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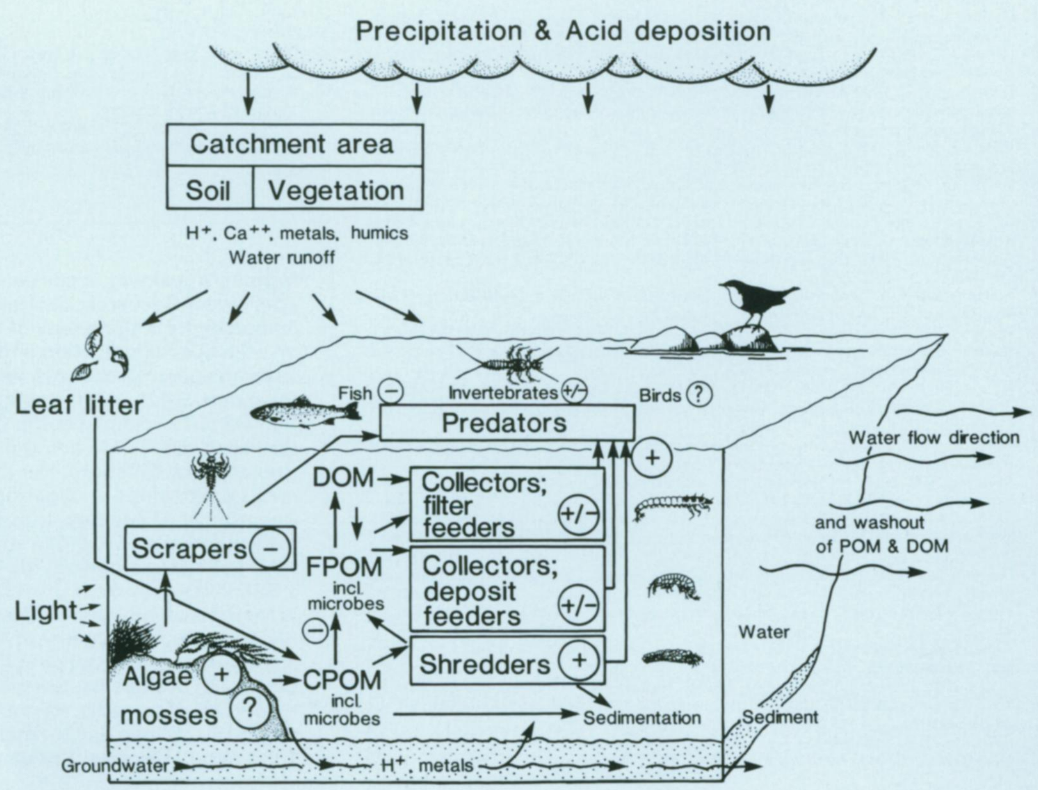
Acid-stress Effects on Stream Biology

Running waters are sensitive and rapid indicators of how whole watersheds become anthropogenically affected by, e.g. acidification. This paper reports and discusses the results of Swedish freshwater acidification research, for the period 1988-1993 and earlier. Changed biotic patterns are exemplified by increased occurrence of those green algae that indicate an increase in nutrients (nitrogen), reduced species richness of invertebrates (especially mayflies, crustaceans, gastropods), a general shift in proportion from invertebrate grazers towards shredders, decreasing populations of fish (salmonids, roach, burbot, minnow). Impact on birds (dipper, grey wagtail) appears less validated. The mechanisms for the changes in individual, population and community levels include elevated hydrogen, aluminum and cadmium concentrations that affect ion balance and respiration in fish and invertebrates, but also various behavior patterns (avoidance reaction, downstream movement, choice of spawning site), and developmental stages (molt and emergence of insects, hatching and growth of early fish stages). Al can ameliorate low pH temporarily but does not biomagnify along food chains, and neither predatory insects nor flycatchers seem to accumulate Al. It seems less likely that cadmium is a serious threat to invertebrates in "normal" concentrations at low pH. Iron precipitation can affect feeding ability and respiration of mayfly nymphs. That humic substances may mitigate metals still seems uncertain for fish and invertebrates. Generally, most changes in the biotic patterns of streams seem to be related to abiotic impact routes. Fewer changes are due to changed biotic interrelations, but some examples of changed competitive situations are given for invertebrates and fish. In all these cases of sublethal acidification stress, the ultimate effect is that growth, development and reproduction of the organisms are retarded. Relevant and sufficient knowledge seems to be lacking in three research fields of acidification impact on streams; viz. increasing occurrence of green algae in acidified streams; role of invertebrates in decomposition of leaves in acid waters; and recovery processes of fish and invertebrates after liming.

INTRODUCTION

Streams and rivers are more susceptible to human influences than lakes: a running water is like a mirror of the whole catchment area (1). The directional flow of the water exposes aquatic organisms to the harmful substances contained in the water itself, but may also be a rapid conductant for the stressors. Watershed processes caused by acidifying deposition and/or human activities can, therefore, profoundly affect lotic ecosystems. Especially in headwater streams, organisms are exposed to large variations in the composition of the water. Chemical conditions in running

Figure 1. A stream section, showing the functional feeding groups and the flow of organic matter between these. CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter, DOM = dissolved organic matter. The functional-feeding groups; *Scrapers* consume periphyton from stones and leaves; *shredders* consume CPOM; *deposit feeders* consume settled FPOM; *filter feeders* consume suspended FPOM, incl. small organisms and colloidal DOM; and *predators* consume animals. Known or supposed effects of acidification on the functional feeding groups indicated by + and – signs. Drawn by G. Marklund from ideas by A. Gerhardt and J. Herrmann.



waters—low pH, rising metal levels—become most severe during spring snowmelt and autumn rain (2).

Acidified lakes and streams have pH levels below 6, often in the interval 4.5–5.5, coupled to alkaline values, in meq L^{-1}, around or below zero. The soil acidification causes increased solubility and washout of metals into acid surface waters, the most serious being aluminum (1000 $\mu g\ L^{-1}$), cadmium (0.3 $\mu g\ L^{-1}$), iron (3000 $\mu g\ L^{-1}$), manganese (500 $\mu g\ L^{-1}$), and mercury (0.01 $\mu g\ L^{-1}$) (These figures imply normal upper limits in acid waters). For some metals, the biological availability and the adverse effects are related only to a fraction of the metal occurrence, often the inorganic ions. Toxicity might be lessened by increased concentrations of calcium or humic substances. The particulate or dissolved humus, up to several hundred mg Pt L^{-1}, may also contribute to acidity (3).

During the 1970s and early 1980s, most acid deposition research was descriptive. However, during the last 5–10 years (mid-1980s to 1993) the focus has shifted towards the underlying active mechanisms (4). In contrast to lake studies, stream research has mainly focused on the dominating regulatory abiotic factors, i.e. chemical impact, and less on biotic interrelations (5, 8). Furthermore, abiotic regulation is perhaps even amplified by acidification.

In this paper, effects of stream acidification on various biotic components are reviewed and the underlying mechanisms discussed. The data are compiled mainly from Swedish research in 1978–1992, especially the latter part of this period. Recent reviews of stream acidification effects, encompassing a range of biotic components, are given by Elwood and Mulholland (6), while Sutcliffe and Hildrew (7), and Herrmann (8), focus on invertebrates.

ALTERED PRIMARY PRODUCTION

Streams are predominantly heterotrophic systems, that rely on input of organic matter and, thereby, food energy from surrounding catchment areas (Fig. 1). Nevertheless, algae and aquatic mosses may be abundant, constituting a food resource and bottom-structure element. Lotic vascular plants can be abundant locally but, so far, their response to acidification has not been studied in streams.

During the last decade, there have been several observations on increasing occurrence of filamentous green algae in Swedish and Norwegian running waters (Fig. 2), particularly in ion-poor and acidic streams (9, 10). In North America, artificial acidification of streams, decreasing pH by c. 2 units, has resulted in a significant increase of periphytic algae (6, 11). Possible explanations include decreased grazing pressure of invertebrates; reduced microbial decomposition; increased phosphorus load; and a switch towards more acid-tolerant algal species, previously hampered by competition.

An additional possibility is that increased amounts of nitrogen in acid deposition fertilize the water. This aspect has recently been investigated in an extensive survey of algal communities in about 60 rivulets in the mountains in central Sweden. These waters were carefully studied during the 1970s (12), and revisited again in 1991 and 1992. This area periodically receives large quantities of

Figure 2. Green algae from a stream in SW Sweden, where pH has decreased distinctly, but nitrogen has increased. Earlier this stream showed very sparse visible vegetation. Photo: J. Herrmann.

acid deposition, and the amounts of nitrogen deposited have increased since the 1970s (13). Increased nitrogen deposition (snowmelt) has been recorded early in spring in the form of a nitrate pulse in small mountain streams (9), whereas there are no indications of changed phosphorus levels in these remote streams.

Detailed results of this survey will be published elsewhere, but the general changes in the algal communities are (i) number of species and total abundances increased; (ii) a shift from blue-green algae towards green algae, mainly of the genera *Zygnema* and *Mougeotia* often occurred; (iii) algae favored by increased nutrient levels (genera such as *Ulothrix, Microspora* and *Spirogyra*) became more dominant, whereas the "acidophilic" diatom *Eunotia* spp. remained at the same level or increased slightly (11). In streams with calcium-rich water, no increase of green algae was observed.

Blue-green algae, e.g. *Rivularia, Tolypothrix* and *Nostoc*, were disfavored relative to green algae, which probably is due to the fact that only the blue-green algae can meet the nitrogen requirements through fixation of N_2 from the air, while the green algae are clearly favored by increased levels of nitrate (and ammonium) ions which makes them the more successful competitors. The green algae *Bulbochaete* sp., however, decreased, probably due to its sensitivity to nutrient-rich conditions.

Thus, both a fertilizing effect, probably by nitrogen, and an acidifying effect appear to be responsible for the increasing occurrence of green algae in acidified streams, at least in central Sweden. Similar observations have also been made in southern Sweden, but no detailed study has been performed. Increases of periphytic green algae in Norwegian streams at moderately low pH levels, c. 6, were attributed to slight increases in nitrogen concentration (14). It is also possible that micronutrients cause increased primary production (15). However, the possible effect of reduced grazing pressure cannot be ruled out.

Expansion of *Sphagnum* mosses, noted in lakes (16), has also been observed in acidified streams (Lingdell and Engblom unpubl. data), whereas occurrence in acidified streams of the bulrush *Juncus bulbosus*, which has been shown to increase in acidified lakes, is not known (5).

Mayfly nymphs were found to starve when given algae from acid streams. This fact could possibly lead to expansion of the algal species that were previously outcompeted or grazed (17). Most results that indicate an increase in periphyton and a decrease in grazers seem to be correlative or circumstantial (6), and it is possible that neither low pH nor fewer grazers can explain the expansion of diatoms (18).

INVERTEBRATE SPECIES: RESPONSE PATTERNS

The role of invertebrates in consumption, storage, degradation and bioturbation of benthic organic matter, nutrients and energy is considerable, but often overlooked (19). These small animals, rarely exceeding 20 mm in length, dwell in the sediments of shallow surface waters. They are important because (i) their feeding facilitates the microbial degradation of the particulate organic matter; and (ii) they are an important food resource for littoral and pelagic fish as well as aquatic and terrestrial birds, but also for predatory invertebrates; and thus (iii) they form energy transfer links over the ecotones from streams and lakes to their shores.

It is well-established that a lowered pH of the stream water and/or raised metal concentrations, have a negative impact on many invertebrates, thus reducing species numbers (6, 8, 20–24). To some extent, lost species can be replaced by other more acid-tolerant but, at normal pH, less competitive species. In a review of synoptic studies, Degerman et al. (9) concluded that in the southern part of the Swedish mountains, both abundances and number of species of lotic invertebrates had declined, particularly in the early 1980s. The changes were primarily attributed to lowered pH, but possibly also to elevated metal concentrations, and were often more pronounced at higher altitudes.

Mayfly nymphs are well known indicators of acidification, most species being unable to withstand a pH below 5–5.5, although a few mayfly species are among the most acid tolerant benthic macroinvertebrates (20, 22, 25–27). Not only pH and metals, such as Al, can be limiting (6, 24), but also the quantity and quality of the food resource, the microalgae (17).

Gastropods and crustaceans are even more restricted to pH levels above 5.5, due to the insufficient Ca content of acidic water (26, 28). The larvae of some trichopteran and a few plecopteran species, are negatively affected in acidified water (20, 23). However, shredding caddis larvae, mainly limnephilids, seem to be less affected by low pH, possibly due to the increasing pool of nondegraded coarse detritus (20, 29).

Number of species, as a function of pH, based upon a huge Swedish data set, are presented in Figure 3. Total number of species shows a clear decline with decreasing pH levels (Fig. 3a). The curves for mayfly and gastropod numbers are clearly displaced towards higher pH levels, ≥6 and 6.5, respectively (Fig. 3b, c), and gastropods are seldom found below pH 6. Also, slightly more caddis larvae species occur at higher pH, whereas pH does not seem to affect species numbers of stoneflies (Fig. 3d, e). Odonates show a plateau from pH 5.5 to 7.5, but with lower numbers outside this interval (Fig. 3f).

Effects of acidification on abundance within the functional feeding groups are presented in the section on community and ecosystem levels. Lowered pH has been reported to reduce the total invertebrate density (24), and the total invertebrate biomass (30). However, other studies have not been able to confirm these findings (22, Henrikson unpubl. data, Lingdell and Engblom unpubl. data).

The unpredictable acidification depauperates the lotic invertebrate fauna, which can threaten the existence of species at low abundances or patchy distributions. In the southern part of the Swedish mountain area, species like *Baetis lapponicus*, *Ephemera danica* and *Philopotamus montanus* now seem to be on the retreat, the latter two species have, however, been observed to colonize after liming (31). The crustacean *Gammarus lacustris* has gradually disappeared concurrent to acidification (9). The stream-living pearl mussel *Margaritifera margaritifera* has declined drastically during this century in Sweden and in other countries, a probable explanation being low pH or high Al levels (Henrikson unpubl. data).

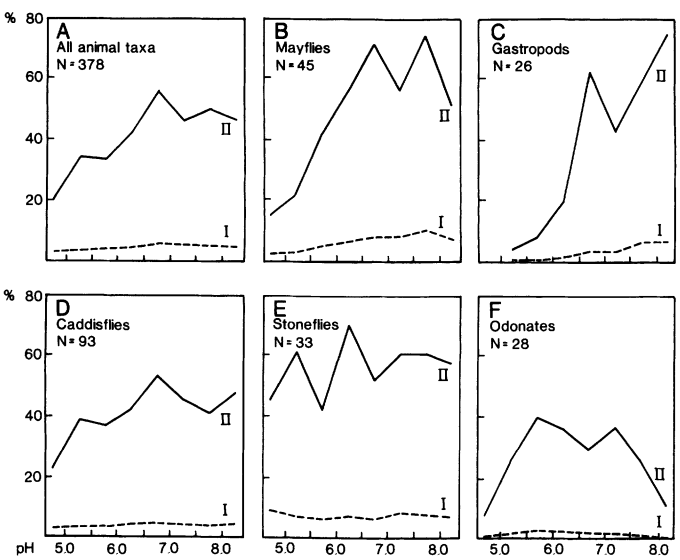


Figure 3. Number of invertebrate species of various taxonomic groups (A – F) found at various pH intervals. For each pH interval, 30 streams with a breadth of 2–5 m were chosen randomly from a large data base of c. 3800 localities all over Sweden. (I) Average number of species found in a typical (average) stream of each pH interval, as a percentage of all found species (N value) for the group. (II) Total number of species from all 30 streams at each pH interval, as a percentage of all found species (N), thus taking into account the replacement of species along the pH gradient. (Source: Limnodata / Engblom and Lingdell).

TOXIC EFFECTS AND MECHANISMS FOR THE INVERTEBRATES

The occurrence patterns of many mayflies, which conform to areas of particularly extensive acidification, are supported by several low-pH laboratory tests (Box 1). Al is often regarded as the most toxic metal for invertebrates in acidified waters (32). Elevated concentrations of hydrogen and Al ions affect osmoregulation in mayflies, a stress impact leaving less energy for growth and reproduction (33, 34). However, it has also been reported that Al can, at least temporarily, ameliorate the toxic effects of low pH on survival and osmoregulation of these species (35, 36). This phenomenon has also been observed in fish, daphnids and stoneflies, and can be due to Al blocking the membrane permeability of hydrogen ions (8). Accumulation of Al in aquatic insects seems less significant, as most Al is shed at each molt (change of larval skin) (Box 1), and no significant biomagnification along food chains seems to occur (Herrmann unpubl. data).

Besides Al, metals such as Cd, Pb, Zn, Cu and Fe can become more soluble at low pH, and the effects of these metals on stream invertebrates were summarized by Gerhardt (37). The LC_{50} concentrations (lethal concentration for 50%) for Cd are very high compared to levels occurring in natural surface waters at lowered pH, implying that generally the potential toxicity of Cd might have been overestimated (Box 2). The acute toxicity of Pb and Fe for the mayfly *Leptophlebia marginata* was higher at low pH than at neutral pH (Gerhardt unpubl. data). Campbell and Stokes (38) concluded that Cd toxicity (growth, uptake and mortality) to algae and fish often decreased at lower pH, whereas the reverse was true for Pb. Most studies seem to indicate that none of these metals show biomagnification along food chains (37).

At pH 5, increased Cd levels lowered escape behavior and general activity of the mayfly *L. marginata* (Box 2), and many animals died. When exposed to 20 µg Cd L^{-1}, the activity of *Baetis rhodani* decreased over three weeks, irrespective of pH, and also Pb and Fe lowered the escape behavior for this species. Increased drift behavior of invertebrates, i.e. passive transport with the water current caused by both abiotic and biotic factors, have been shown to occur at lowered pH (8), and at increased discharge levels (39).

At a pH drop from 7 to 4.5, Fe caused a significant and clear dose-dependent (range 0–50 mg Fe L^{-1}) decrease in feeding activity of the mayfly nymph *L. marginata*, while these Fe concentrations had no affect at pH 7 (40). Being an essential element, Fe can to some extent be regulated, thus avoiding the negative effects for some time. At the highest Fe concentration at pH 4.5, most animals showed a constipated midgut (Fig. 4). This was followed by death, probably due to starvation. The gut membrane was covered with a thick layer of Fe-humus-hydroxides, which blocked food uptake (Fig. 4). Fe precipitations occurred also on the body and gills. Further, uptake of Cd by mayflies became reduced in the presence of Fe, possibly due to co-precipitation of Cd together with Fe-humus-hydroxide complexes, which make Cd less bioavailable (Gerhardt unpubl. data).

Molting frequency of larvae of the low pH sensitive mayfly species *B. rhodani* was found to be threefold at pH 5 compared to pH 7, but we have no explanation for this. At pH 5, frequency of emergence, i.e. final metamorphosis to adult insects, was only a third, compared to that pH 7 (Box 2). Presence of Cd seemed of less importance for development. Molting mayfly nymphs (*Heptagenia sulphurea* and *E. danica*) showed substantially increased sodium fluxes, probably being more "physiologically" sensitive to low pH and elevated Al levels at that stage (42). Fe has also been observed to cause increased molting of *L. marginata*, possibly ridding the animal of precipitates of Fe (Fig. 4). Molting, and especially emergence, are energy-consuming processes. At low pH, these will compete with the energy demand for the increased osmoregulation, and can, therefore, affect growth and development, especially the final stage, i.e. the reproducing mayfly.

To summarize, it appears that Al in concentrations following acidification can be harmful for many invertebrates. In the long term, Al adds to the pH stress itself, even though in some instances it may at first ameliorate the low pH. The Cd levels used in these experiments are 2–3 magnitudes above realistic levels, which was necessary to show clear effects and mechanisms, thus indicating that the negative role of Cd may have been overestimated.

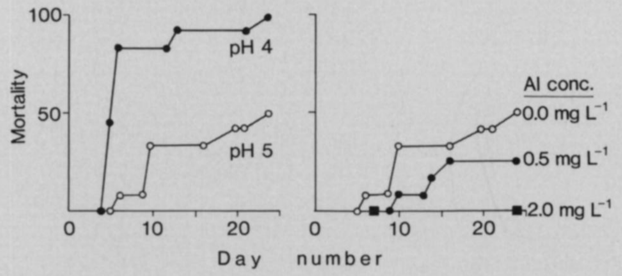
Chemical stress is most critical during acid surges in spring (2), and may continue to be a problem even after liming. Due to groundwater with higher pH and lower oxygen content entering the surface waters, metals may precipitate in the mixing zone. Mayfly nymphs with pronounced precipitations on the gills, abdomen and legs have been found in several streams in Sweden (Lingdell and Engblom unpubl. data, Gerhardt unpubl. data). Such precipitates (Fig. 4), mainly consisting of Fe and Mn, probably also humic substances, might be deleterious for some species, by hindering normal chemical processes and activity. On the other hand, other species can gain by its camouflage.

Dissolved humic substances seem to reduce the survival of some mayfly and caddis nymphs, amphipods and daphnids (43, Henrikson unpubl. data). Conversely, at low pH, moderate levels of humics seem able to form metallo-organic complexes (e.g. with Al), possibly lowering the metal toxicity. This might explain that at low pHs, modest levels of humics were beneficial, allowing more species of stream invertebrates (29). Further, it was observed that of most streams at pH 5–7, those with low water color (<10 mg Pt L^{-1}) hold a considerably lower number of mayfly species than more stained streams (Lingdell and Engblom unpubl. data). This might be interpreted as inhibiting metals, but also that humus

Box 1. Effects of Aluminum on Invertebrates

Mortality

The mortality of several species of mayfly nymphs has been studied at various pH and Al (inorganic) levels. *Ephemera danica* showed the expected sensitivity for low pH, but Al lowered this sensitivity. Species less sensitive to low pH showed the same patterns, but less pronounced. (Source: J. Herrmann, unpubl. data).

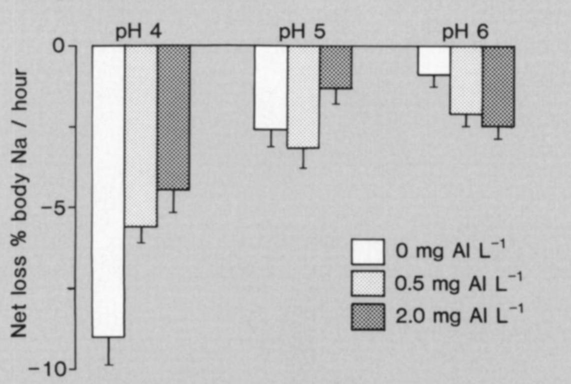


Accumulated percentage mortality at pH 4 and 5 (Al = 0).

Accumulated percentage mortality at different Al concentrations (pH = 5).

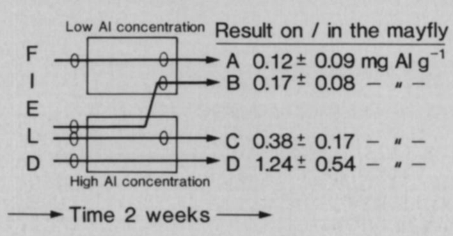
Osmoregulation

Fluxes of ^{22}Na through mayfly nymphs showed a higher net loss at lower pH, indicating more disturbed osmoregulation. As an example are shown results for Ephemera danica. At low pH, however, Al (inorganic) seemed to ameliorate this negative pH effect. Species less sensitive to low pH showed the same patterns, but less pronounced. Source: 77.



Accumulation

Simplified view of Al contents of nymphs of the mayfly *H. sulphurea*, after rearing in different regimes of Al concentrations. Most Al is left behind at change of larval skin (exuvium), indicated by a ring. 95% confidence limits are given. Animals in regime C are significantly different from all the others. Redrawn from (42).



can be a food resource and buffering agent, although both are controversial. It has also been suggested that *B. rhodani* and *G. lacustris,* in moderate water color, survive better at lower pH due to inactivation of harmful metals (35, 44). However, it must be emphasized that as the beneficial metallo-organic complexes are stable only under stable pH conditions (45), this being less common in natural waters, metals can easily become free and potentially dangerous. In addition, such complexes can increase mobility and bioavailability, and thus, the toxicity of metals (43). Further aspects of humic substances are discussed by Kullberg et al. (3).

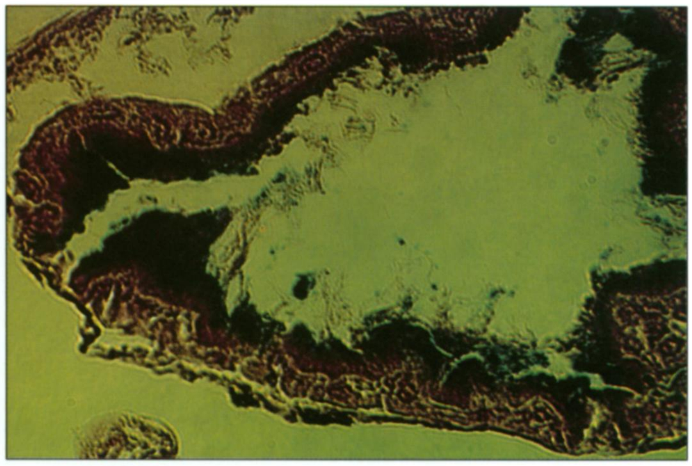
FISH SPECIES RESPONSE PATTERNS

There is no overall estimate of the total loss of species or production of fish in Swedish streams, but approximately 1/3 of

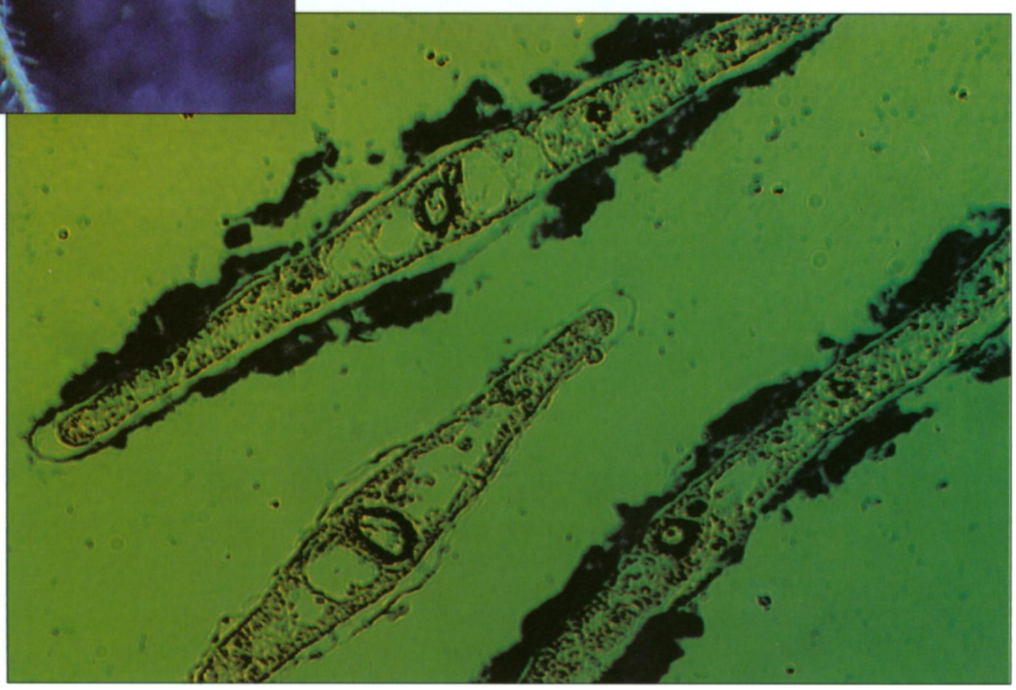
a.

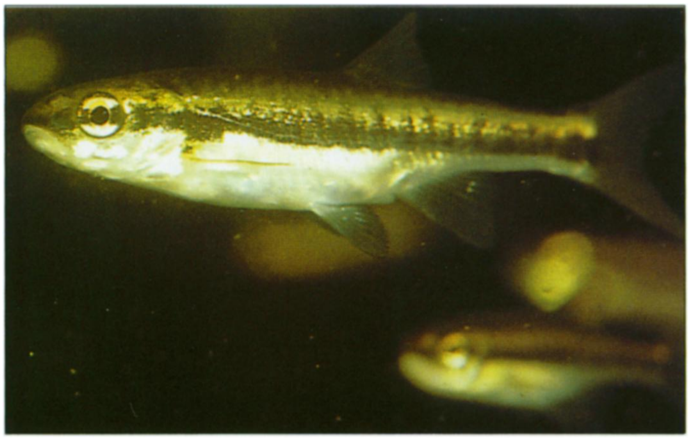
Figure 4.
Fe precipitations on the mayfly *Leptophlebia marginata*;
a) the whole animal, showing gills and abdomen;
b) histochemical sections of gut membranes with Fe-humus-hydroxide (blue);
c) the same of the gills.
Photos: A. Gerhardt.

b.



c.





The European minnow (*Phoxinus phoxinus*), typical for clean streams, is very sensitive to acidification. Photo: F. Ehrenström.

the streams in Sweden show pH values below 6 (13), thus, many fish populations would be affected significantly. Without liming, c. 40% of the Atlantic salmon smolt production on the Swedish west coast would have been lost (46). The impact of acidification on fish is partly an effect of osmotic stress on adult fish, but is primarily related to reproductive impairment, resulting in reduced recruitment (47, 48).

In Sweden, the negative effects of low pH on natural fish populations begin when pH falls below 6, but populations are seldom lost until pH reaches 5.5 (47). Documented disappearance of brown trout (*Salmo trutta*), Atlantic salmon (*S. salar*), burbot (*Lota lota*), roach (*Rutilus rutilus*), European minnow (*Phoxinus phoxinus*) and grayling (*Thymallus thymallus*) from Swedish streams coincided with pH levels of 5–6. Occasionally, even a total loss of fish species resulted from one single acid spate (49, 50). In 50 Swedish west-coast lakes, species dependent on running waters were often the first to vanish (51). In particular, brown trout and European minnow have been affected severely, since these species spawn in small streams, which are often more susceptible to acid spates (52).

In small streams, the abundance of salmonid parr (juveniles) declines with reduced pH (49, 50, 53, 54). Most critical are the acid spates during snowmelt, which cause fish abundance to decrease even in water systems where the pH is above 6 for most of the year. Average abundances were reduced to only 10% (salmonid parr) and 40% (European eel, *Anguilla anguilla*) of those found in similar streams, but with mean annual alkalinity higher than 0.1 meq L^{-1} (55). Decreased recruitment, i.e. a loss of sensitive individuals, of Atlantic salmon and bullhead (*Cottus gobio*) has followed acid spates during snowmelt with lowest recorded pH in the interval 5.5–5.9, in streams with a pH above 6 during the rest of the year (49).

TOXIC EFFECTS AND MECHANISMS FOR FISH

In all observations of the occurrence of low pH-sensitive fish species and populations, there is a variation due to the innate biological variation of each property. In addition, some traits can, with altered selective pressure, change over time, also leading to variations.

Acid tolerance consists of physiological superiority (e.g. buffering capacity in the perivitellinear fluid of the egg, osmotic stress tolerance) and behavioral adaptations (e.g. avoidance reactions, choice of spawning substrate). In addition to increased mortality, at low pH and advanced gill lesions after exposure to Al in acid water, the European minnow behaved abnormally and tried to escape from the Al-rich inlet (56). Quick downstream migrations

Box 2. Effects of Cadmium on Invertebrates

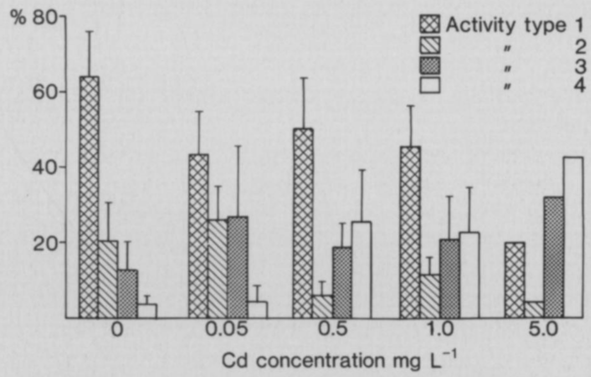
Acute mortality

High short-term tolerance to Cd was found for several invertebrates, mostly irrespective of pH 5 or pH 7. Below are shown LC_{50} values, i.e. lethal concentration for 50% of animals exposed for 120 h. Levels are in accordance with earlier findings. Data from (41).

Baetis rhodani	2.3 mg Cd L^{-1}
Leptophlebia marginata	> 5 mg Cd L^{-1}
Pisidium sp.	>> 5 mg Cd L^{-1}
Polycentropus flavomaculatus	> 2500 mg Cd L^{-1}

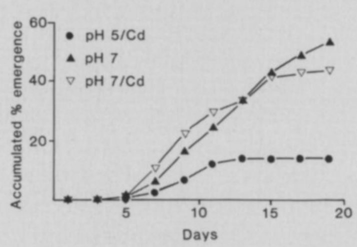
Sublethal effects; behavior

Displayed behavioral types in % of total registration time of the mayfly *L. marginata* changed in a dose-dependent way on Cd exposure, using an impedance converter and a computerized response-treatment system. With increasing concentration of Cd, the escape behavior decreased, and slow movements increased, as did also the degree of inactivity, all measured for 1 h after exposure of 120 h and pH 5. Source: (Gerhardt unpubl. data).



Behavioral responses of *L. marginata*, exposed to various Cd concentrations at pH 5. Behavior types are 1 = realized escape behavior; 2 = rapid movements; 3 = slow movements; 4 = inactivity. Standard deviation is shown. At the highest Cd level n = 1, for the others n = 6.

Sublethal effects; development



Emergence of *B. rhodani* after exposure to various pH and Cd regimes (0.02 mg Cd L^{-1}) during 16 days. Source: (94).

coinciding with acid and metal-rich spates in spring have been observed for several fish species (49). This behavior could be induced by metal (Al, Fe, Mn) flocculation in the water, leading to respiratory dysfunction in brown trout, and 100% mortality within a few days (57). Species or local strains of fish that display avoidance reactions and migrate back will probably survive better in systems with acid spates, but this behavior can be complicated by obstacles to migration, e.g. dams, which are common in Swedish streams (50).

Another possible mechanism for survival in acidified streams, is the optimal choice of spawning site (58). Whereas brook trout spawn exclusively in areas of (neutral) groundwater seepage, brown trout utilize locations with or without groundwater outflow and can therefore be more tolerant to acidification (59).

Osmotic stress on fish at low pH caused reduced growth rates in laboratory studies (60), but under natural conditions this effect may be of less importance as temperature, food availability and quality, interspecific and intraspecific competition also determine fish growth rates (47).

Eggs of Atlantic salmon and brown trout were exposed *in situ* in the river Mörrumsån and some of its acid tributaries (48). Low hatching frequencies were recorded for both species at acid localities. The mean mortality of yolk-sac fry (newly hatched) exposed to acidic waters was higher for Atlantic salmon than for brown trout. Disturbances, i.e. increased mortality and pathological alterations, were recorded at pH levels as high as 5.7. Enlarged intercellular spaces, lack of normal epithelium due to loss of normal cell junctions at low pH, and the direct uptake of Al may have caused the electrolyte depletion in fry, due to an increased leakage over gill epithelia; an effect which may partly be compensated for by increased chloride-cell proliferation. The ion-regulating chloride cell seems to be an important target for aqueous Al, which may thereby disturb normal cell functions and ion regulation.

It has repeatedly been advocated that Ca can *per se* protect fish against adverse effects of low pH and high Al but, at least for brown trout, this now seems uncertain. The uncertainty can be explained by the fact that Ca is so intimately coupled to at least pH (61).

Yearlings were also studied in field experiments. Survival, developmental rates and otolith growth rates were lower in acid streams (minimum pH < 5.6) than in less acid streams (pH > 6.3), again salmon being more severely affected than brown trout (Mosegaard unpubl. data). A complex interaction between the effect of pH and rising spring temperatures has been found in the field. Both an apparent higher yolk conversion efficiency and larger otolith to body-weight relationship was found at lower pH. Laboratory experiments, however, indicated that this effect was due to prolonged developmental time in more acid water. Thereby, a greater part of embryonic growth took place under higher and subsequently more optimal temperatures.

EFFECTS ON COMMUNITY AND ECOSYSTEM LEVELS

As opposed to lakes, only few food-web mediated changes have been confirmed for running waters, also in connection with acidification. This may be interpreted to indicate that mainly abiotic factors are responsible for the occurrence and dynamics of lotic invertebrates (8). This may be true, but it should be emphasized that the prospects of detecting biotic interrelations in streams are smaller than in lakes (5, 62). The physical environment (e.g. water velocity, instability of the bottom substratum) is more unstable in streams, compared to lakes and, of course, man-induced impact like acidification adds to the list of stress factors (63). The reduced effectiveness of biotic interactions and regulations, such as predation, in combination with inefficient study methods and the rapid dispersal of stream-living organisms, make it difficult to demonstrate such impacts (64). Nevertheless, evidence for the importance of predators in structuring and regulating stream invertebrates is now accumulating and in the future we will probably be able to find decisive changes in the biotic interactions in acidified streams.

Lake studies have shown that after moderate acidification, the growth rate of fish often increases because of reduced competition (65), whereas fish surviving in severely acidified water may show reduced growth (66). It can be assumed that this will be shown also for stream populations, unless the invertebrates serving as food are reduced too much. This is also supported by observations of both higher and lower growth potential (Fulton's condition factor) for stream-dwelling brown-trout parr (juveniles) in acid streams, than in well-buffered streams (54, 55).

At declining pH values, the competitively superior amphipod *Gammarus pulex* may retreat, which allows the more acid-resistant, but competitively inferior isopod *Asellus aquaticus* to expand (67, 68). In addition, the low pH-tolerant mayfly *L. marginata* seems to expand in abundance in acidified streams (25).

Dominant, but acid-sensitive fish species, can be replaced by more acid-tolerant subdominant species. However, after liming many acid-sensitive species are often re-established (49). Although fish populations in small streams are regulated mainly by abiotic factors, interaction between species has also been found to be of importance (69).

Thus, acidification undermines the biotic regulation and allows subdominant species to thrive until they are also eradicated. Alpine bullhead (*Cottus poecilopus*) increased in numbers in some years following low pH during snowmelt. This was mainly due to reduced brown-trout recruitment and competition (49). In years of higher spring pH, the brown-trout recruitment was resumed and the abundance of alpine bullhead decreased again.

After changes in various abiotic and biotic niche components following acidification, the result is an altered fish or invertebrate community, often with less diversity, because sensitive and rare species have been lost. Such changes, combined with the available ecological knowledge, have shown the diverse stream invertebrates to be useful and popular as indicators of acidification in Sweden (70, 71) and Norway (35, 72). Due to the variable and unpredictable chemistry in streams, the use of biological indicators is highly recommended in the assessment of the acidification status, since these integrate the conditions over time and distance along the stream.

The food-web structure is also valuable in assessing the status of a stream locality. The five functional groups, revealing the different feeding habits of stream invertebrates, are commonly used parameters (Fig. 1). Scrapers, most of which are mayflies, are positively correlated with pH, but negatively correlated with the water color (6, 20, 29); probably due to the dependence of primary production on these parameters. Changed composition of algal species may affect food quality for macro-invertebrates. Nymphs of the mayfly *B. rhodani* survived less well, when fed on algae from acid streams than algae from more circumneutral conditions (17).

The increasing proportion of shredding caddis larvae in acidified streams could be due to the elevated amounts of coarse detritus that remain undegraded over a longer period in acid streams (20), or the absence of fish predators (8). Declining decomposition rates have repeatedly been attributed to lowered bacterial and fungal activity (73, 74), though probably less so in fine-grained bottom substrate, such as lakes and slow-running streams (6). Lowered invertebrate-depending decomposition seems less important for the lowered breakdown (75), in accordance with lower degradation of Coarse Particulate Organic Matter (CPOM), but not Fine Particulate Organic Matter (FPOM), in an acid stream, compared with a control stream (20). There is an obvious need for better knowledge on the decomposition processes.

It seems less clear how acidification affects filter and deposit feeders. The latter group can be protected against severe chemical impact by being buried in the sediment (8). Many predators can switch between different food items, irrespective of water chemistry. They can also benefit from altered behavior of their prey species, these becoming more easily caught.

Nyholm (76) observed breeding impairments in the pied flycatcher (*Ficedula hypoleuca*) and elevated Al levels in eggs and medullary bones. As the cause, he suggested Al from acidified runoff to a lake, via insects, mainly stoneflies. The hypothesis for conveying Al through the food web from aquatic to terrestrial organisms was also supported by the absence of similarly affected birds in an area with well-buffered soils and waters. Normally, most Al is left in the larval skins when insects emerge, thus preventing significant amounts of Al from reaching terrestrial birds (20, 77). However, stonefly larvae can also crawl on the geolittoral part of the shore, thus exposing themselves as food. Nevertheless, in recent follow-up studies Nyholm found no differences in the contents of Al, Ca and P in emerging stoneflies between the area with breeding impairments and an area with no such effects. As a correctly attained result, the suggested Al route was discarded (78, 79). However, the high Al levels in the flycatchers still have to be explained.

RESTORATION OF ACIDIFIED WATERS

Liming is the most widespread method to improve chemical conditions after acidification. Raised abundances or numbers of species of benthic invertebrates, and a general increase in abundance of several fish species can follow liming (80). However, fish colonization often seems weak, because species of Swedish fish fauna are limited in numbers. But even migration obstacles (dams) in the streams are important factors (51). The realized colonization of plants and animals depends on various abiotic and biotic factors (81), e.g. stability; predictability and quality of bottom substrate and water chemistry; the number of species available for recruitment; the distance to the nearest location with potential colonizers; their dispersal biology; and the composition of the new invertebrate community. Acid surges in springtime can be a definite hinder for successful colonization, even after liming (80).

Before liming, Atlantic salmon parr showed decreasing abundance, and after liming, at the same localities, brown-trout parr increased significantly, but did not reach previous levels (49, 50). After liming, Atlantic salmon soon recovered and the abundance of brown trout again decreased. Reduced competition has been reported between year-classes within brown-trout populations, during acid stress conditions, as well as resumed competition after liming (49, 82).

Invertebrate colonization can be rapid, show a succession of species assemblages, and random composition (83). In most cases, it is probably not possible to achieve identical biotic composition, and often one does not even know which organisms were present under pristine (pre-acidified) conditions, or which would have existed currently if no perturbation had occurred. There are reports of improvement in invertebrate fauna, like colonization of mayfly species without liming or spontaneous chemical recovery of the stream (Lingdell and Engblom unpubl. data). This indicates the risk of misinterpretation by attributing a positive faunal change to a performed countermeasure, a relation which is not necessarily causal.

Even if streams, as acidification proceeds, gradually become devoid of fish and invertebrates, portions of the stream or adjacent streams with the same conditions may continue to support animals. Such inter- and intraspecific genetic variations in acid sensitivity are important for potential natural resilience. To achieve an acceptable colonization of fish and invertebrates, one might need complementary measures besides liming, such as arranging migration paths, and increasing bottom complexity, including promoting riparian vegetation recovery (81, 84). In some cases, it may be necessary to restock with plants and invertebrates after liming.

STREAM-RELATED BIRDS

Acidification effects on birds have focused on metal mobility and effects, notably breeding impairment, and changed food supply, that affect foraging success. The lentic species are reviewed by Appelberg et al. (5) and Eriksson (85). Among the species related to Swedish acidified running waters, the main focus has been on the dipper (*Cinclus cinclus*). It was suggested that it has disappeared from streams due to heavy acidification, but this now appears to be doubtful (86). Scattered observations have implied dwindling numbers, but the birds migration and their dependence on favorable winter weather make interpretations uncertain.

Recently (1990–1992), c. 90 stream localities in the western part of Sweden were revisited for which dipper breeding information was available from 1975–1978. The numbers of breeding dippers remained essentially the same, both at acidified localities ($pH < 6$, alkalinity < 0.1 meq L^{-1}), and more neutral ones (Åhlund and Eriksson unpubl. data). No indication of decreasing brood sizes was observed. On both acidified and neutral sites, food during the nesting period was dominated by limnephilid caddis larvae, which are both fairly resistant to low pH and provide a good food source. No relation between stream pH and consumed food items of the dippers was observed.

The possibility that dippers could be affected by raised metal levels via their food has not been studied in Sweden. Dippers breeding close to a Norwegian acid stream contained higher levels of Al and Pb, compared to a reference area (87). Unfortunately, no comparison was made of breeding success. In Wales, breeding densities were lower near acid streams, due to effects on several breeding components (88), e.g. switch from preferred, but declining mayfly to smaller stonefly nymphs (caddis larvae also declined), and calcium deficiencies in the diet. Al and heavy metals did not seem to be an explanation for the impaired breeding.

So far, no changes in the grey wagtail (*Motacilla cinerea*) population, in Sweden, have been related to acidification (85), probably due to its habit of feeding mainly on flying and terrestrial insects (89). Nothing has been reported in the literature on the possible effects of acidification on the kingfisher (*Alcedo atthis*). However, as this species mostly breeds along larger and lowland streams it is probably less affected by acidification. Several ducks breed along streams, especially the goldeneye (*Bucephala clangula*), and these are favored by the increasing food stock in fishless acidified surface lakes (85), but the significance of this phenomenon is not known.

CONCLUSIONS

It has been suggested that competition and other biotic regulations are of less importance in harsh and variable systems (63, 69), probably including acidified waters (5). Food-chain regulations of fish upon invertebrates are rarely reported from running waters (90), whereas abiotic regulation seems to be more important, especially in low-order streams (24, 91). Acidification accentuates this by adding further abiotic stress on the stream system. In a comprehensive review of acidification effects in streams, Elwood and Mulholland (6) seemed more inclined to abiotic explanations. However, this could be due to bias as studies on abiotic factors are conducted more easily and more frequently in streams.

Nevertheless, also in streams there are competitive interactions, which change with acidification. If the increase in green algae depends on increased nitrogen, the relation can be assigned abiotic, but this expansion also outcompetes the blue-green algae, i.e. a biotic factor. Most changes in the invertebrate communitities seem to relate to abiotic factors. Low pH and rising Al can cause osmoregulatory disturbances, whereas changed proportions between functional groups are more biotic events, due to changed food availability. When pH decreases, salmon disappear and trout are favored, and at even lower pH are replaced by bullhead (49). However, below pH 5.5 abiotic regulation increases, the acute cause often being electrolyte depletion and hatching obstacles. For invertebrates the interval where pH effects occur is longer (pH c. 4–6), due to the multitude of species, and variability between the species. At lowered pH levels, the decomposition of organic matter seems to decrease, however, the cause of this is not clear.

Several sublethal responses, e.g. physiology, development, and behavior, have been presented in this paper and may provide better parameters as early warnings of anthropogenic stress than does mortality. As some invertebrate species are affected at levels as high as pH 6, even moderate acidification will, eventually, disturb the animals. Of the metals, Al appears to be more dangerous at low pH conditions, also in the absence of a tendency to increase upward in the food-chains to insects and birds (flycatchers) as earlier suggested. However, it has been suggested that with less discrepancy between background concentrations and least-known-effect levels, heavy metals such as Hg, Cd, Cu and Pb may still be expected to be more toxic (92).

An intermediate disturbance has been suggested to promote diversity in streams (93), but as all effects of acidification on the organism are unpredictable, even moderate stress will, in the long run, cause an adverse impact on most species. Irrespective of the mode of negative effects at a lowered pH, with concurrently enriched metals, the impact on the organisms diverts energy from its main purpose, i.e. to promote the growth, development, and reproduction of plants and animals.

Natural selection would, with time, favor those characteristics and individuals that can adapt to and survive under adverse conditions. No significant genetic changes have been demonstrated so far, but acclimation and changed tolerance do occur, also as a result of changed behavior. Genetic changes are less likely to have occurred in fish, but may have occurred in invertebrates. Restoration of acidified surface waters by liming has often been successful chemically, but sometimes less so biologically, because (re)colonization has proven to be a much more unpredictable and time-dependent than anticipated.

Future research needs on acidified surface waters have been proposed by Fleischer et al. (4). For streams, the most urgent needs are: (i) How and why are decomposition processes affected at low pH in different types of sediment? (ii) How can we explain observed or failed biological recovery after liming? (iii) Can we be certain about the original flora and fauna composition in pristine streams? (iv) Are changes in biotic relations in streams after changed pH really so unusual as inferred from existing observations? (v) Is there evidence that populations have adapted genetically to lowered pH levels? (vi) How is the trade-off between environmental stress against growth and reproduction manifested?

Since running waters are positioned in the immediate interface between terrestrial and aquatic ecosystems, studies of the interplay between the two, in terms of chemistry and biology, will provide the earliest possible information on anthropogenic effects. The sensitivity and usefulness are also due to the fact that streams are much more dynamic and variable both in space and time than are lakes. Thus, studies of the ecotones of running waters should be given higher priority to assess human impact on entire catchment areas.

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