrosis during heart muscle arrest seems to be caused by Ca "overload" in the cell (Wiercinski 1989), and similar cell necrosis could also be suggested to take place in gill epithelia. The overall effects of the possible interference of Al with basic processes in the gill epithelial cells may thus be severe effects on the epithelial barrier properties (trans- and paracellular transport) and accelerated cell death (Excely *et al.* 1991).

Sometimes extensive mucus-clogging of the secondary lamella has been observed (Muniz and Leivestad 1980, Rosseland 1980, Rosseland and Skogheim 1984). This response is not universal, as fish dying in field in natural acidic waters at labile Al-concentrations of 59 - 110 $\mu\text{g/l}$ have not shown excess mucus despite an Al-accumulation on the gills (Skogheim *et al.* 1984, Rosseland *et al.* 1986a, Rosseland *et al.* 1992). Adding excess aluminium as $\text{Al}_2(\text{SO}_4)_3$ to such waters ($\text{LAl} > 130 \mu\text{g/l}$) rapidly induced mucus clogging (Muniz and Leivestad 1980, Rosseland 1980, Rosseland and Skogheim 1984). The relevance of the mucus clogging might therefore be questioned with respect to natural conditions, although increased number of mucus cells on gills of Atlantic salmon in an acid river has been observed (Jago and Haines 1990).

Both histopathological changes and an increased mucus layer will serve to increase the diffusion distance for O_2 and CO_2 between the water and blood. This can lead to a decreased oxygen tension in the arterial blood, reduced hemoglobin oxygenation and pH, and increased blood CO_2 and blood lactate (Neville 1985, Malte 1986, Wood and McDonald 1987). At low pH, the increased mucus layer will reduce the rate of ion loss, thereby temporarily increasing the resistance, as observed by Baker and Schofield (1982), Hutchinson *et al.* (1987) and Wood and McDonald (1987). At such high concentrations of H^+ and aluminium, the primary cause of mortality might thus be respiratory rather than osmoregulatory failure (Rosseland 1980, Muniz and Leivestad 1980, Neville 1985, Wood and McDonald 1987).

In general, there is an increase in metabolic cost when an organism is exposed to stressful conditions (Calow 1991). In acid waters, metabolic activity, measured as oxygen uptake, is not affected by H^+ alone, but increases as a response to aluminium in the water (Rosseland 1980, Neville 1985, Malte 1986, Wood and McDonald 1987). The increased respiratory and heart rate observed in acidic waters (Rosseland 1980, Muniz and Leivestad 1980, Ogilvie and Stechey 1983, Giles *et al.* 1984, Fivelstad and Leivestad 1984, Neville 1985, Malte 1986, Leivestad *et al.* 1987, Wood and McDonald 1987) are not believed to cause the increased energy expenditure *per se*, as the increased metabolism

rather reflects the increased activity of the intrinsic compensatory mechanism trying to restore homeostasis (Rosseland 1980). In long-term experiments, both low (Sadler and Turnpenny 1986) and high concentrations of Al (Muniz and Leivestad 1979, Siddens *et al.* 1986) have reduced growth. A reduction in growth has also been observed in a population of brown trout from a lake undergoing reacidification after a previous liming (Barlaup *et al.* 1992) Hyperventilation in acidic waters is a specific response to the labile Al-concentration, as the addition of chelator such as citrate depresses hyperventilation (Leivestad *et al.* 1987).

Prolactin and cortisol are important hormones related to osmoregulation (Potts and Flemming 1970, Johnson 1973); prolactin reduces ionpermeability and increases mucus production, while cortisol stimulates the onset of cellular proliferation and differentiation in the primary gill epithelium, and increases the specific activity of Na-K-ATPase. Both hormones are affected by acidic waters (Wendelaar Bonga and Balm 1989, Witters *et al.* 1991). Plasma cortisol increases in fish exposed to low pH and high aluminium concentration, presumably as a response to compensate the H⁺/Al-response (Kjartansson 1984, Witters *et al.* 1991), as well as in fish exposed to low external NaCl-concentration (Perry and Laurent 1989) and chronic stress in general (Pottinger and Pickering 1992). Prolactin production increases in acidic waters mainly as a response to a drop in plasma electrolytes (Wendelaar Bonga *et al.* 1987). As this is a time dependent increase, an increased prolactin production is clearly a mechanism of resistance.

Although hormones plays an important role in various resistance mechanism towards acid waters (Exley and Phillips 1988, Rosseland and Staurnes 1993), an important and yet undiscussed aspect, is the potential negative effects of an increased level of cortisol as a response to prolonged (chronic) exposure to acid aluminium-rich waters. As a permanent increased level of cortisol has a negative effect on the immune system (Mazeaud and Mazeaud 1981, Pickering and Pottinger 1985), such a response might thus have a negative effect on the health status of fish populations in acid lakes in general. Another important aspect is a possible post-episodic effect. A combination of a primary sublethal physiological stress (a.o. osmoregulatory and circulatory problems) and a secondary reduced immunity caused by a cortisol respons, might lead to an increased mortality over a long periode. The overall effect might thus be substantially greater than the direct observed mortality during and shortly after an episode or an exposure to a "mixing zone chemistry" (Rosseland and Staurnes 1993).

Avoidance reactions to low pH waters have been observed when plasma cation concentrations have been reduced by acidic waters (Pedder and Maly 1987). Olfaction is an important part of behavioural response and can lead to both positive and negative chemotaxes including avoidance. Low pH alone reduces the olfactory response to aminoacids and increases the mucus layer in the olfactory organ (Thommesen 1975, Klaprat *et al.* 1988). Adding aluminium to the water depresses olfactory response even more and causes histopathological changes such as irradiation of the microvilli, swelling and disformation of the olfactory epithelium (Klaprat *et al.* 1988). During episodic changes in water quality related to snowmelt or heavy rain, fish are often observed gathered at the outlet of, or having migrated into, a less acid brook or stream (Muniz *et al.* 1978, Rosseland 1986). Also during more chronic acidic conditions, preferences towards better water quality has been observed. In the limed Lake Hovvatn, brown trout during reacidification migrated into an adjacent pond with better water quality in spite of higher fish density and higher competition for food (Barlaup *et al.* 1989). Also in relation to acid episodes

with elevated Al-concentrations, brook trout have been observed drifting downstream or actively seeking chemical refugia (Carline *et al.* 1992). Downstream drift has also been observed by Atlantic salmon during a naturally occurring and highly toxic episode of low pH and high Al-concentration (Skogheim *et al.* 1984). These studies indicate that the avoidance/escape reactions are important resistance mechanisms under acid conditions, and therefore important for survival and selection of more tolerant fish.

Chronic exposure to sublethal acidic conditions causing disturbances of the olfactory sense prior to a toxic episode, might reduce the chance for a fish population to find refuges and survive in their environment. A sensitive olfactory organ, but still insensitive to the negative effects of pH and aluminium, might thus be one of the most important factors for natural selection and resistance in nature (Rosseland and Staurnes 1993).

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