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Effects of Acidification on Aquatic Ecosystems

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Abstract—Effects of acidification on aquatic ecosystems are analyzed on the basis of an analytical synopsis of relevant data. Major active agents influencing aquatic organisms and main trends in the reorganization of microbial, phyto- and zooplanktonic, benthic, and fish communities in an acidified environment are described. A generalized concept of changes in ecosystems caused by acid precipitation and accompanying factors is formulated. These changes include the reduction of biodiversity of all structural elements due to the disappearance of species sensitive to acidification, modification of trophic structure, and decrease of fish stock.

Key words: water acidification, changes in communities, microorganisms, primary producers, zooplankton, benthos, the fish component of communities.

In the 20th century, global pollution of the atmosphere with acid-producing substances (sulfur and nitrogen oxides) emitted during fuel oil and coal combustion and ore smelting created problems of acid precipitation and the consequent acidification of soil and waters. Despite a considerable reduction of SO_2 emission in Europe and North America, sulfate fallout onto drainage areas in the past 20 years has exceeded that in the preindustrial period by a factor of no less than ten. The emission of NO_x in recent decades has been either stable or increasing, and prognoses for several countries indicate that it may become comparable to that of SO_2 (Kuylenstierna *et al.*, 2001). Water acidification on the global scale remains an acute problem for the 21st century.

Water acidification is a complex process. Along with decrease in water pH, the direct and indirect influence of precipitating acid-forming substances and their dry absorption by the underlying substrate entail a complex of adverse phenomena. Saturation of soils with exchangeable bases occurs in the drainage area and, consequently, their content in surface and ground waters decrease; hydrocarbonates are displaced by stronger technogenic acids, so that water alkalinity becomes lower; and metals (Al, Cd, Zn, Mn, etc.) are leached from rock. An abrupt drop of pH in streams during spring and rain floods, referred to as pH shock, is especially dangerous for biological systems.

Investigations dealing with the effects of water acidification on biological systems are numerous. However, most of them were made in America, Canada, and Scandinavian countries, where this problem has received special attention. In Russia, such studies performed in Murmansk, Leningrad, and Vologda oblasts and the Karelian Republic confirmed the development of anthropogenic acidification of humid areas (Abakumov *et al.*, 1990; Flerov and Komov, 1991; Moiseenko, 1994, 1998; Golubkov *et al.*, 1997; Il'yashchuk, 1998; Yakovlev, 1998; Moiseenko *et al.*, 1999; Sharov, 2000; Korneva, 2000; Vandysh, 2002). However, the ecological consequences of water acidification have not been assessed comprehensively.

The purpose of this study was to make an analytical synopsis of relevant data obtained in Russia and abroad and, on this basis, to formulate a general concept of events occurring in aquatic ecosystems under conditions of acidification.

ACTIVE AGENTS

Adverse effects on aquatic organisms result mainly from changes in water acidity (pH), which involve an increase in the concentrations not only of hydrogen ions (H^+), but also of cations, such as inorganic (ionic) monomeric aluminum Al^{3+} and other metal ions. The toxic properties of Al^{3+} manifest themselves in acidified waters at concentrations as low as 30 μg/l (Rosseland and Staurnes, 1994). The impact of increased doses of aluminum leads to disturbances of metabolism in aquatic organisms, especially of mineral metabolism (Cronan and Driskol, 1990). Some investigations have shown that organisms living in an acidified environment accumulate the excessive amounts of harmful elements (Hg, Cd, Zn, Pb, etc.), which is due primarily to the low content of calcium in water and the resulting increased uptake of other elements (Haines *et al.*, 1992; Manio, 2001; Moiseenko and Kudryavtseva, 2001).

Anions of strong acids (SO_4^{2-} and Cl^-) may also take part in the impact on aquatic ecosystems. Nitrate (NO^{3-}) and ammonium (NH^{4+}) inflict damage indirectly: NO^{3-}, together with sulfate ions, contribute to a reduction in the acid-neutralizing capacity (ANC) of water; ammonium produces hydrogen ions (H^+) in the course of oxidation and is an additional source of biogenic elements for primary producers (Schindler, 1988). Secondary effects of acidification manifest themselves upon phosphorus binding by precipitating aluminum (Jansson, 1986). This may lead to a deficiency of biogenic elements, on the one hand, and to increasing water transparency, on the other (Dillon *et al.*, 1984); the latter provides conditions for a higher productivity at greater depths. The heat balance of acidified lakes changes under the combined influence of vertical mixing, decrease in the content of dissolved compounds, and the consequent increase in water transparency. The complex of aforementioned factors has an effect on the structural elements of the ecosystem.

MICROORGANISMS

The abundance of bacterioplankton in acid lakes is lower than that in lakes with pH values close to neutral (Rao and Dukta, 1983). This results in a lower rate of organic matter decomposition in aquatic ecosystems. Previous investigations demonstrated the displacement of bacteria by fungi in an acidified environment (Traaen, 1980). Flerov and Komov (1991), who studied anthropogenically acidified water bodies of the Darwin Reserve, demonstrated that the level of bacterial processes in aquatic ecosystems decreases upon acidification; the abundance of saprophytic bacteria decreases, whereas that of fungi increases due mainly to the development of pink yeast. Acidification entails a change of dominants in the fungal complex on plant substrates, favoring the development of a limited number of aquatic hyphomycete species.

An important aspect of the problem is that acidification, suppressing the microflora, has an inhibitory effect on the decomposition of organic detritus, a key process in water bodies. The accumulation of coarse organic debris (leaves and branches) in some acid water bodies may be used as an indicator of reduced microbiological activity (Andersson, 1985; Stenson and Erikson, 1989). Liming as a method of water acidity control aids in restoring microbial communities and increasing the rate of organic matter decomposition (Hultberg and Andersson, 1982).

PRIMARY PRODUCERS

Most investigations provide evidence that the biodiversity, biomass, and primary production of phytoplankton in acidified water bodies are reduced, and the composition of dominant species is transformed (Siegfrid *et al.*, 1989). According to Almer *et al.* (1978), the species diversity of phytoplankton decreases upon acidification from 30–80 species in neutral lakes to 10–20 species in lakes with water pH 5.0 and to only three species in lakes with water pH 4.0. Under such conditions, acidification-tolerant dinoflagellates (*Peridinium inconspicuum* Lemm.) and chrysophytes (*Dinobryon* sp.) may account for up to 30–50% of the total biomass (Stokes, 1986). These species are less competitive under neutral conditions, but acidification facilitates their development (Havens and DeCosta, 1987). Their ability to gain dominance at strong acidity may also be related to their protective morphological features, such as a hard shell (often of silicon) and jelly surrounding the body (Schindler *et al.*, 1985).

Korneeva (2000) showed that the algoflora of lakes with a low water pH has a reduced species diversity and is formed of monotypic species: as the proportion of stenobiontic species increases, the abundance of green algae, chrysomonads, and cryptomonads increases as well, whereas that of blue-green algae decreases. Changes in the structural and functional organization of phytoplankton occur when water pH decreases from 6 to 5. In acidified lakes of the mountain tundra (northern Fennoscandia), an increase in the proportion of acidobiontic and acidophilic species was observed against a background of general decrease in the species diversity of phytoplankton (Moiseenko *et al.*, 1999; Sharov, 2000).

According to Flerov and Komov (1991), the seasonal average content of chlorophyll *a* in the lake phytoplankton averaged 1.1–1.7 μg/l at low values of water pH and color, 5.4–8.1 μg/l in waters with a similar pH but enriched with humus, and 40–77 μg/l in neutral eutrophic waters.

Periphyton develops abundantly in acidified water (Stevenson *et al.*, 1985). In naturally acid water bodies, periphyton is usually less abundant (Stokes, 1981); in anthropogenically acidified aquatic systems, species of the genera *Mougeotia, Zygogonium*, and *Spirogyra* develop abundantly. At higher acidity, their development leads to an increase in the phytomass of algal periphyton per unit area. This increase in productivity and biomass is also conditioned by the decreasing abundance of invertebrate consumers (e.g., crustaceans) and even herbivorous fishes, such as gudgeon (Howell, 1988). Other relevant factors include changes in water transparency, thermal conditions, and alleviation of competition due to the inhibited development of organisms sensitive to acidification. In addition, the growth of periphyton in acidified lakes is promoted by an increasing content of readily accessible carbon (Stokes *et al.*, 1989).

In North America, the number of macrophyte species in lakes decreases, which is attributed to acidification and accompanying factors, especially an extremely low calcium content in acid oligotrophic lakes (Jackson and Charles, 1988). In some regions of Central Europe and Scandinavia, increasing water acidity results in the expansion of sphagnum mosses (Grahen, 1986) but restricts the distribution of species dominating in subneutral (pH 6.5) lakes, such as *Juncus bulbosus* L., *Lobelia dortmanna* L., and *Littorella uniflora* L. (Roels, 1983).

At the same time, as the transparency of acidified waters increases, higher aquatic vegetation expands to greater depths, and species tolerant of the acid environment (water mosses) develop more actively. Production of mosses in acidified Lake Goluboe (Karelia) is several times higher than in neighboring neutral lakes, while the content of chlorophyll *a* is an order of magnitude lower (Il'yashchuk, 1998; Golubkov *et al.*, 1997). This fact indicates that the contribution of bottom plant communities to primary production increases in acidified water systems. Sphagnum forms a dense layer on the water—bottom boundary, which limits the development of many organisms and interferes with processes occurring in the water body (Dillon *et al.*, 1984). Sphagnum actively absorbs cations and releases H^+ in the course of metabolism, thus contributing to water acidification (Brakke *et al.*, 1987).

Neutralization of acidified lakes and their natural reclamation upon the reduction of acid load lead to a decrease in the abundance of filamentous algae (Griffiths, 1987; Keller, 1990) and acidophilic macrophytes (Hultberg and Andersson, 1982), which is accompanied by the recovery of acid-sensitive species, because the concentration of bicarbonates in water increases (Eriksson *et al.*, 1983).

ZOOPLANKTON

Acidification of the aquatic environment leads to changes in the species composition, abundance, and ratios of particular taxonomic groups, which is reflected in the structure of zooplankton. Some representatives of this group may suffer from both the direct influence of low pH and higher doses of Al^{3+} and indirect effects resulting from changes in the abundance and composition of primary producers and species of higher trophic levels: large invertebrates, plankton-eating fishes, and predators, including waterfowl.

The species diversity of zooplankton decreases at higher acidity, especially when water pH decreases below 5.5 (Harvey *et al.*, 1981). This fact has been confirmed by numerous observations in nature (Flerov and Komov, 1991; Moiseenko *et al.*, 1999; Vandysh, 2002; Hobaek and Raddum, 1980; Certer *et al.*, 1986; Tessier and Horowitz, 1988; Abakumov *et al.*, 1990) and in experiments on lake acidification (Malley and Chang, 1982). Studying the effects of acidification on zooplanktonic communities of lakes in Norway, Hobaek and Raddum (1980) found that the average number of species decreased from 16 to 7 when water pH changed from 5.5–6.0 to 5.0 or a lower value. In Canadian lakes, *Mysis relicta* and three other species of crustaceans disappeared when pH decreased from 6.7 to 5.0–5.1 (Jeffries, 1997). Most species of daphnias cannot exist in lakes with low pH (Nilssen, 1980; Carter *et al.*, 1986). In Canadian lakes, *Daphnia galeata* proved to disappear at pH 5.5–5.0 and appear again when pH increased to 5.6 (Jeffries, 1997). In laboratory experiments, the critical pH value for this species was estimated at approximately 5.1 (Malley and Chang, 1986). Disappearance of some daphnia species sensitive to acidification is explained by the direct impact of active agents on their organism, which results in disturbances of osmotic regulation, reduced oxygen consumption, and precipitation of aluminum on the filtering apparatus (Alibone and Fair, 1981).

In acid lakes of the Darwin Reserve, in contrast to water bodies of Western Europe, the bulk of zooplankton biomass (90%) consists of the bidominant complex of *Eudiaptomus graciloides* and one cladoceran species. Rotifers are absent from these lakes. According to Salazkin (1976), cladocerans dominate in highly acidified water bodies with pH < 4.7. Svirskaya (1991) notes that the group of species most resistant to acidification includes *Scapholeberis mucronata, Alonopsis elongata, Alonella nana, Polyphemus pediculus*, and *Bosmina obtusirostris.* Some lakes are characterized by active development of *Eucyclops serrulatus* and *Acantholeberis curvirostris*, the species preferring water with higher acidity (with a limit at pH 3.5–4.0). Large cladocerans *Limnosida frontosa* and *Leptodora kindtii* are infrequent, as they avoid waters with increased acidity and high content of humic substances.

In small mountain-tundra lakes exposed to anthropogenic acidification, the species composition of zooplankton is poor and its quantitative parameters are low (abundance 6500–12000 ind./m^3, biomass 0.3–0.5 g/m^3), which is characteristic of acid lake ecosystems (Vandysh, 2002). Biodiversity fluctuates within a range of 1.4–2.1 bit/ind. Its decrease is due to both the reduction of species number in the community and the increasing dominance of species resistant to acidification (Lazareva, 1994). Water reactivity may limit the number of species in lakes at pH < 5.5.

Numerous biological tests on some zooplanktonic species have shown that the effects observed in laboratory experiments are comparable with those occurring in natural acid lakes. The disappearance of the copepod *Cyclops scutifer* at pH < 5.0 apparently results from disturbances of normal reproduction and population replenishment, rather than from direct poisoning of adult individuals (Tessier and Horowitz, 1988). An adult *Cyclops scutifer* can live in highly acidic water (pH 4.0–3.5), but its progeny fails to develop (Arvola *et al.*, 1986). The decrease in reproductive efficiency observed in *Daphnia pulex* was related to disturbances of its maturation.

Changes in the structure and biomass of zooplanktonic communities in acidified water bodies are often related to changes in the trophic structure of the entire aquatic ecosystem. In some cases, the abundance of large specimens in zooplankton increases with an increase in acidity, because the rate of their consumption by fishes becomes lower, whereas small-sized zooplankters are actively consumed by large predatory forms (Dillon *et al.*, 1984; Flerov and Komov, 1997). In other cases, small zooplanktonic forms dominate, which may be due to the presence in these lakes of plankton-feeding fishes (Stenson and Eriksson, 1989).

Experiments on water neutralization by liming in acidified lakes showed that their communities recovered very slowly (Hultberg and Andersson, 1982). Water neutralization in an acid lake in the vicinity of Sadbury, Canada, provided for the return of species sensitive to acidification, such as *Epischura lacustris* (Gunn and Keller, 1990).

Thus, although the altered complexes of the zooplanktonic community in acid lakes are formed in different ways, acidification always favors the development of a limited number of species resistant to this factor, which leads to the reduction of biodiversity.

BENTHOS

The impact of water acidification on benthic communities manifests itself within a short period due to the high sensitivity to acidification of many species of mollusks, crustaceans, and aquatic insects (mayflies, stoneflies, caddis flies) (Okland and Okland, 1986; Raddum *et al.*, 1988; Golubkov *et al.*, 1997; Il'yashchuk, 1998; Yakovlev, 1998; Raddum and Skjelkvele, 2001).

An abrupt decrease in the abundance of mayflies was observed upon a decrease of pH to 6–5.5 (Raddum and Fjellheim, 1984). However, some species of *Leptophlebia* proved to survive even pH 4.5–5.0 (Mackay and Kersey, 1985). Upon acidification to pH 5.5, the abundance of mayflies decreased by 60%, whereas that of stoneflies increased by more than 30% (Raddum and Fjellheim, 1984).

The effect of acidification on amphipods is similar: *Hyalella azteca* in acidified lakes of North America (Stephenson and Mackie, 1986) and *Gammarus lacustris* in Scandinavia are either absent or very rare in waters with pH 6.0, which is indicative of their high sensitivity. An isopod of the genus *Asellus* is more tolerant and occurs at lower pH (Okland and Okland, 1986). Crustaceans *Orconectes viriis, O. rusticus*, and *O. propinquosus* are absent from North American lakes with pH < 5.6. The Scandinavian species *Potamobius astacus* is still more sensitive and rarely occur at pH 6.0 (Berrill *et al.*, 1985).

The mollusks, including gastropods and small bivalves (Sphaeriidae), are similarly sensitive (Muniz, 1991), and their abundance decreases at higher acidity. In Norway, gastropods (including widespread species typical of oligotrophic lakes) were generally absent from waters with pH decreasing to 5.2, while bivalves disappeared at pH 4.7. A similar effect was observed in the United States (Singer, 1984), Canada (Jeffries, 1997), and Great Britain (Sutcliffe and Carrick, 1973). Mollusks and crustaceans need calcium for building their shells, and its shortage in acidified waters may be the main factor limiting their development.

Mysids *Mysis relicta* disappeared at pH 6.0–5.8; crustaceans *Orconectes virilis* poorly reproduced at pH 5.6 and disappeared at pH 5.0. The decrease in the abundance of these crustaceans was attributed to the high sensitivity of juveniles to acidification and disturbances of gamete maturation under the effect of this factor (Davies, 1989).

Periodic acidification of streams and elevated concentrations of labile Al entail an increased mortality and drift of sensitive mayfly species (Ormerod *et al.*, 1987). As a consequence, their communities in the upper reaches of rivers become impoverished even at the early stages of acidification. This phenomenon was investigated in 1937–1942 and 1984–1985 in Canadian streams (Hall and Ide, 1987). Similar changes were observed in many streams exposed to acidification in Scandinavia (Mossberg, 1979; Engblom and Lingdell, 1984) and Germany (Matthias, 1983). In general, the number of genera in all groups of large invertebrates decreases in acidified waters from 25 to 8, i.e., by two-thirds.

In acidified waters of the Darwin Reserve, the species composition of benthos is extremely poor. Chironomid larvae dominate, whereas the abundance of oligochaetes is low (Flerov and Komov, 1991). In northern Europe, benthic organisms of the lotic and lentic systems that are most sensitive to decrease in water pH are as follows: amphipods; gastropods Valvatidae and *Lymnaea*; and the nymphs of mayflies (except Leptophebidae, *Heptagenia fuscogrisea*, and *Caenis horaria*) and stoneflies (except *Nemoura* spp.). The amphipod *Gammarus lacustris* is absent from water with pH < 6.5. Of gastropods, only *Gyraulus albus* occurs at pH < 6.0. On the contrary, oligochaetes, isopod *Asellus aquaticus*, mollusks *Pisidium* spp., Hydracarina, beetles Dytiscidae, bugs Corixidae, and the larvae of chironomids, mayflies, dragonflies, orl flies (*Sialis* spp.), mayflies Leptophebidae, stoneflies *Nemoura* spp., and caddis flies (Phryganeidae, Limnephilidae, *Cyrnus flavidus, Polycentropus flavomaculatus, Neureclipsis bimaculata*, and *Plectrocnemia conspersa*) are common inhabitants of acidified lakes and streams. As water pH decreases, the species diversity of mollusks, mayflies, and stoneflies consistently decreases as well, and changes occur in the complex of dominant species (Yakovlev, 1998, Table 1).

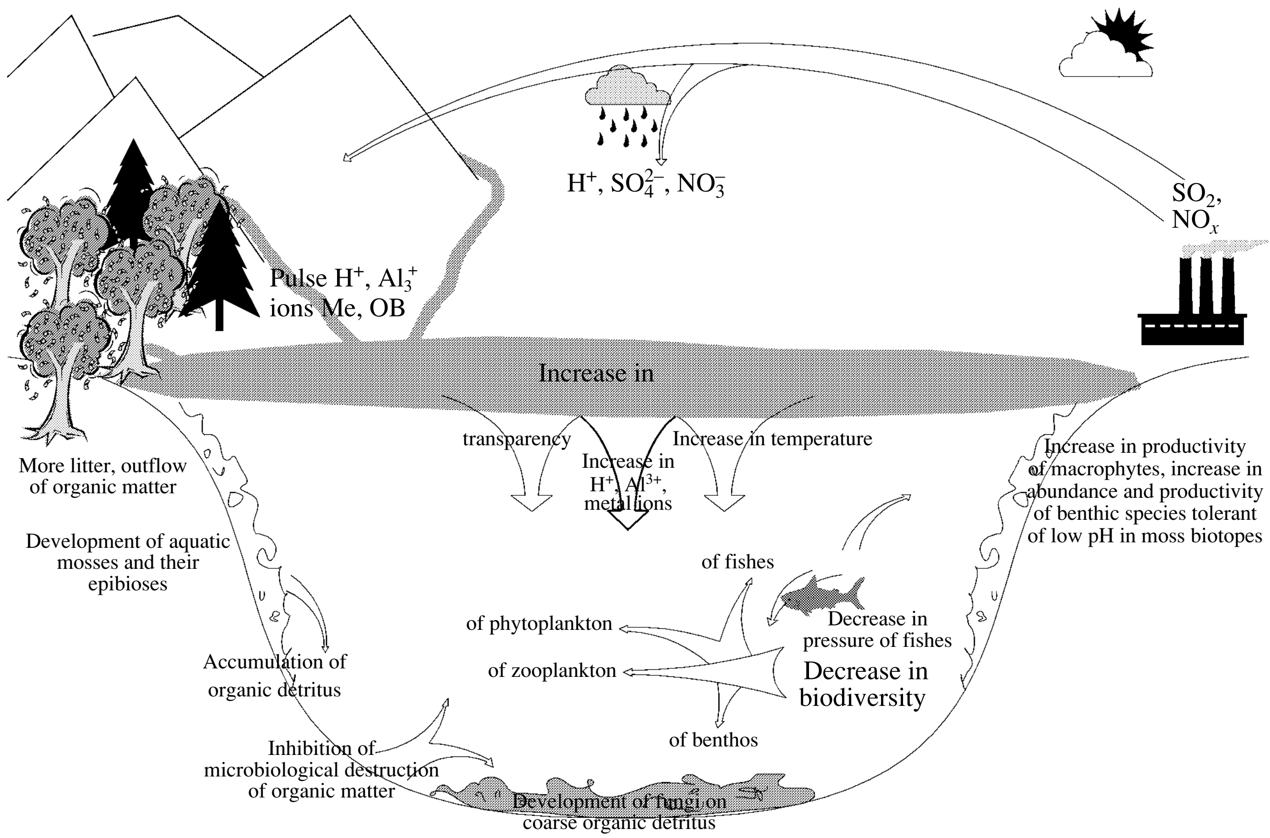
High acidity exerts its effect on aquatic invertebrates in different ways: in some cases, they are chronically exposed to constantly low pH; in other cases, they suffer from abrupt pH drops (pH shock), which, combined with mobilization of metal ions, may destroy the aquatic fauna. Organisms living on the surface and in the littoral zone are more vulnerable to occasional acidification than those living in bottom sediments, burrows, and the deepest parts of a lake (Raddum, 1980).

Table 1. Distribution of species and higher taxa depending on acidification level of surface waters in northeastern Fennoscandia and the Kola Peninsula (Yakovlev, 1998)

Taxon, species	Acidification
Gastropoda: *M. margaritifera, G. lacustris, Baetidae* spp. (except *B. rhodani), Ephemera* spp., *Metretopus* spp., *A. ladogensis, B. minutus, N. ciliaris, Ph. montanus, Tinoedes waeneri, W. subnigra*	None or weak, pH > 6.0 (may temporarily decrease to 5.5 during floods)
Himdinea: *Daphnia* spp., *A. inopinatus, B. rhodani, Caenis horaria, Centroptilum luteolum, Heptagenia* spp., *Siphlonums* spp., *Capnia* spp., *Diura* spp., *Isoperla* spp., *L. fusca, L. hippo–pus, Limnius wolckmari, Apatania* spp., *Hydropsyche spp., L. hirtum, Oxyethira* spp.	Medium, pH 6.0–5.5 to 5.0 during floods or rains
Pisidium spp., *Heptagenia fuscogrisea, D. nanseni, Nemoura* spp., *Elminrhidae* spp., *Limnephilidae* spp., *Polycentropodidae* spp., *Rh. nubila, Phryganeidae* spp.	Considerable, pH 5.5–4.8, to 4.5 during floods or rains
Diptera: *A. aquaticus, Leptophlebidae* spp., *Odonata* spp., *Corixa* spp., *Dytiscidae* spp., *Sialidae* spp.	Strong, pH < 4.7

Hydrogen ions have a differential effect on bottom invertebrates at different stages of the life cycle. Laboratory experiments have shown that water acidification is especially harmful to gametes, juveniles, and molting individuals (Davies, 1989). This finding was confirmed in field studies on *Gammarus* (Engblom and Lingdell, 1984) and *Hyalella* (France and Stokes, 1987). The impairment of reproduction and growth was observed in mayflies *Ephemerella funeralis* and gastropods *Amnicola* spp. (Muniz, 1991). These effects are apparently characteristic of all acidification-sensitive species.

The destructive effect of low pH on invertebrates is related to physiological processes, such as disturbances of ionic and osmotic regulation and, in some groups, the loss of NaCl. Inorganic aluminum in combination with H^+ can also affect physiological processes. In some bottom invertebrates, disturbances of the respiratory function were revealed (Muniz, 1991).



General scheme of direct and indirect effects of acidification on aquatic ecosystems.

The effect of acidification on the total biomass of bottom communities is ambiguous. There is evidence for its decrease (Okland and Okland, 1986), but some authors have shown that it increases due to changes at the upper level of the trophic structure of the ecosystem. In acidified streams of northern England, Schofield *et al.* (1988) observed an active development of predatory forms tolerant of acidification, including caddisworms *Plectrocnemia conspersa.* This phenomenon may be explained by alleviated competition among these forms and reduced pressure of fish predation. Great numbers of larger predatory invertebrates, including damselfly and dragonfly larvae, were found in acid lakes in Sweden, and this could also be attributed to the reduced pressure of predation by trout and other insectivorous fishes (Erikson *et al.*, 1983).

The development of water mosses provides additional substrate for epibioses and, thus, improves food supply for benthic species feeding on periphyton; on the other hand, water mosses serve as shelter from predatory fishes. As microbial decomposition of allochthonous material in acid water bodies is inhibited, species capable of utilizing coarser organic detritus (gnawing species) prevail over species feeding on microalgae (Stenson and Eriksson, 1989).

Recent investigations (Golubkov *et al.*, 1997; Il'yashchuk, 2002) demonstrated the increasing significance of the benthic subsystem in the general metabolism of acidified water bodies. The most productive communities are formed in the biotope of water mosses. They play the main role in the regeneration of phosphorus. The productivity of benthic animals in the biotope of water mosses is several times higher than the average productivity of benthic communities in neutral water bodies. In an acidified lake in Karelia, the seasonal average ratio of production to total expenditures for metabolism in zoobenthic communities was close to 1.0, whereas that in a nearby nonacidified lake was approximately 0.4. A high value of this ratio is a direct consequence of simplification of the community structure (Golubkov *et al.*, 1997). These data show that acidification of the aquatic environment has both direct and indirect effects on benthic communities. Decrease in the number of taxa is a direct effect, whereas the expansion of littoral communities and acidification-resistant species to greater depths and the consequent increase in the contribution of benthic communities to total ecosystem production are indirect effects.

Experiments on liming and investigations on lakes recovering their acid-neutralizing capacity upon reduction of acid load have shown that acidification-sensitive species repopulate their biotopes under such conditions, and the abundance of benthic organisms is restored (Raddum *et al.*, 1986). However, the initial characteristics of communities are not recovered (Gunn and Keller, 1990).

Table 2. Relative sensitivity of different fish species to water acidity according to data on 50 lakes in Sweden (Almer *et al.*, 1974)

Sensitivity	Species
Higher	*Leuciscus rutilus*
↓	*Phoxinus phoxinus*
	Salvelinus alpinus
	Salmo trutta
	Coregonus albula
	Perca fluviatilis
	Esox lucius
Lower	*Anguilla vulgaris*

FISHES

In thousands of lakes in Scandinavia (Henriksen *et al.*, 1989; Muniz, 1991), Europe, and North America (Dillion *et al.*, 1984), acid precipitation has reduced or even completely destroyed fish stocks, dramatically demonstrating the hazard of acidification. Freshwater fishes living in oligotrophic streams, rivers, and lakes are highly sensitive to this factor. Numerous facts show that acidification is responsible for the disappearance of some species or for changes in the species abundance ratio in fish communities. Since the 1950s, some fish species have gradually disappeared from remote lakes (not exposed to economic activities) in the mountains of Ontario, Canada, as a consequence of their increasing acidification (Beamish *et al.*, 1975; Harvey and Lee, 1980; Jeffries, 1997). The following example is illustrative: of eight fish species inhabiting Lake Landsen in the 1950s, *Perca flavescens* and *Lota lota* have not been caught since 1960; *Salvelinus namaycush* and *Cottus cognatus* disappeared between 1960 and 1970; and the abundance of *Catastomus commersoni, Coregonus arteedi*, and *Couesius plumbeus* has decreased. The dependence of the decreasing number of fish species on increasing water acidity was established (Harvey and Lee, 1980; Matuszek and Beggs, 1988). Similar results were obtained in American lakes, in the Adirondack Mountains: lake trout and stream trout were usually absent from these water bodies if water pH was below 5.4 and 5.1, respectively (Schofield and Driscoll, 1987). The disappearance of minnow, roach, and, finally, pike and eel (the most resistant species) according to the same scenario was observed in Swedish lakes (Almer *et al.*, 1974). Table 2 shows comparative data on the sensitivity of various fish species to low pH.

The main factor responsible for degradation of fish populations upon acidification is the direct impact of low pH and Al^{3+}, which results in biochemical and physiological disturbances (Rosseland and Staurness, 1994). The target systems in fishes are gills and sensory organs, and the most vulnerable stages of the life cycle are larvae and fry.

For anadromous fishes, the zones where acid river waters mix with more alkaline lake or sea waters present a serious hazard: under these conditions, dissolved aluminum coagulates on the gills, and the effect may be lethal (Rosseland and Staurnes, 1994). In acidified waters with a low calcium content, fishes more actively accumulate many elements, including highly toxic Hg, Pb, and Cd, even when their concentration in water is below the sensitivity threshold of analytical methods. Thus, fishes may be used as indicators of the indirect effects of water acidification (Moiseenko and Kudryavtseva, 2002).

Special attention has been given to the causes of a sharp decrease in the abundance of Atlantic salmon in Norwegian rivers in the 1970s and 1980s. Analysis of statistical data on fish catches showed that the reduction of fish stock was due to acidification of spawning rivers. The tendency toward the recovery of Atlantic salmon populations in the past decade is explained primarily by a decrease in acid load and restoration of the buffering properties of waters (Krogland *et al.*, 2001).

SUMMARY

(1) The fallout of acid-forming substances on drainage areas and water acidification have both direct and indirect effects on biological systems, causing changes in individual organisms, communities, and whole ecosystems.

(2) At all levels of ecosystems, biodiversity decreases upon acidification due to elimination of species that are most sensitive to low water pH. The microflora and destruction processes are inhibited, whereas fungi gain dominance; as a result, coarse organic detritus accumulates on the bottom of acidified lakes and rivers. The trophic structure of bottom communities changes towards a prevalence of gnawing species. Water transparency increases, and macrophytes expand to greater depths, with water mosses resistant to acidity developing most actively. Changes in production processes are ambiguous: they are usually inhibited in strongly acidified waters, but the productivity of communities consisting of acidification-tolerant species often increases due to modification of their trophic structure and alleviation of competition with acidification-sensitive species and predation by fishes.

(3) Decrease in acid fallout has a favorable effect on biological communities. In recent decades, a tendency toward their recovery has been revealed in water systems with increasing pH values and alkalinity. In some lakes of Canada and the United States, repopulation of biotopes with acidification-sensitive species and increasing biodiversity of aquatic communities have been observed. However, communities and ecosystems generally do not recover their initial (natural) characteristics.

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