

Functioning

So called dystrophic lakes (the term introduced by Naumann 1931), recently named more frequently humic lakes (Wetzel 1983), are as a rule small (surface area of several to twenty hectares) and shallow (mean depth of several to twenty meters) mid-forest lakes without or with weak outflow. The lakes are hydrologically linked with mire systems and moss peatlands. Their drainage basins are covered primarily by coniferous forests. The lakes are typical constituents of boreal and cool temperate forests. Their characteristic features include low calcium content (several mg l⁻¹ vs 40-60 mg l⁻¹ in meso-eutrophic lakes, therefore being termed soft-water lakes), browncoloured water (therefore being termed stained, coloured or brown-water lakes) due to run-off and accumulation of humic compounds, and high transparency due to typically low productivity. Water, and most of all sediments, are clearly acidic (pH of 4.5-5.5) or weakly acidic (pH of 5.5-6.5) (Starmach et al. 1976). Low pH is a biological effect of peatmoss (Sphagnum) occurring around a

lake or even expanding over its water table in the form of a mat with water pH about 4.0-5.0 or even as low as 3.0 (Wetzel 1983). Such a peatmoss system causes cations to be continuously exchanged, with calcium and magnesium ions being captured, and carboxyl-associated hydrogen ions being released (Wetzel 1983). Presence of peatmoss littoral as well as acid raw humus loading from the conifer catchment is a constantly acidifying factor that maintains the relatively low pH of these ecosystems (Halsey et al. 1997). These factors render acidic, humic (lowland) lakes different from acid clear water lakes characteristic of lowland areas on granite bedrocks (e.g. in Scandinavia or Canada), and of mountainous or piedmont areas where the low pH is an geological effect (lack of cal-

cium in the soil and slow weathering of parent rocks).

Humic lakes are relatively low productive, this being related to plankton rather than littoral, as the latter one may be composed of various rich communities of aquatic and mire plants as well as fila-

mentous and periphyton algae. This is a consequence of allochtonous matter input, i.e. humus and humic compounds (humic and fulvic acids, humins) of typically high-molecular weight (over 1000 daltons) (Jones 1992a, b, Tulonen et al. 1992), imported from the terrestrial and peatland surrounding and then accumulated in these lakes. Humic compounds are principal constituents of organic carbon pool in these lakes (De Haan 1992). These compounds are produced during decomposition of lignin - a component of terrestrial and aquatic plants (Jones 1992a, b). Strong metalbinding ability of humic compounds leads to complexation with iron (giving brownish-coloured water), aluminium, phosphorus as well as aminoacids. As an effect, large and fairly stable complexes of aggregate, colloid or even flock (particles larger than 0.02 µm) types are often produced. The deposited material, being at different stages of fragmentation and decomposition of plant remnants, forms sediments of Dy type characterised by C:N ratio exceeding 10 and semi-liquid consistency (Wetzel 1983). Chemical oxidation in stained lakes is usually much more higher than biological oxidation, the latter being related to a fraction of organic matter easily decomposed by bacteria. A pool of potentially bioavailable and recycled phosphorus is usually very low. Labile P is bound to a fraction of organic matter containing compounds of low-molecular weight (about 100 daltons) and constitutes not more than 10% of total P in sediments (Rzepecki 1997). Humic compounds are thereby a trap for phosphorus, which can be released either photochemically (UV radiation) or through the enzymatic bacterial decomposition (Wetzel 1983). Under such conditions, production of pelagic planktonic algae is low or even negligible when compare with that of eutrophic lakes. Turnover time of phosphate phosphorus is very long (Jones 1992b), and P³²O₄ added disappears quickly as it is captured by macrophytes. Jones (1992b) and Salonen et al. (1992 a, b) have revealed that functioning of a humic lake is based on heterotrophic food chain. The chain consists successively of: DOM (dissolved organic matter) pool of allochtonous (mainly low-molecular) origin and metabolised by bacteria - bacterial biomass - microzooplankton (flagellates, ciliates) and larger plankton grazers. The principal mechanism of P regeneration does not consist in P release from deposits but in P excretion by zooplankton. The metabolised (low-molecular) DOM fraction is small and presumably does not constitute more than 30–40% of the total DOM pool. Tulonen et al. (1992) has revealed that 63% of DOM consists of high-molecular compounds (over 10000 daltons), probably resistant to decomposition or of long decomposition time (especially under conditions of low pH). Resistance to bacterial decomposition is also characteristic of a large POM fraction (particulate organic matter), which is therefore not available as food for Daphnia, this having been experimentally proved by Kairesalo et al. (1992). On the other hand, bacterial biomass produced through metabolising DOM, the structure of which is prone to enzymatic decomposition by bacteria, displays high P-cell quota which, according to Hes-

sen's opinion (1992), indicates strong P-limitation.

Conclusions important for lake management, protection or manipulation which may be drawn from the above concise description of humic lake functioning are following: – A humic lake constitutes a part of a unified functional system where peatmoss and forest surrounding the lake maintain its low pH (with overall consequences like slow decomposition, specific biota), may prevent possible pH increases, control phosphorus cycling through P complexation by humic compounds excreted by mosses or through P adsorption on humus particles;

– Energy and matter fluxes through the system are based primarily on allochtonous material received from the outside and from its own littoral. The incoming matter (humus) is highly resistant to bacterial decomposition. Some small fraction of it which is metabolised by bacteria enters trophic web of the lake through microbial loop (bacteria \rightarrow microzooplankton \rightarrow larger zooplankton). Nutrients are principally regenerated through *in vivo* excretion by heterotrophic components, not by bottom deposits.

- The peatland surrounding the lake as well as in-lake pools of POM and DOM (including deposits) are basically a trap for P and therefore production of autochtonious plankton dependent on bioavailable and regenerated P is low, so is algal biomass, this leading to a strong competition among herbivors.

Thus, the lakes are strongly P-limited and low-productive, which means that they are particularly susceptible to any nutrient supply, especially when pH tends to be increased or in cases when peatmoss and coniferous forest surrounding the lake are eliminated.

Protection

In the hilly lakelands prevailing in north-eastern part of Poland lowland humic lakes are important components of post-glacial landscape. These lakes particularly stabilise water retention in a region and contribute to nature resources and ecosystem diversity. No precise estimates exist of number, distribution nor water resources of humic lakes in Poland. There are about 6000 of small (1–10 ha) lakes in Poland constituting 65% of the number of all natural lakes, but not more than 6% of their total surface area (Chojnowski 1986, after Majdanowski). Vast majority is located in northern (e.g. Masurian or Pomeranian) lakelands. Although there is no precise information which of them are humic, it may be assumed that such lakes constitute a large fraction of shallow lakes in that region of Poland. Humic lakes together with associated peatlands provide refuges of unique, relict and rare species of plants and animals (particularly invertebrates)

and thereby are of special importance for biological diversity. According to e.g. Lewandowski's (1994) list of protected lakes (excluding these ones which are situated in national parks) about 150 isolated humic lakes are protected as nature reserves. It may be assumed that further tens of protected humic lakes are located in national parks. These are for instance so called "suchary" in Wigry National Park (North-eastern Poland), between ten and twenty of which have already been described since 20-ties as well as in recent years (Zdanowski 1992). An example of typical humic lakes, between twenty and thirty of which are reserves, are so called "lobelian" lakes characteristic of Pomeranian Lakeland. These lakes have low ($\leq 20 \text{ mg l}^{-1}$) calcium content, pH between 5 and 6 and rare, relict (boreal) plant species such as Lobelia Dortmanna, Isoëtes lacustris, Littorella uniflora and others (Kraska 1994).

Sparse distribution, small size, and closed hydrological system, all these factors render humic lakes particularly sensitive to human activity. Among the most important, acidification resulting from external (precipitation, drainage basin) supplies of acid-forming compounds is to be mentioned as it may lead to a decrease in water and sediment pH below a natural level, i.e. below 5.0. Equally hazardous is eutrophication that may occur as an effect of e.g. nutrient loading combined with acidity neutralisation (through e.g. liming), introducing fishery, fertilisation or forest clearance. Another important threats to the biogeochemical balance and to biodiversity of lowland humic lakes are lowered ground water table and wetland drainage in their watersheds.

Acidification

Acidification of waters, sediments and soils by acid precipitation has commonly been documented in lowland and mountainous areas of northern and central Europe (Scandinavia, England, Germany) supported by international programmes (M a s o n 1990). Results of the various studies have served as a base to recognise such direct effects of enhanced acidification like sequential extinction of particu-

as well as in North America (Canada, United States), where for geological or biological reasons buffering capacity of waters and sediments is low (R off and K w i a t k o w s k i 1977, S t o k e s *et al.* 1989). The process is also analysed in Poland (P a w ł o w s k i 1997).

Acidification mechanisms have been described following recognition of long term effects of acid deposition and hence reduced pH of surface waters (K w i a tk o w s k i and R o f f 1976). The findings have been supported by experimental studies with simulated acid rain (B r ez o n i k *et al.* 1986, 1993), using bioassay method, in-lake enclosures (L o c k e 1991, H a v e n s 1992a, G o n z a l e s and F r o s t 1994), by whole-lake experimentation (S c h i n d l e r 1991) and paleolimnological studies (R e n b e r g *et al.* 1993).

Numerous global and regional syn-

and communities with lar species decreases in water and sediment pH and arrangement of the biota in order of increasing acid sensitivity (e.g., MacIsaac et al. 1986, Stokes et al. 1989, Morling and Willen 1990, Olem 1991, Siegfried and Sutherland 1992, Marmorek and Korman 1993). It has been shown that pH of about 5.0-5.5 is critical for majority of fish, crayfish and invertebrates (e.g. Mierle et al. 1986, Stokes et al. 1989, Olem 1991, Locke et al. 1994). When pH falls below 5.5, toxic aluminium ions are being mobilised. The ions are believed to be the main factor responsible for extinction of ichtyofauna (Nyberg et al. 1986, Dickson 1988) as well as higher plants from the acidified lakes through phosphorus capturing by Al ions at pH < 4.5 (Motowicka-Terlak 1993).

theses have been made for Scandinavia and other areas of northern Europe, North America, e.g. mountain areas of Adinrondack (Hörnström and Ekström 1986, Adriano and Johnson 1989, Henricksen 1989, Norton *et al.* 1989, Stokes *et al.* 1989), these being

However, many authors have claimed that biocenotic and ecosystem consequences of lowered pH of lake waters are fairly diversified and must not be necessarily explained by laboratory studies on tolerance of single species or organisms to pH gradient and related metal toxicity. Some detectable changes may already occur between 5.5 and 6.5 pH. Schindler (1991) and Schindler *et al.* (1991) have pointed out that in the above pH range noticeable changes in biodiversity occur (development of some species at the expense of some others), whereas functional properties such as primary production or respiration show little, often undetectable changes.

Different rates of acidification-related structural changes has also been emphasised by Stokes et al. (1989) and Locke and Sprules (1993, 1994) who have shown that stability of planktonic food web (e.g. species richness of each link and link number) does not change markedly unless pH falls below 5.0. Studying food webs in tens lakes ranging from 4.7 to 7.3 pH, Havens (1993a, b) has found that, stability and complexity of their trophic structure declined with pH decrease. However DOC resources alleviated the direct effect of lowered pH owing to e.g. humus ability to bind the toxic aluminium (Fleischer et al. 1993). According to Porcella et al. (1989), the above phenomenon indicates that transformations in humic and clear water lakes exposed to similar pH changes may proceed at different rates, showing generally a lower rate in lakes rich in organic matter. However, investigations of humic lakes response to acidification indicate that the particular components of a biocenosis react to lowered pH on different rate. The whole-lake response not only depends on the magnitude of pH deviation from its natural levels or the pool of humus resources. The possible elimination of "top" predators, mainly fish brings about secondary changes in the plankcommunity of invertebrates tonic (Stokes et al. 1989, Steinberg and Wright 1994). Thus, indirect effects seem to be more important than the direct ones such as consequences of physiological stress caused by low pH and metal toxicity. The direct effects seem to be generally restricted to fish and certain (usually predatory) invertebrates and this is why acid or acidified lakes are practically fishless. This fact is important as it secondarily affects the functioning of a lake.

In some acidified lakes, decline in predatory Chaoborus larvae affects zooplankton to a higher degree (Y a n et al. 1991) than acidification itself. A p pelberg et al. (1993) have pointed out that two mechanisms are involved in the indirect effects of acidification: "topdown" - associated with fish and other predator elimination, and "bottom-up" consisting in CO₂ changes in a system and resulting in fixed dominance of such plants as Sphagnum and Juncus in the littoral. According to Fleischer et al. (1993), reduced decomposition of dead plant material (especially at initial stages) in acid lakes results from elimination of invertebrates - shredders that break up plant remnants rather than from a direct effect of low pH of water or sediments. Bell and Tranvik (1993) have found that under acidic conditions bacteria and phytoplankton are co-limited due to their similar nutrient requirements, and that changes of phytoplankton influence bacterial production to a higher extent than lowered or raised pH does. Nyman (1990) has noticed that Calanoida dominance in zooplankton following decline in Cladocera (the group more sensitive to acidification) is an additional factor removing and inactivating phosphorus, because slowly degradable faecal pellets of copepods, when deposited in sediments, remain practically intact, not decomposed under conditions of low sediment pH.

Recovery

To mitigate acidification problem in surface waters, liming is commonly used in case of lakes and streams having low buffering capacity. The measure was used in Scandinavia as early as in 70-ties (Olem 1991) and since then it has become common in every area endangered by acidification, i.e. where alkalinity was lower than 0.05 meq l⁻¹, and pH constantly ≤ 6.0 (Nyberg and Thörnelöf 1988, Rosseland and Hindar 1988, Henricksen et al. 1995, Svenson et al. 1995). There are series of long term observations, including those made under experimental conditions where whole-lake response has been studied. Some examples of such investigations include the famous Lake Gardsjön in Sweden (Dickson 1989, Wright and Haubs 1991), Lake Hovvatn in Norway (Raddum et al. 1986), lakes in the Netherlands (Bellemakers et al. 1994), Scotland (Brown et al. 1988) or mountain lakes in Montana in USA (Weither et al. 1994). Lime is sometimes applied to a lake and its catchment area, like in the case of Lake Gardsjön (Brocksen and Wiśniewski 1988, Brown et al. 1988) or a comparison is made between a limed lake versus reference lake (Elser et al. 1986). There are various liming techniques (e.g. by air), limestone forms (powdered, liquid etc.) (Lessmark and Thörnelöf 1986, Svedrup and Warfringe 1988), and calculation methods of the

Liming has also been carried out in Poland. There were the efforts to use dolomite in running waters on granite, calcium poor bedrock in mountainous areas (W r ó b e l 1989, 1991).

Liming is often combined with fishing (mainly brown trout) in order to recover fish stocking (R a d d u m *et al.* 1986). Stenson and Svensson (1994) have suggested that changes in limed fishless lakes should be divided into direct and indirect effects of both liming itself and fishing.

A question arises whether acidification would be reversible if neither liming nor other measures accelerating recovery are used, and only input of acid-forming substances by precipitation discontinues. In Steinberg's and Wright's (1994) opinion this is a fundamental question, as recently the principal acidforming component, i.e. sulphur comin precipitation decrease pounds (resulting from relevant regulations and international agreements) while nitrogen compounds simultaneously increase. Results of a Norwegian experiment (Wright and Henricksen 1990, Wright and Haubs 1991) with controlled acid precipitation have indicated that acid exclusion reversed soil acidification, however, simultaneous nitrate input with precipitation and from the catchment area disturbed this recovery process. Sullivan et al. (1997) stressed also the under-estimation of role of nitrogen during inferred history of acidification of surface waters in Adirondack Mtn. (USA). By analysing sediments (diatoms) of a lake from the pre-acidification, liming and re-acidification periods, Renberg and Hultberg (1992) have found that primarily dominating Cyclotella community did not re-appear.

amount of calcium needed for water and sediment neutralisation. This is made by assessment of so called dissolution efficiency dependent on e.g. retention time (N y b e r g and T h ö r n e l ö f 1988), the factor which also determines necessity of reliming (F l e i s c h e r *et al.* 1993).

Many a time fertilisation has been used, sometimes combined with carbon addition and liming (Blömqvist et al. 1993), to attain desired phytoplankton composition and abundant zooplankton that provides introduced fish fry to survive. Such an accelerated eutrophication of formerly an acid lake is particularly hazardous in the sense it results in rapid and irreversible changes. Oligotrophic character and strong P-limitation preventing algal blooms and providing high water transparency render humic lakes more sensitive to eutrophication. A response of an acid humic lake (pH ~4.5) to liming combined with fertilisation may be exemplified by Lake Smolak in Masurian Lakeland where algal production and abundance were by several times higher, diversity was altered, and macrophyte biomass increased. The lake has begun to resemble an eutrophic lake. The treatment effects have persisted not only for several years after (Wegleńska et al. 1975, Zdanowski et al. 1975, 1977, Hillbricht-Ilkowska et al. 1977, Hillbricht-Ilkowska and Zdanowski 1983) but also for more than 20 years after treatment (Zdanowski and Hutorowicz 1998). The above comments on recovery of the endangered lakes through liming suggest that structural and functional changes are not predictable and may continue over different time periods, which makes reliming to be necessary. This results primarily from permanent activity of factors acidifying waters and soils (precipitation, peatmoss surroundings). In a synthesis describing ecological effects of lake liming in various countries, Olem (1991) has expressed a positive opinion about the treatment. Liming effectively eliminates acidification effects, and in vast majority of cases it gives predictable physico-chemical changes providing suc-

cessful fish introduction and improved diversity. Moreover, it enhances nutrient cycling, decomposition and primary productivity of the lakes. To support the above, other researchers (e.g. Steinberg and Wright 1994, Henricksen et al. 1995, Svenson et al. 1995) have put forward positive results of liming attained in Scandinavian countries. However, some authors have given attention to possible threats caused by liming of lakes and their catchments. These consist in extinction of acidophilous, often rare, unique, endemic plants from peatmoss and littoral zone of the lakes. Furthermore, Steinberg and Wright (1994) have emphasised that even in case of those recovery measures that give predictable effects synergistic effect of climate change in the future, changes in water cycling, intensity of UV radiation, soil saturation with fertilisers, etc., have to be taken into account. Although north-eastern part of Poland (including Masurian Lakeland) belongs to relatively unpolluted regions of the country (Pawłowski 1997), surface waters in that area may also been threatened by acidification. Data from the Suwałki region (22° 45' E, 54° 13' N) given by Hryniewicz and Przybylska (1993) as well as unpublished data from the Station of Background Monitoring indicate that precipitation pH has constantly been about 4.5 for nearly two decades, i.e. since continuous measurements have started. It should be noted, however, that precipitation reaching surface of a lake must not be necessarily so much acidic. According to Kufel (1996), pH of bulk precipitation (wet and dry) in the vicinity of Lake Flosek examined in this paper, and measured at the ground level near the forest edge ranged from 5.0 to 7.0 (data for the period 1986-1987). Nevertheless, the precipitation that

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can possibly reach the surface waters suggests potential threat of anthropogenic acidification to abundant humic lakes of Masurian Lakeland. Having low buffering capacity, water pH of these lakes may fall below a threshold value, i.e. 5.0–5.5.

To recognise how a weakly acidic, humic lake having low calcium content will respond to a sudden high input of this element, experimental liming of Lake Flosek (Masurian Lakeland, NE Poland) – a typical humic, mid-forest lake – was performed. The experiment was established in 1970, following yearly period of pilot control studies, and was supplemented by four-year-studies of liming effects (W e g l e ń s k a *et al.* 1975, Hillbricht-Ilkowska *et al.* 1977, E j s m on t - K a r a b i n *et al.* 1980, E j s m on t - K a r a b i n and W e g l e ń s k a 1985). Unlike in the case of previously mentioned humic Lake Smolak (pH = 5.5) where long-lasting transformations were attained by liming combined with fertilisation (Zdanowski et al. 1977, Zdanowski and Hutorowicz 1998), Lake Flosek was intended to be limed only and then examined for its response to this treatment alone. Liming is a measure required in case of real threat of water acidification, and presumably does not lead to as fundamental and longlasting alterations as liming combined with fertilisation does. Another objective of liming performed was to recognise to what extent a single lime application and related increase in Ca concentration in water and sediments may alter conditions under which communities and species typical of humic lakes and decisive for their unique biodiversity exist.

