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Defensive reactions of freshwater ecosystems against external influences

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Abstract

Eutrophication and toxic loading of freshwater occurred even in early geological epochs as a result of natural factors (*e.g.*, large animals, volcanism), and nutrients and xenobiotics are more quickly integrated in material cycling in aquatic than in terrestrial systems. Therefore, aquatic ecosystems show many defensive mechanisms against organic and toxic loading. Many other defensive reactions can be described in addition to the well-known example of microbial self-purification.

Freshwater ecosystems possess compartments which cooperate towards the function and protection of the whole system but, in opposition to these "euoecisms", there are also "dysoecisms". The defensive reactions of an ecosystem are founded largely on species-egoistic adaptations that have an (accidental) system-altruistic effect. The whole ecosystem reacts only seldom, and it is not clear whether there are selection processes which favour water bodies with a slow eutrophication and therefore slow silting-up, because the freshwaters are important for the global water balance.

It is possible to compare organismic with ecosystemic defensive reactions but the origin of both reactions is very different.

Key words: Freshwater ecosystems – defensive reactions – eutrophication – natural loadings – euoecisms and dysoecisms

1. Introduction

Aquatic ecosystems can be influenced by the input of foreign substances – both degradable organic and inorganic toxic substances – and by the immigration of foreign species, and they react more sensitively to these loads than terrestrial systems. Whereas in terrestrial ecosystems, especially in soils, most of the nutrients and dangerous substances are bound to, and stored on, soil particles, in aquatic ecosystems nutrients and xenobiotics are diluted and suspended. In this way, they enter the element cycling more quickly than in terrestrial systems. Therefore, it was especially important for limnetic ecosystems to develop defensive reactions against additional load. In contrast to waters, heavy metal resistant bacteria are absent in soils, because their contact with heavy metals is relatively weak.

As a result of this additional high load of externally supplied nutrients, accelerating eutrophication occurs, and aquatic systems can show signs of "diseases". The main part of this external load is caused by the input of degradable organic substances. However, the final products of decomposition – especially nitrogen and phosphorus – are also used by plants as nutrients. Nitrogen

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and phosphorus sources can alternatively contaminate water bodies directly from anthropogenic sources, *e.g.*, sewages and agrochemicals. This means of eutrophication has become highly important since human interference with nature began, and is the result of urbanization and of industrial and agricultural development.

In contrast to that of degradable organics, the role of inorganic and toxic substances, either as organic or inorganic compounds, is difficult to judge. The influence of these substances to ecosystems is very different, and it can be supposed that such substances already affected aquatic environments before human interferences with nature took place.

Of decisive importance for the existence of aquatic ecosystems, however, is the process of eutrophication. Because ecosystems are complex systems – not merely a group of individuals – it is not possible to equate exactly nutrient-driven eutrophication with the feeding or overfeeding of individuals. All individuals, whether they receive too little or too much food remain identifyable as individuals until they die, and even then we can often find their remains. It is otherwise with aquatic ecosystems since, with increasing eutrophication, they loose their identity by changing trophic state. The changes result in a completely different ecosystem. In principal, we can say that each stage of eutrophication results in the "death" of the former system, but, unlike with individuals, we never find "corpses" – because a new ecosystem develops instead.

The process of accelerating eutrophication leads to the aging of lakes or streams, passing through several ecosystem stages – one after the other – until the dissolution of the final system. This means that the basin or the channel previously containing the ecosystem completely disappears.

In the following, some details of these processes are given. Extreme eutrophication limits aquatic ecosystem functioning. If the hypertrophic state is exceeded (nitrogen >30 mg l^{-1}; phosphorus >3 mg l^{-1}) transparency (Secchi depth) decreases and as a result of this light limitation aquatic plants cannot use the high nutrient concentration. Biodiversity consequently declines and benthic producers can disappear completly. Because the phytoplankton shades itself, its photosynthetic activity is reduced and, in consequence, the concentration of oxygen shows aperiodic oscillation; a high production of oxygen (±20 mg l^{-1} d^{-1} O$_2$) is accompanied by high respiration rate (±30 mg l^{-1} d^{-1} O$_2$) (UHLMANN 1966; KALBE 1996).

Another characteristic of the instability of a hypertrophic aquatic system is the extreme oscillation in the density of planktonic algae (BARICA et al. 1992). The mass development of planktonic algae also influences the feeding behaviour of the zooplankton, first reducing the efficiency of filter feeders and then the rate of predation (BURNS 1968). Energy transfer may then be

blocked, resulting in the destabilization of the whole system (ROSENZWEIG 1971).

We can conclude that – together with its nutritional aspects – eutrophication is a real symptom of illness in a limnetic ecosystem. Therefore, in limnetic systems, different defensive mechanisms are necessary against organic and toxic loads. Just as individuals react to stress situations and symptoms of diseases, ecosystems have also developed specific defence mechanisms, but these are frequently misunderstood.

The aim of the present paper is to give – after an introduction to natural eutrophication – an overview of the different defence strategies, from the well-known self-purification to the features and structures of ecosystem compartments that cooperate towards the function and protection of the whole system.

Another emphasis of this paper is the invasion of water bodies by foreign species (neophyta and neozoa) which may have occurred since freshwaters are existing. These species are frequently introduced for anthropogenic purposes or promoted by anthropogenic impacts. The role these organisms play in limnetic ecosystems and also the systems' reactions to these interventions will be described.

2. The natural load of aquatic systems

Allochthonous eutrophication and toxic loads have existed ever since water has been available on Earth; even without anthropogenic impact these waters were subjected to external stress situations. At the latest in the Mesozoic, with the advent of the first large land animals, polysaprobic waters have existed. High toxic loads also occurred in connection with vulcanic activities (i.e. acidification, high concentrations of heavy metals). Human disturbance of water bodies also has a long history, however namely since the first permanent settlements.

One of the main factors contributing to the natural allochthonous eutrophication of waters is large land animals. Today, tropical lakes and rivers are eutrophied by buffalo, elephant and antelope. The result of their occupation of water bodies in tropical regions is an enormous mass development of algae and macrophytes. Also carnivores, for instance the tiger, frequently hunt their prey in water and crocodiles pull big game (grazers) into the water and tear them to pieces there. In addition, wallowing by big game and disturbance of bottom sediment by crocodiles severely clouds the water. These processes are accompanied on the one hand by a remobilization of nutrients from the sediments, in the direction of accelerating eutrophication, but on the other hand, the growth of plants – and therefore also the results of the eutrophication – will be inhibited.

This coupling of loading and relieving processes can be found frequently in ecosystems. One example is the activities of buffalo. These big game eat land plants and may deposit their excrements in water, but in contrast to these eutrophication-activities they also eat great amounts of aquatic macrophytes and then leave the water, thus reducing eutrophication. Another example from tropical waters are the hippopotami. The bulls mark their territories by fanning large amounts of excrement and often they prefere the banks, especially of bights for this purpose. This leads to considerable fertilizing. By grazing aquatic plants hippopotami could counteract the eutrophication but they very often eat land plants.

Waterfowl are another cause of eutrophication; not birds that live permanently or only in the breeding time on water and feed on aquatic organisms; but to high concentrations of waterfowl in autumn, winter and spring which cause an immense nutrient supply. Geese, in particular, contribute to accelerating eutrophication when they eat land plants during the day but over-night on water.

The highest concentration of nitrogen is found in the excrement of grey herons, the smallest in the excrement of ducks (including swans) and cormorants. Phosphorus is concentrated in the excrement of grey herons and cormorants, less in such of ducks. At present 36 species of aquatic fungi are known to grow on avian excrement and mineralize them (CZECZUGA & MAZALSKA 2000).

Natural eutrophication must have been enormous also in former geological periods. In the Upper Carboniferous, already *Edaphosaurus* was living. In the Permian, *Moschops*, a big reptile fed on plants in desert rivers.

In the Jurassic many grant dinosaurs also used waters. *Brontosaurus* (with a length of 18 m) lived both on land and also in water, where it fed on aquatic plants as did *Diplodocus* (length 27 m). Another saurian, the 22 m long and 11 m tall *Brachiosaurus*, used deep lakes and fed upon benthic plants (Fig. 1). In the Upper Cretaceous period the enormous *Protoceratops* grazed both on land and water plants.

Very important for water bodies during the Cretaceous period were also the world-wide occurring Hadrosaur (length up to 11 m) which have had webs on the feet and a duck-like beak. They were plant feeding animals living close to water.

These big reptiles undoubtedly had the same effects as big mammals. They would cause accelerating eutrophication if they deposited their excrement into water. But simultaneously, they may have counteracted this nutritional load by grazing aquatic plants – one of these sites has predominated and therefore decided on loading or relief.

In the Tertiary, the explosive radiation of the Mammalia coincided with an extremly high density of big mammals which in some cases populated lake shores in such numbers that the lakes became hypertrophic. One example is the well-known Messel quarry, near Darmstadt, Germany, where in the Eocene a permanent algae bloom occurred. This resulted in the formation of oil shale, a material which favours fossilization. The hypertrophic Lake Messel produced methane in such high concentrations that it killed many bats flying over the lake that then fell in and were fossilized.

Fossiliferous deposits are also known from other Tertiary lakes. The fossils show for instance, that European
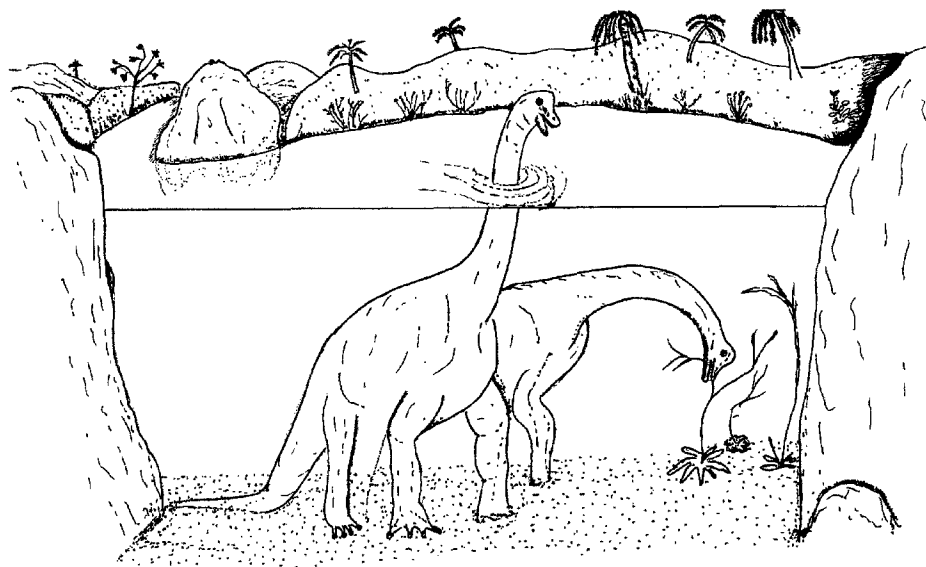

Fig. 1. The jurassic *Brachiosaurus* grazing waterplants in a lake. (Half-schematic drawing, in the style of a pattern from the Czech Academic Artists, Z. BURIAN).

water bodies were then populated by hippopotami. Also tapirs, Mastodonts, the gigantic and monstrous hoofed animals of the genus *Uintatherium* and the Deinotheria – animals similar to the elephants – brought a high nutrient load to the waters of the Tertiary swamp forests. All of these animals fed on submersed plants.

Likewise, the sediments of shallow lakes from the Pleistocene (about 200.000 years ago) indicate strong eutrophication. In these deposits fallow-deer skeletons were found, their backwards bent cervical vertebrae pointing to an abnormal cause of death. The high amounts of methane produced by hypertrophic lakes could also have been responsible in this case (MANIA 1992). There is also a Pleistocene lake in California which has been thoroughly profoundly investigated by palaeontologists. Its high shores show thick layers of oil shale containing the fossils of large mammals. When these animals came to drink they stuck in the oil shale where they were often attacked by carnivores, for instance by the big cat *Smilodon*.

But big animals were not only important for eutrophication in former periods. By their wallowing activities they also changed the morphology of waters, especially of streams and rivers, which influences of course also the trophic state of the waters and also produces new pools. The dinosaurians uprooted great woodlands by their long and strong tails, and this process was continued in later periods by large mammals, using – as do elephants – their trunks and tusks. This uprooting thus destroyed the nutrient-rich vegetation along lakes and rivers with its high diversity of plant species and coincidentely influenced the water.

The nutrient load introduced by heavy rain should also not be forgotten. In combination with erosion in the areas denuded of vegetation by animals rain could have been of decisive importance.

All these examples show that high nutrient load of aquatic ecosystems has occurred during the whole biological development of the Earth. Gigantic natural eutrophication processes led also in times past to polysaprobic conditions. These conditions were outside the range of the currently used limno-saprobity index which would have to be expanded to include eu-saprobic conditions, comparable to wastewater-saprobity.

One great ecological problem of our day – cattle grazing, which affects water as well, especially rivers – is harmless in comparison to the eutrophication processes of former times. In the inter-glacial periods, in present day central Germany, enormous large mammals lived and polluted the water. Only as a result of human activity, for instance the hunting of these animals, did the water quality probably improve (MANIA 1995).

It can be concluded that natural eutrophication of waters in the course of the Earth's history has greatly surpassed the eutrophication caused by anthropogenic influences. Where nowadays are inland waters where big animals are killed by high concentrations of methane or where animals coming to drink stick to oil shale?

The palaeontological examples of natural eutrophication given above should lead to a reorientation of the field of limnolgy. The examples make obvious the role of great Tetrapoda and birds as sources of a high environmental load during the Earth's history.

Because of these loads it was necessary for aquatic ecosystems to develop defence mechanisms comparable with the reaction of individuals to diseases. Because, as shown above, the natural loads persist for extended geological periods, the waters were well prepared for a new enormous challenge – the disturbances caused by human impacts. Without the possibility of developing these defence reactions through such long periods of time, the waters would presumably not have survived the anthropogenic loads.

In the following an overview about the different defence mechanisms of aquatic ecosystems is given.

3. Defensive mechanisms

3.1. Microbial self-purification

The best investigated defensive reaction against eutrophication is the well-known microbial self-purification. Primarily, microbial decomposition was generally the basis for a continuous evolution of organisms. Without microbial decomposition there would have been an accumulation of organic remains on the Earth which would have prevented any existence of organisms. This mechanism has been retained for the self-purification of all habitats. The majority of microbial decomposers does not live primarily in water bodies, but come into rivers and lakes together with allochthonous matter or dead organisms. Therefore, microbial self-purification may be only compared with reservation with the immune system of organisms (compare chapter 7.6.).

The bacteria were one of the first groups of organisms on Earth and – despite the process of evolution – they are also at present integrated in all ecosystems, and many of them inherited the function of decomposers of organic matter. This function, so to speak, was offered to different ecosystems, which were thus not required to develop these systems themselves. This process was probably supported by selection, because without saprophytic bacteria all forms of higher life on earth are impossible.

But microbial self-purification can not be regarded as an universal remedy. The final products of protein decomposition are plant nutrients and therefore a potential of eutrophication. At a permanent load the microbial

self-purification leads only to a mitigation of the eutrophication processes in water bodies. In standing waters with a longer water residence time, nutrients can be accumulated even at short-term loading in sediments and algae and remain in this way available.

3.2. Drift and throw-off of load

Apart from microbial self-purification, limnic ecosystems possess also other defensive mechanisms. Algae, higher plants and, to a low degree, microorganisms as well can accumulate great quantities of nutrients and transform them into biomass. Water bodies possess mechanisms to remove this biomass or a great part of it from the whole system or from a compartment of it. In running waters this mechanism is drift and in standing waters it is the throw-off of load by floatation ashore (flotsam).

• Drift

In the drift of biomass from running waters the green alga *Cladophora* plays an important role. This algae occurs even in oligosaprobic stream reaches, but with increasing load mass production occurs. This mass production is caused by the high nutrient accumulation; the accumulation factor for N and P amounts to 5000 and 20 000 respectively. When eutrophication is advanced, *Cladophora* clumps can grow up to 4 m within a few days (SCHÖNBORN 1996). Nearly 16% of its fresh weight consist of seston (detritus), filtered by the filaments. For optimal growth *Cladophora* needs a current velocity of at least 0.5 m s^{-1}. Clumps above 1 m length detach and drift downstream if the current velocity exeeds 1 m s^{-1}. A reach may thus be freed from high amounts of biomass, but also from nutrients and xenobiotics, e.g. heavy metals (SCHÖNBORN 1995). Depending on the roughness of the stream bed the drifting *Cladophora*-clumps can be transported about different distances. Rough stream beds may catch and detain the drifting clumps thus hindering the drift mechanism, but with smooth beds the algae can reach the sea.

As an example for the importance of the drift some values should be given for the River Ilm, a low mountain range stream in Thuringia (Germany). The stretch investigated was a headwater with pebbles and stones. The first 120 m of the stretch were unshaded and in this part 1.5 tons *Cladophora*-biomass were produced in a week. This weight even increased to 1.74 tons within one month by filtering seston. But after a high discharge the whole stretch was freed from *Cladophora* which was transported downstream. Within the next hundred metres or so nearly 70% of the drifting biomass were attached to protuberant stones and artificial elements, for instance piers and weirs. Shading by bank trees led to rapid death; nearly 30% of the dead

Cladophora-clumps were stored as detritus, so stopping further decomposition (SCHÖNBORN 1997). After the total loss of *Cladophora* and reduction in the discharge, the mass production of algae immediately resumed.

Other algae like *Ulothrix* and *Oedogonium* also show the same drift mechanism, but it seems not to be as effective as in *Cladophora*. The diatom *Melosira* also develops long, fragile filaments in brooks, covering stones and sediments at a high density. They break up with even the slightest increase in the discharge, and are then carried away. This mechanism also contributes to removing load from water bodies.

Among microorganisms, the polysaprobic filamentous bacteria *Sphaerotilus*, is involved in drift-events. It develops into clumps, somewhat more than a hand in length, which become detached and show the well-known fungal drift. Similar behaviour was registered in the aquatic fungi *Leptomitus* and *Fusarium*. Of *Sphaerotilus* it is also known that it can accumulate heavy metals. Therefore, the micro-organisms given above affect unloading in a threefold way: by decomposition, by the drift of biomass and by the drift of xenobiotics.

In running waters, small portions of *Cladophora* and *Sphaerotilus* may be continously removed, not only during high discharge, but also during low water, demonstrating that biomass has a relatively short residence time in running water.

• Throw-off of load (floatation ashore)

The load throw-off by floating ashore (flotsam) is related to the above described drift mechanisms, but occurs in standing water. In eutrophic standing water, algae detach from the sediment and float to the surface, where they continue to grow and develop into algal mats. The mats are drifted landwards by the wind and some will be washed ashore. Important algae with this mechanism are *Cladophora fracta*, *Oedogonium*, *Spirogyra*, *Zygnema*, *Mougeotia*, *Rhizoclonium* and the blue-green alga *Microspora*. *Cladophora fracta* can also participate in the purification process in running water, whereas *Cladophora glomerata* occurs only in running waters and in the surf-zone of lakes.

Important for the growth of algae on sediments are the light conditions at the bottom of the water. Light and an increasing supply of nutrients lead to mass development of algae. But when algae-aufwuchs on sediments reaches a certain density its surface becomes progressively rougher. If the laminar boundary layer of mat surfaces exeeds a certain roughness, turbulence occurs, with the result that the aufwuchs detaches even at low water movements.

The algae mats can also drift into the reed-belts and a great part of the biomass of the whole lake can be "ban-

ished" into this zone. Within the plant belt, as a consequence of strong aeration, rapid decomposition is favoured, particularly by the aeration of the rhizosphere and the released nutrients are quickly taken up by the littoral vegetation. Therefore the pelagic eutrophic level is mostly lower than that of the littoral.

The wash-ashore-mechanism was already described by CEEB (1972) who recorded >2 kg m⁻³ (fresh weight) of blue-green algae washed ashore from a lake. Recently, KIES & DWORSKY (1982) and SCHULZ-STEINERT & KIES (1996) have described these processes in *Vaucheria sessilis* which also detaches from the bottom and can drift ashore. In shallow waters with a drying period, the algae mats frequently form paper-like layers over the dry sediment. These layers are converted by terrestrial organisms until the water body next fills. *Vaucheria compacta*, distributed from the fresh waters to mesohaline zones of estuaries, also forms extensive mats on sediments. Like *Cladophora*, this species filters great amounts of seston from the water and is a habitat for many animals. During storm surges *Vaucheria* detaches and is washed ashore (KÖTTER 1961; SIMONS 1974). The production amounted to ~16 g C week⁻¹ m⁻². Comparable values for *Cladophora* in streams are 140 g (River Saale, Thuringia; see SCHÖNBORN 1980) and 40 g (River Ilm, Thuringia; see SCHÖNBORN 1996). Both species of algae show the same behaviour and have similar functions in aquatic ecosystems.

In Central Europe stranded algae are found mainly on the east side of standing waters, because westwinds predominate. Frequently stranded algae are concentrated in

bights which function as "sputum rooms". The more bights a lake has, the better its recovery mechanisms seem to function. In heavily loaded Central European lakes, algae stranded along shores with many inlets are frequently up to 0.5 m wide. On 1 m of shore up to 1 kg fresh weight of algae can be found.

The blue-green alga *Aphanotheca* on sediments produces jelly-like masses the size of pigeon-eggs that drift on the water surface and then to the shore. They are occupied by diatoms and small animals, and inside the jellies calcite precipitates and oxygen is produced, which accelerates their decomposition.

Even in the inlets of oligotrophic lakes masses of *Cladophora*, *Bulbochaete*, *Spirogyra* and *Mougeotia* drift onto the shores after they have been detached by animals, or these days by bathers, in the water.

Not only filamentous algae and mats produced on the sediment can be drifted by wind ashore, but also **waterblooms**. These consist mainly of algae which, because of embedded gas vacuoles, float on the surface. If the nutrient level is high these blooms can occur in masses. An important bloom-forming green alga is *Botryococcus braunii* (Fig. 2). It forms colonies 0.5 mm in diameter and stores enormous amounts of oil in its cell walls thereby reducing the specific gravity. Large quantities of starch are stored in the cells. This alga has existed since the Palaeozoic and it is a main component of oil pools. Stranding of this algae has probably been an important factor in unburdening water bodies throughout the Earth's history.

The majority of waterbloom-forming algae are Cyanophyceae. Their gas vacuoles are composed mostly of molecular nitrogen (*Microcystis*, *Anabaena*, *Gloeotrichia*, *Coelosphaerium*, *Gomphosphaera* and *Aphanizomenon*). The drift of blue-green algal blooms, especially those of *Microcystis*, has been intensively investigated (GEORGE & EDWARDS 1976; VAN DER VEER et al. 1993). Drifts are particularly concentrated in bights on the lee side of water bodies and they rot quickly. VAN DER VEER et al. (1993) have developed a model that decribes the accumulation rate of drifting masses of blue-green algae on the shore. The drift is dependent on the quantitity of algae, lake surface area, wind course, and wind velocity. In a shallow, hypertrophic, lake over 75% of *Microcystis* blooms were washed ashore! But the blooms must be distinguished from the other phytoplankton which colonize the whole light-exposed waterbody and is only seldom drifted by wind. In this case other defensive mechanisms are effective that will be explained later in this paper.

Also the **neuston** participates in the wash-out effect. If mass colonization of the boundary layer of the water surface occurs the wind can transport this neuston film shoreward. A particular role in this case is played by the green alga *Ankyra* (*Characium*) *ancora* which frequent-
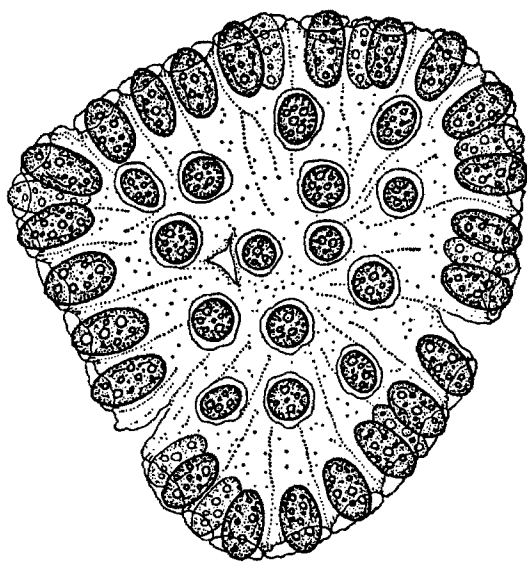

Fig. 2. The green alga *Botryococcus braunii*, an important storage organism which can be easyly removed by wind from lakes. (From STREBLE & KRAUTER 2002).

ly occurs in high densities and has hydrophobic resting spores. The resting spores from *Ankyra*-films, driven ashore by the wind, quickly reach the land and can be distributed to other waters (FOTT 1954).

The **pleuston**, like the neuston, is integrated in the defensive mechanisms. *Lemna* and, in the tropics, also *Salvinia molesta* and *Eichhornia crassipes* spread carpet-like over the surface of lakes and slowly flowing streams. Then they are drifted ashore, where they die. Especially in lakes with a strongly varying water level, the removal of pleuston plants leads to significant immobilization of nutrients. During falling water level pleuston plants dry out very quickly and will be metabolized by terrestrial organisms (HARPER 1992; HARPER et al. 1993).

These wash-ashore mechanisms occur not only in standing waters but also in slowly flowing streams. In such streams, filamentous algae can form large mats which drift bankward, also *Lemna*-carpets are frequently pushed to the edge. Furthermore, macrophytes in the middle of slow and shallow streams catch great quantitites of seston, drifting algal mats and *Lemna*, producing enormous concentrations of biomass and other organic matter. These concentrations of organic matter, representing in a hydrographic sense "transport-bodies" will be drifted downstream by the next high discharge.

Not only lakes and rivers have inherent disburdening mechanisms, but so do periodic and episodic waters, and not only in the manner of drying algal mats mentioned above. During dry periods deposited matter is oxydized and the bacteria get oxygen for decompositon (imitated by rotating biological discs). When shallow waters freeze, nutrients are probably released (DABORN & CLIFFORD 1974), which will mostly be washed out by heavy rainfall in the next spring.

3.3. Terrestrial outlet-systems

Systems of biomass release from waters that are based on food chains, only have long-term effects. The unburdening is delayed, for instance, because defecation by terrestrial grazers and predators in water bodies is always possible. Respiration (metabolization) also belongs to the biomass release systems, but this process will not be referred to in this paper.

Defensive reactions concern not only the reduction of nutrient levels, as will be shown in the following remarks, but also improvement of water quality. This means that the water becomes physiologically more tolerable, for instance, through increased transparency and decreased fluctuations in pH-values as well as CO_2- and O_2-concentrations.

In the following the main terrestrial outlet-systems are explained.

• Skimming

Floating algal mats and pleuston plants are used by terrestrial animals. Parts of consumed biomass will be deposited as faeces on land. This process may be designated as **skimming** (Abschöpfen). A well-known case of skimming in Europe is *Lemna*, which is used as food for ducks (Anatidae). Additionally, algal mats are also frequently used as food by ducks, above all because the mats contain many small animals. Many aquatic birds eat filamentous algae especially in spring, and ducks also use the fungal drift previously described. They eat *Sphaerotilus*-clumps, including the microfauna inhabiting the clumps. Drifting *Sphaerotilus* and fungal clumps are deposited by degrees and yield a fertile sediment. This sediment is colonized by a high density of tubificids. Ducks filter the tubificids from the sediment, and by this process consume great quantities of biomass, including nutrients.

• Grazing

Another terrestrial outlet-system of biomass and nutrients is the **grazing** of waterplants by terrestrial animals in which in addition to mammals birds (*e.g.*, ducks, coots) also partizipate. According to REICHHOLF (1993) coots can consume up to 90% of the waterplants of lakes (*e.g.*, reservoirs of the river Inn). The more the animals defecate on land, the more intensive is the output of nutrients. Anatids can reduce the trophic and saprobic level enormously.

But these relationships may be more complicated than at first supposed. For instance, geese grazing in the daytime on fields and sleeping at night on the water are a significant factor in eutrophication (BAZELY & JEFFERIES 1985; ZIEMANN 1986). The faeces of herbivorous waterfowl deposited in water produce rapid eutrophication, because they make available nitrogen and phosphorus previously bound in water plants. Coot (*Fulica atra*) and also rudd (*Scardinius erythrophthalmus*) can consume great stocks of *Elodea*. This gap is used by *Ceratophyllum* that spreads quickly and takes up nitrogen and phosphorus by its leaf. *Elodea*, on the contrary, takes up nutrients from the sediment (VAN DONK et al. 1993). However, *Ceratophyllum* is not eaten by most animals and this mechanism counteracts the availability of nutrients from the faeces.

There are many mammals that eat waterplants, for instance elk, elephant, rhinoceros and hippopotamus, but also wild boar. Wild boar do not deposit faeces in water bodies but often emerge garlanded with floating algal mats which are thus transported landward. A special role is played by seacows (*Sirena*), which can push up into streams and consume great quantities of waterplants. Because they remain in the water, they do not really belong to the terrestrial outlet system, but they keep even

strongly eutrophic streams free of plants and therefore they prevent the realization of the nutrient potency in waters.

• Predator-prey-relationships

The **predator-prey-relationships** represent the most intensive outlet-system. In this mechanism the initial link of the food-chain is a limnic organism, and the end of the chain is a terrestrial predator.

Widely spread is the system alga – fish – terrestrial predator which should be described in the following. The majority of fish species eat algae and the typical fish smell comes from algae. In fresh waters we can find more herbivorous fish species than in the sea.

Especially among the cyprinids many algal consumers are found. For instance, species of *Varicorhinus*, an acient genus, living in South Asia and Africa, scrape off the algal aufwuchs with the help of their under-standing mouth and their pointed underlip. Their long intestine may also be an adaptation to this form of feeding. The species *V. capocta*, occurring in the Sewan area (Armenia), even eats the toxic green alga *Botryococcus brauni*, which forms blooms and is rich in nutritious matter. This alga plays a key role in the cleaning-systems of many waters, as mentioned above.

Other algae-consuming cyprinids are the nase (*Chondrostoma nasus*), living in the same part of rivers as graylings and barbs, many barb species, the chub (*Leuciscus cephalus*), the rudd (*Scardinius erythrophthalmus*), the black belly (*Xenocypris*), the genus *Discognathichthys* and other species. In mountain brooks of South-East Asia species of *Gyrinocheilus* feed on algae. The North-American minnow (*Campostoma anomalum*) also eats filamentous algae (*Spirogyra*, *Rhizostomum*) and can significantly reduce the algal density (POWER et al. 1985). Even the carp (*Cyprinus carpio*) eats filamentous algae if there is not enough zoobenthos. The silver carp, *Hypophthalmichthys molitrix*, filters great quantities of phytoplankton. The Indonesian fish species *Tilapia mossambica*, *Chanos chanos* and *Thynichthys* species have also a high consumption rate of microalgae. According to LAKSHMI-NARAYANA (1965) the fish species *Hilsa iliska*, *Gadusia chapra* and *Barbus stigma* eat planktonic diatoms in the River Ganges.

Some of the fish species mentioned are used in algae control. The grass carp, *Ctenopharyngodon*, introduced into Europe for waterplant control, eats macrophytes but also the macrophytic algae *Spirogyra*, *Cladophora* and *Chara*. But it can not be regarded as a cleaning factor, because nutrients are released in its excrements, which contain nearly 77% of the phosphorus-uptake, resulting in a strong development of phytoplankton.

Frequently, the aquatic food-chain is lengthened by predatory fish species. One example is the minnow,

Campostoma, which is captured by perches and has been used in attempts to control the eutrophication of running waters (POWER et al. 1985). Barbs and nases mainly are captured by huchen. Crocodiles and other reptiles, *e.g. Python*, hunt fish in various water bodies. Capybara (*Hydrochoerus capybara*) in South America eat great quantities of waterplants therefore preventing weediness. They are prey of the Anaconda, a top predator in American waters. The snake eats the prey within the waters and also defecates there. Therefore it only prevents realization of the nutrient potential, but does not greatly reduce the nutrient burden.

Water bodies are comparable with steppes or savannas since in both large grazers prevent, respectively, weediness or bushiness. In most cases large grazers scarcely reduce the nutrient level, but its conversion to phytomass is significantly reduced.

The next link within the terrestrial outlet-systems – after algae and fish – are piscivorous terrestrial animals. Because there are a lot of these animals, only a few examples can be referred to.

Among the families of birds *Mergus*-species, herons, storks and cormorants especially control fish densities. Goosander and red-breasted merganser (genus *Mergus*) consumed nearly 3.5 tons salomonids per year in a Swedish stream, this amounts to 350 000 individuals if it is assumed that one individual weighs ~10 g. An adult *Mergus* needs 400 g fish d^{-1} and so *Mergus*-species can control salmonid populations (LINDROTH 1955). Data from another area indicate that *Mergus* consumes similar quantities of non-salmonids.

Appropriate investigations are given for cormorants by LEAH et al. (1980). In a hypertrophic shallow lake cormorants (*Phalacrocorax carbo*) caught fish in such high quantities, that water transparency greatly increased. This led to an increase of macro-zooplankton species and also of macrophytes and zoobenthos. Of course, the nutrient level remained constant, because a long time is necessary before the influence of the birds greatly reduces nutrients. Furthermore, there should be a long distance between the waterbody and breeding colonies and the re-solution of nutrients must be taken into account, especially that of phosphorus from the sediment. Cormorants can empty water bodies of fish and are therefore regarded as a danger for inland fisheries. But it should be taken in account that, at present, cormorants are the most active and natural factor in the improvement of quality of standing waters in the Central European landscape.

In the same way, herons and storks can improve water quality. The *Mycteria*-storks of India and the African yellow-billed stork (*Mycteria ibis*) consume large quantites of fish. One pair can catch >40 kg fish per breeding season, great colonies even some tons in the same time.

Tropical shallow waters and marsh areas support enormous densities of piscivorous birds. To this func-

tional group belongs also the hals (Alcedinidae) which mainly eat young fish that feed mainly on algae.

Not only birds but many terrestrial mammals feed on fish including some soricids living in water, bears, the water mongoose (*Atilax paludinosus*) and the fishcat (*Felis chaus*). Large cats like tiger and jaguar also frequently catch their prey in water.

First of all should be mentioned the family of otters (Lutrinae) because it plays an important role in the relief of all limnetic waters. It is distributed world-wide, mostly in high densities, and occurs from the mountains to the plains and colonizes nearly all types of water bodies. Most important is that defecation takes place outside of water – mostly on prominent points – and serves also for the marking of territory.

All otters need great quantitites of crabs (Decapoda) and fish. Especially the giant otter (*Pteronura brasiliensis*) of the Amazonian region needs decapods and fish in extremely high quantities.

Under natural conditions, decapods occur in high densities in natural brooks, small rivers and shallow standing waters. Decapods consume great quantitites of waterplants (*Chara*, seedlings of *Potamogeton* and other macrophytes). According to NYSTRÖM et al. (1996a, b) they can significantly reduce the stock of waterplants and are regarded by these authors as key species in limnetic ecosystems. One group of Decapoda, the Astacura, feed frequently on *Cladophora* (LE SAGE & HARRISON 1980; HART 1992; ANWAND & VALENTIN 1996). This species, which plays a very important role in the cleaning system, removes biomass, nutrients and xenobiotics not only by a detachment-mechanism, but additionally with the help of a food chain. Like the food-chain explained above (algae – algivorous fish – terrestrial

predator) the food-chain *Cladophora – Astacus* – otter can be used for biomanipulation and is thus a major factor in reducing of the trophic level. But it may also be important, that decapods detach more *Cladophora* than they consume (SCHMALZ 1999), and thus the two removal-systems are connected (Fig. 3).

To the terrestrial outlet-systems also belong Amphibians, above all frogs and toads. Their tadpoles assimilate different matter from the water, which is, at their metamorphosis, transported out of the water (DICKMAN 1968; SEALE 1980). The tadpoles feed intensively on algae and take up also the animals which inhabit algae mats. The tadpoles of *Rana dalmatina*, e.g., intensively consume swimming mats of *Spirogyra*, *Zygnema*, *Mougeotia*, *Cladophora* and *Oscillatoria*. Because the tadpoles eat some of their own proteinaceous faeces, release of nutrients to the environment is decreased as a result of repeated cycles of digestion (WARINGER-LÖSCHENKOHL & WARINGER 1990).

Terrestrial outlet-mechanisms must have already existed in the Mesozoic. Since this time eutrophication or disburdening depend on the place of defecation and the proportion of landplants in the food. Many saurians fed on waterplants and it can be assumed that the hydrosaurians filtered swimming algae and pleuston from the water. *Pterodactylus* and other flying saurians captured great quantities of fish during flight. In this way, these land animals may have relieved the water bodies significantly.

In the Tertiary the otters occur in a high diversity, more than 10 genera were distributed world-wide. They may have disburdened the water bodies considerably which were polluted by many mammals living in high densities in this earth period.
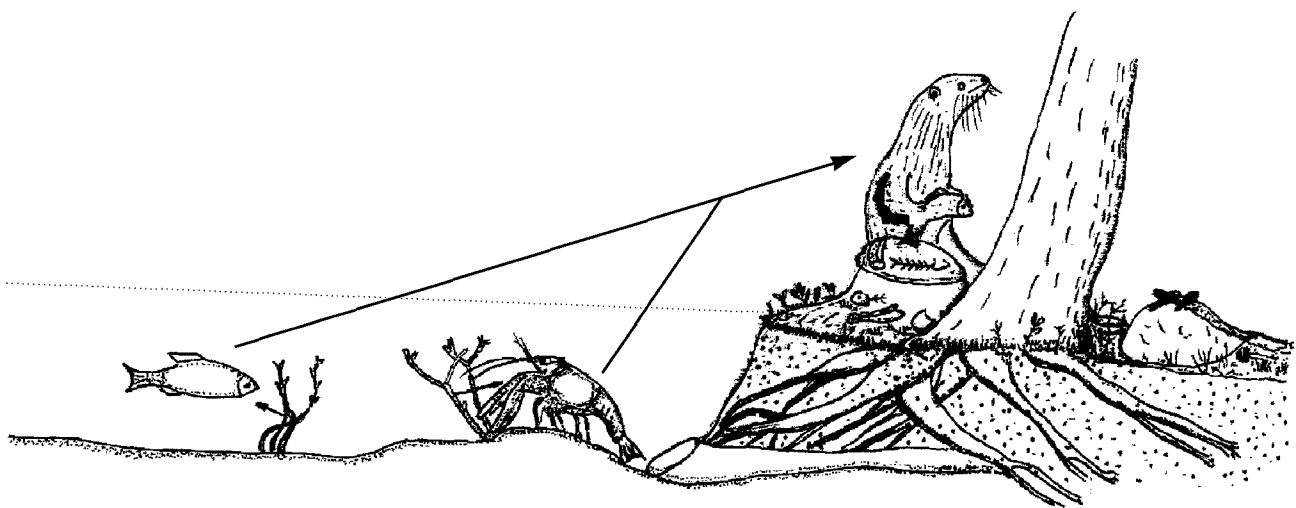

Fig. 3. Example of a terrestrial outlet-system: algae, fish, *Astacus* and otter. In the water body can be seen the cave of the crayfish, providing the alder rhizosphere with water. Above the bank lies a food- and defecation-place of the otter. (Half-schematic drawing).

In a completely different way hippopotamuses and other large animals decrease eutrophication, especially in African lakes. The movements of their ponderous bodies continually destratify and therefore detoxify eutrophic lakes.

3.4. Marine outlet-systems

Marine outlet-systems are represented by catadromous fish, which migrate for spawning from fresh waters into the sea. The most important group of this system are eels (*Anguilla*) which are extreme predators of decapods and fish and migrate fattened for spawning in the sea, from which they do not return. This output is probably not compensated for by the immigration of eel-larvae (faeces from marine food).

In contrast to catadromous fish, anadromous fish species, spawning in running waters, can be a significant eutrophication factor. A well-known example is the Pacific salmon, *Oncorhynchus nerka*, post-spawning deaths of which can significantly increase the primary production in some stream reaches (RICHEY et al. 1975), and at some points also the saprobity. The existence of these two counteracting mechanisms means it may be difficult to estimate the result of marine outlet-systems.

3.5. Filtration

Filtration of suspended matter occurs both mechanically and by the activity of organisms. The most important mechanical filter-system in running waters are large clumps of filamentous algae, especially *Cladophora*. *Cladophora* can clarify seston-loaded streams (SCHÖNBORN 1997). With the help of detachment-mechanisms, the filtered seston is transported downstream (see chapter 3.2). In standing waters the stock of another plant, *Myriophyllum*, store much detritus, but without drift. The effect of this storage of suspended matter is unknown, but it may contribute a little to clearing the water.

Filtering organisms occur in standing as well as in running waters, in the pelagic and benthic zone. The most important filter-system among pelagics are cladocerans, and there is an immense literature on their role in this respect. The biomanipulation programme developed for lakes is based fundamentally on the filtering ability of, above all, *Daphnia*. High densities of *Daphnia*-species in lakes can produce a clearwater stage within a short time. This process does not lead to a reduction in nutrients, but results in an improvement of the water quality in a biological sense. Biomanipulation imitates natural defensive mechanisms, but only incompletely, as indeed, natural defensive mechanisms were also incomplete. The influence of cormorants and otters, as described above, comes closest in type to the biomanipulation applied.

The main benthic filter-mechanisms are large mussels and the role of *Dreissena polymorpha* has been especially well investigated. During one hour, one mussel can filter 300 ml of water free from particles (REEDERS 1989); but there even higher values have been published. Around 10 000 mussels can reduce by 69% the suspended matter of a middle-sized water body with an average load (VOOGT 1989; REEDERS 1990). In this way *Dreissena* can significantly decrease the degree of the trophic status of a water body, it is, for instance, "the greatest sewage treatment plant of Lake Constance" (KLEE 1971). The filter-system of *Dreissena* has probably been active since the Pliocene (KINZELBACH 1992).

It may be important that the filter feeders are frequently connected with terrestrial outlet-systems. This is possible because fish (rudd, bream, barb and especially eel), diving ducks, coots and otters eat mussels. But decapods are also great *Dreissena* predators, with the result that they are integrated in this important food-chain for the relief of water (PIESIK 1974).

Other big mussels, e.g. unionids, also have a filtration effect comparable to *Dreissena* but they are unfortunately insufficiently investigated.

The role of other benthic filter feeders like ciliates, rotifers, sponges, bryozoans, some trichopterans and simuliids should not be underestimated. They metabolize a part of their high quantities of food and are integrated in outlet-systems.

3.6. Precipitation (calcite precipitation)

With the increase of the nutritional level the density of phytoplankton in standing waters also rises. This leads to an increase in CO_2-concentration with the result that the $Ca(HCO_3)_2$ can not remain in solution and precipitates as $CaCO_3$, in the form of microscopical calcite crystals. Sand grains, shells of diatoms and probably bacteria act as crystallization germs. Sinking calcite crystals transport nutrients from the pelagial into the depth. This can happen mechanically by the crystals pulling down of organic particles and algae, but also by adsorption of dissolved phosphorus on crystal surfaces. This process, long since known as "biogenic decalcification" or "whiting" was investigated anew by KOSCHEL (1990) who concluded that it is a cleaning reaction in hardwater lakes. The effect of calcite precipitation on phosphorus content is given in Fig. 4.

Integrated in this process is the phytoflagellate *Phacotus* (Fig. 5) since its empty calcareous shells sink (KOSCHEL & RAIDT 1988). By this process *Phacotus* belongs, like *Cladophora* or *Botryococcus braunii*, among the key groups for the relief of waters.

More information about calcite precipitation as an important defensive reaction of lakes will be given later in this paper, but the incomplete nature of these mechanisms will also be described.
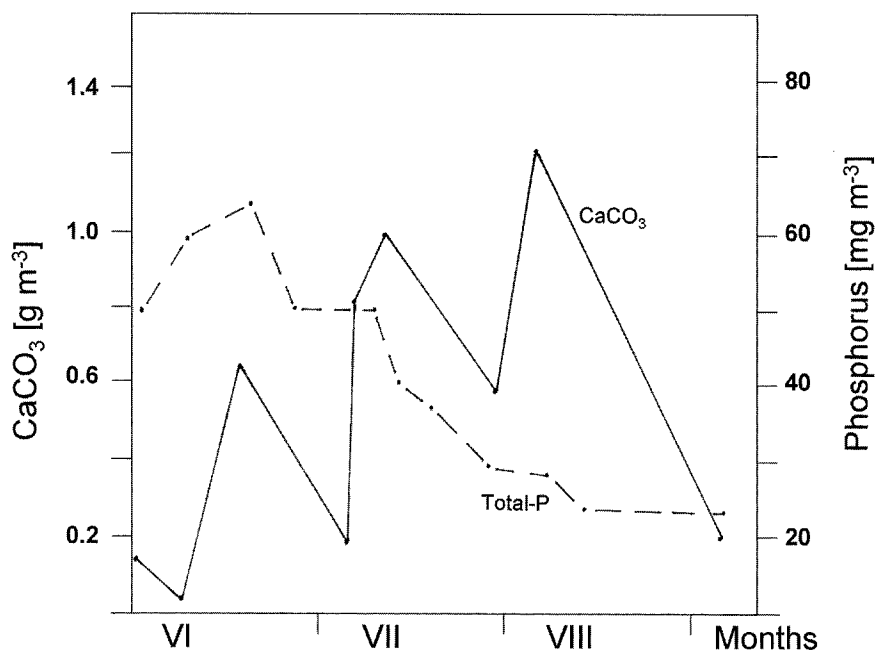
Fig. 4. The effect of calcite precipitation on phosphorus content. (Modified after KOSCHEL et al. 1988).
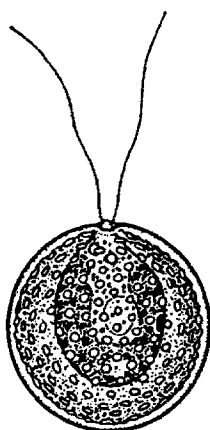

Fig. 5. The phytoflagellate *Phacotus lenticularis* is integrated in the calcite precipitation, an important relief process of the pelagial zone of lakes. (From STREBLE & KRAUTER 2002).

3.7. Concentration and centralization

We have seen that there are different processes in water bodies which ease removal of biomass and solid matter. To these processes belong the formation of neuston, pleuston and rising algae, which develop expanded mats near the water surface, but macrophytes can also store suspended matter.

This applies particularly to the macrophytic green alga *Cladophora* in streams. *Cladophora* shows mass production, accumulates nutrients and xenobiotics and filters great quantities of suspended matter and these masses can be transported away completely by a single high discharge. By their mass production *Cladophora* can be regarded as a **center of primary production**.

But *Cladophora* is also a habitat for a lot of animals which play important roles in matter cycling. For instance, in the filamentous system of *Cladophora* are

concentrated chironomid larvae in a high density, using the filtered detritus as food and for building their tubes. Simultaneously, the chironomid larvae tubes fix detritus within the filamentous system, facilitating in this way the quantitative detritus drift. The emergence period of the larvae is adapted to this detachment-mechanism (SCHÖNBORN 1997). Furthermore, in the *Cladophora*-clumps the leech *Erpobdella octoculata*, a main predator of the chironomid larvae, occurs in high density and thus *Cladophora* also becomes a **center of habitats**.

But the process of concentration is not be finished yet. Parallel to the increase of stream eutrophication, both the density of bacteria and of bacteriovorous animals rises, above all the density of ciliates. The ciliates, again, are prey of various small metazoans which are absent from oligotrophic stretches.

Bacteriovorous animals similarly need predators if their populations are to remain in the exponential growth phase. The most important predator of ciliates is the predaceous naidid oligochaete *Chaetogaster diastrophus* which, in turn, is the prey of the leech *Erpobdella octoculata*. *Erpobdella* also captures great numbers of chironomid larvae and of the detritivorous naidid *Nais* which frequently occurred in *Cladophora*-clumps (SCHÖNBORN 1985a). *Erpobdella* is from 3 mm (emergence from the cocoons) to nearly 60 mm and all development-stages are predaceous, occurring in high densities and controlling the whole meio- and macrozoobenthos. In streams with severely shortened food-chains (*e.g.*, lack of predaceous fish, piscivorous birds and mammals) *Erpobdella*, beside cyprinids and salmonids, can be a second top-predator and becomes a **predation-center** (SCHÖNBORN 1985b, 1992, 1995, 1996, 1998).

In summary, we can say that there are three centers which lead to a **concentration** of the ecosystem processes in loaded streams, whereby the ecosystem relationships are simplified. What does it mean in regard to the defence against eutrophication?

- Parallel to the density of bacteria the density of bacteriovorous animals increases, stopping stationary phases in bacteria growth and leading to permanent stimulation of bacterial production and consequently to the decomposition of organic matter.
- Many bacteriovorous species are found in the group of ciliates, which play a key role in self-purification. Other groups, like rotifers, have also a great number of bacteriovorous species. Especially important in this connection are the sediment feeders (oligochaetes, chironomid larvae), as explained above. These groups increase with eutrophication, because of the enrichment of sediments with bacteria, the main food of the larvae. In the River Saale (Germany) the oligochaete worm *Nais* digests up about 280 g bacterial biomass m^{-2} a^{-1}, whereas by ciliates only 182 g m^{-2} a^{-1} were consumed in the same time (SCHÖNBORN 1985a).
- The last link in this predator-chain is *Erpobdella*, which controls great parts of the macrozoobenthos (SCHÖNBORN 1987; see also Fig. 6).

The **concentration** leads simultaneously to a **centralization** of the ecosystem, in response to the increase of eutrophication. Therefore the ecosystem can react as an entirety against eutrophication. All the facilities that are involved in defensive reactions therefore act in concert.

3.8. Accumulation

Accumulation can be interpreted as a defensive reaction against toxic loading, initiated in the earliest geological periods in connection with increasing volcanism.

In the present paper, accumulation is defined as the enrichment of nutrients and xenobiotics in organisms. The importance of nutrient enrichment is described above (see chapter 3.2.). The accumulation of xenobiotics refers to heavy metals and today also to pesticides.

In waters of the temperate climate, primarily *Cladophora* and water mosses accumulate xenobiotics. The accumulation factor can be more than 10^6. In adaequate ecosystems these plants have a similar function to the liver in higher organisms. In the case of *Cladophora* the accumulated xenobiotics are removed from the stream reach concerned by a detachment-mechanism. Drifting *Sphaerotilus* also accumulates heavy metals, however, especially copper. Mosses, indeed, are great accumulators, but very resistant against drift. They are
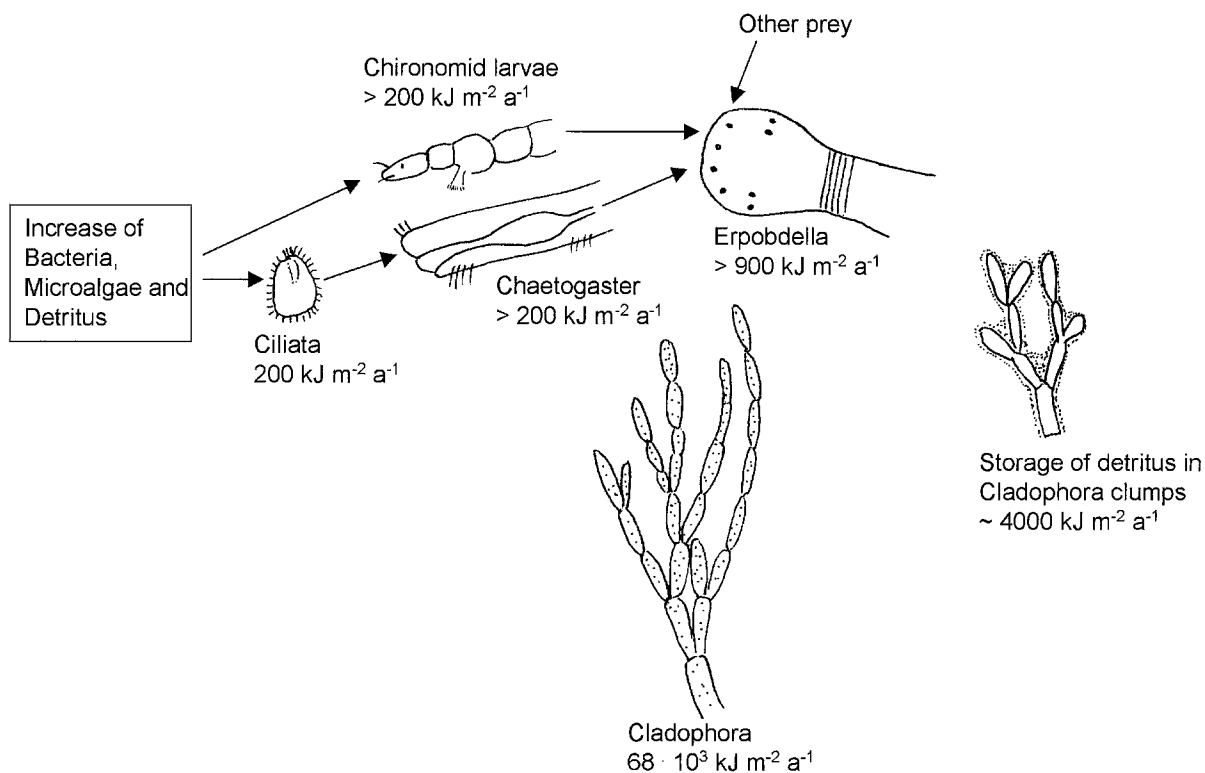

Fig. 6. *Cladophora* clumps as a center of primary production, habitats and predation. The values give the production of the named organisms or the storaged detritus, respectively. The detritus storage referred to a supposed vegetation period of *Cladophora* of four months. The arrows indicate the energy transfer. (Compiled from several papers, compare SCHÖNBORN 1992).

scarcely used as food by animals, whereby the accumulated matter is isolated from the water.

The immense literature on aquatic toxicology has not been taken into account in the present paper.

3.9. Other relief processes

• Resuspension

Resuspension, the churning up of sediments, is caused by bioturbation and in shallow waters additionally by wind. Oligochaetes, chironomid larvae and, especially, benthivorous fish (by rooting up sediment) participate in the bioturbation, but also large mammals by bathing and food seeking.

The churned up sediment increases water turbidity and therefore inhibits phytoplanktonic primary production. This can partially suppress realization of the eutrophication potential. Resuspension is prevented frequently by macrophytes, but on the other hand churned up sediment is deposited on leaves and thus restricts their production.

Resuspension also simultaneously leads to the remobilization of phosphorus locked in the sediment. So it seems that two contrary effects occur: on the one hand, realization of the eutrophication potential is reduced, and on the other hand more phosphorus is available for primary production.

The storage of phosphorus, especially in sediments, can also be interpreted as aimed against eutrophication, and furthermore, its release from sediment by bioturbation brings it more quickly to outlet-systems than it may happen by degrees. But this is not supported by facts.

• Denitrification

Another relief-system is denitrification which is integrated into limnetic ecosystems and probably very efficient. Nitrate can be denitrified wherever an oxygen deficiency occurs. Most important is denitrification on the surfaces of stones and other substrates. It can be observed even in oxygen-rich headwaters because it takes place on the basis of PRANDTL's boundary layer. Even some 100 μm above this layer oxygen occurs. Such oxygen-rich habitats represent an important cleaning-system if their area is great enough. In running waters epilithic denitrification rates of 16 mg m^{-2} d^{-1} have been measured (NAKAJIMA 1979). Animals can also take part in nitrate respiration and an important role in eutrophic profundals is played by the ciliate *Loxodes*.

3.10. Morphological defensive systems

The banks of running and standing water are frequently colonized by trees. In Europe, these are alders (*Alnus*) and willows (*Salix*), in other geographical regions *Ficus* species, gallery forests and mangroves.

With eutrophication, standing waters in shore and littoral areas expand their waterplant zone. This vegetation zone has characteristic stratification. But only emersed waterplants are important as defense mechanisms because they can occupy wide zones of both standing waters and slowly running waters. Like organisms many waters possess a "skin". In this case it is a two-fold stratification: a tree-belt and an emerse belt. In mountain brooks, the emersed plants are frequently replaced by sloping-plants, *e.g. Petasites* and *Phalaris*. This "skin" of water bodies takes an important protective function against eutrophication.

The alder zone: Alders' system of dense filamentous roots block the diffusion of matter into water. A 10 m broad strip of trees along running waters reduces nitrogen input from the surrounding fields by 10–15% and phosphorus input is reduced by about 20–30% (MANDER 1985). The alders' hydrophilic thick roots stabilize stream- and river banks. Their filamentous roots, thin as a hair and swinging in water, serve as habitat for many small animals which take part in decomposition. Land roots of alders possess tubercles with symbiotic bacteria (Actinomycetes, especially *Frankia*), that fix the air nitrogen in the soil. Therefore, alders can grow in nutrient-poor soils. The high nitrogen content of alders is distributed up to the leaves. In contrast to many other tree species, prior to leaf abscission alders stop the removal of nitrogen from the leaves. Therefore, the C/N-ratio of alder leaves that fall into the water is relatively low and makes the leaves an important food source for aquatic invertebrates. The input of nutrients by alder leaves does not cause an increase of eutrophication, because the decomposition of the leaves by hyphomycetes, by bacteria and by intestinal passages of shredders occurs slowly and successively. Animals in extremely nutrient poor brooks feed on alder as well as willow leaves.

The belt of emersed plants: A belt of emersed plants, especially the reed, *Phragmites australis*, provides an effective protection against eutrophication. The main mechanisms of this protection are basing on the following principles:

– Emersed plants act as a dike against infiltrated matter.
– Shading by emersed plants counteracts the development of algae in shore areas.
– Algae washed ashore from the main body of water are caught by the emersed belt where they die from shading. Emersed plants function as a trap for matter. The dead algae remain in the wind-protected belt, are deposited and decompose quickly due to the high oxygen content.
– The sediment within the plant belt is sufficiently aired because the roots release oxygen (from the assimilation of the leaves and transported through the

aerenchyma). This is primarily an adaptation to oxygen-poor sediments, but it leads simultaneously to an increased decomposition within the belts and therefore also to nitrification and sulphurization that leads finally to detoxification.

- Dead leaves of emersed plants can be found frequently on the sediment surface. Immediately below this layer of leaves are anaerobic conditions. In these flat areas nitrates and sulphates are denitrified or desulphurified, respectively. The mosaic-like distribution of oxygen-rich and oxygen-poor patches in the belt of emersed plants creates a detoxification- and disburdening-system (BÖRNER 1992).

- In anaerobic zones of water, anaerobic decomposition occurs that results in development of H_2S, NH_4^+ and CO_2. But these processes do not damage the reed plants (HÜRLIMANN 1951) because the anaerobic reaches will by bioturbation promptly be aerated. Thus the patch dynamics between aerobic and anaerobic reaches function as an effective protection against eutrophication.

- The plants accumulate nitrogen and phosphorus (per reed stalk ~150–250 mg N and 10.5–18.5 mg P) that is partly released in the summer months (SCHIEFER-STEIN 1999). Therefore, the accumulation of nitrogen and phosphorus does not seem to be an effective protection against eutrophication.

The belt of emersed plants, especially the reed protects against not only organic loading, but also against unorganic and toxic matter. Roots of the reed, for instance, accumulate copper and iron (Fe^{2+}), but frequently the heavy metals stick together with detritus at the reed stocks. Following OSTERKAMP et al. (1999) reed stocks retain:

- 29–91% of filterable matter and
- 16% lead, frequently connected with filterable matter (see Fig. 7).

From studies of wastewater treatments using aquatic plants, it is established that mineral-oil hydrocarbons (MHC) and polycyclic aromatic hydrocarbons (PAH) can be enriched in sediment between reed stalks. Therefore, tree-belts and belts of emersed plants provide water bodies with an effective protection against a wide spectrum of allochthonous matter. If groundwater in floodplains reaches the surface of soils (stressed conditions), marshlands will be formed including swamp forests or, as in the Southern Africa, gigantic *Cyperus* areas. In spite of increased nutrient input by big game, the marsh soils and their vegetation near the water bodies accumulate great quantities of nutrients and thereby prevent a hypertrophication. In this way, the wet soils of floodplains result also in increased denitrification.

4. Euoecisms and dysoecisms

4.1. Euoecisms

Euoecisms are defined as a co-operation of various features of one or some partial systems to the benefit and protection of the whole or greater parts of the ecosystem.
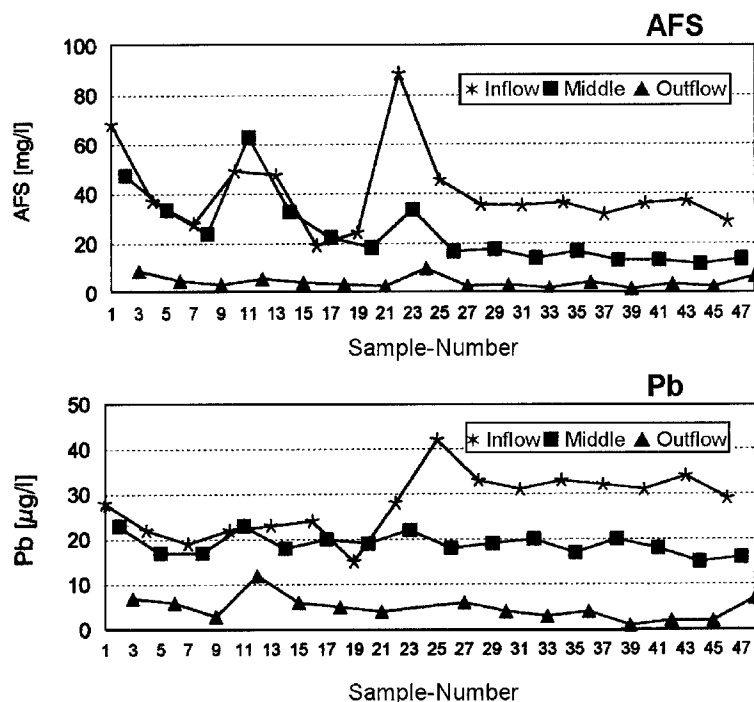

Fig. 7. Detention of particulate matter (AFS) and lead (Pb) within a waste water treatment using waterplants. Measured in inflow, middle and outflow during a storm-runoff-event. (After OSTERKAMP et al. 1999).

We have just described such an euoecism with the alder belt and the belt of emersed plants. The function of alders, for instance, can be completed by forming a canopy. This cools the water and reduces primary production, leading finally to the protection of greatly loaded brooks against weediness. The alder leaves can also regarded as a pharmacy for crayfish (*Astacus*), because the consumption of alder leaves is a protection against fungus diseases. The great importance of crayfish for the healthy of water bodies is decribed above (see chapter 3.3).

When leaves of alders are transported downstream in temperate regions the spring winds blow the deciduous leaves of the hardwood vegetation from along the riverside into the stream. These leaves are heavy decomposable, but in the course of their decomposition the C/N-ratio decreases and the leaves become edible for inhabitants of the stream.

Beside the harmonizing features of the belt of emersed plants in regard to the wellbeing of the whole system, their function as habitat for many birds, especially for herons, is also of interest, because the birds further remove biomass from the system.

Another euoecism begins with such planktonic diatoms which are only moderatley adapted because they sink to the ground relatively quickly and serve as food for profundal animals. Other sinking plankton also increased the nutritive value of the sediments. Many animals that feed on sunken living phytoplankton, or on sediment generally contribute to bioturbation and to the shift of sediment. This leads to the oxidation of sediments and therefore to the stimulation of the bacterial production, decomposition, nitrification, sulphurization and to an increasing release of methane and molecular nitrogen enclosed in the sediment.

Benthivorous fish also contribute to bioturbation in the profundal zone. In Central Europe it is primarily bream (*Abramis brama*) that feed on important sediment-shifting animals, such as chironomid larvae and

tubificids. The food-seeking of bream influences not only the oxidation of sediments and the stimulation of prey species, but also the removal of biomass from the profundal zone. Furthermore, through the oxidation of sediment, more phosphorus is bound in chemical compounds.

These euoecisms seem to be widely spread. Many euoecisms occur only in small spheres of activity without influencing the whole system. Some examples are:

- Floating features of planktonic forms protect also against predators.
- The suppression of secondary leaves of some flowering plants in the water current – mechanically or by loss of assimilates – allows only primary leaves which are adapted excellently to current water.

4.2. Dyseocisms and the "egoism" in limnetic ecosystem compartments

In contrast to the euoecisms, dysoecisms also exist. Dysoecisms are defined as defensive reactions of a compartment of an ecosystem to the detriment of one or several other compartments of the same system (SCHÖN-BORN 1995). From an anthropomorphic point of view, the different compartments can react "egoistically", in regard to other parts of the system.

Such behaviour is exhibited, for instance, in the defensive system of *Cladophora*. Their mass production, which is presumed to be its defensive reaction, impairs the whole stream ecosystem. By its relatively coarse-filamentous system, many invertebrates are excluded from the *Cladophora* clumps. These clumps are dominated mainly by chironomid larvae, leeches and other worms. Young fish, for example, are frequently "caught" in the long filaments (FOTT 1971) and die.

The mass production of *Cladophora* reduces the density of many algae and animals that otherwise would be typical species of the given bed structure or water quality. This refers especially to Ulotrichales and *Vaucheria* and,
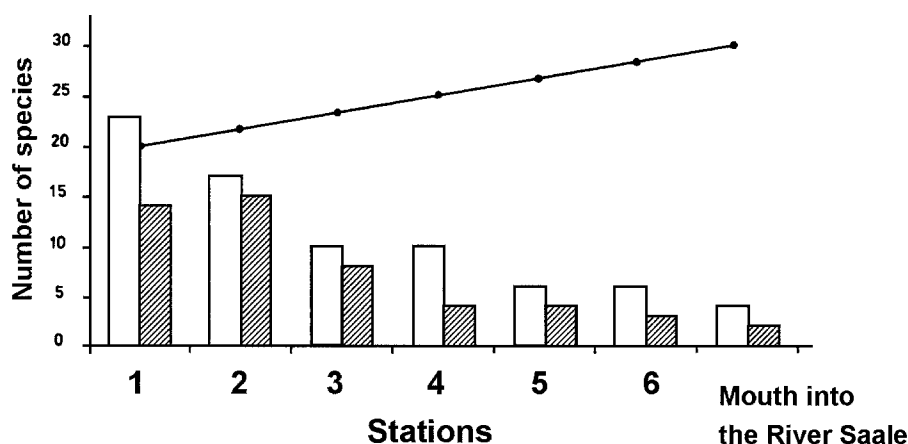

Fig. 8. Number of species of Trichoptera (white columns) and Ephemeroptera (hatched columns) in the longitudinal profile in a stream dominated by *Cladophora* (Ilm, Germany) in comparison with the number of species expected to occur. (After SCHÖNBORN 1996).

in the case of animals, the larvae of ephemeropterans and trichopterans (SCHÖNBORN 1996; see also Fig. 8). The chemical conditions within large *Cladophora* clumps also change. Nitrate uptake, high oxygen production and an increase of pH value (up to 10) are caused by the CO_2 decline resulting from the high assimilation intensity (FOTT 1971).

The detachment and transport of *Cladophora* masses benefit only a particular stretch, not the whole stream. On the contrary, in structure-rich and shaded downstream stretches, *Cladophora* masses are attached on overhanging stones and rotten. The mass production of *Cladophora* is an over-reaction of the system against early stages of pollution. The defensive reaction is directed against the ecosystem itself.

A similar case of dysoecism can be observed in calcite precipitation (SCHÖNBORN 1995). On the one hand, the sinking calcite crystals clean the pelagial but to the detriment of the benthic communities. The crystals block the interstitial system of sediments and the filamentous aufwuchs on stones and macrophytes. This results in high losses of microflora and microfauna, living in the interstitials. In Lake Stechlin, Germany, for instance, 140 taxa of testacean rhizopods were registered within the algal aufwuchs. But during increasing calcite precipitation caused by phytoplankton, these taxa were reduced to about 80.

After calcite precipitation in the aufwuchs of filamentous algae, many calcite crystals were found. Littoral sediments and algal layers on surfaces of stones were covered by calcite precipitation with a yellowish-white, quickly resuspensable coat. It consisted of felted flocks of detritus, in which crystals are included. Most calcite deposits can be found at the north and east shores of lakes, because the wind drifts the crystals to the littoral, and in particular to the surf zone. Whereas by this process the transparency in the pelagial increases, the benthic zone is covered by quickly resuspensable sediments. Shells of phytoplankton and zooplankton are frequently found within these deposits.

To a lesser degree, filamentous algae mats also have biogenic decalcification, especially if blue-green algae occur in high density. But this does not impair colonization of the mats.

We can draw the conclusion that a lake does not react as an entirety to the impact of loadings, but that the defensive reactions negatively impact other system compartments. They "overshoot the mark", comparable with allergic reactions of organisms.

Another example are bacteria, which evolved as destruents and which are of fundamental importance to the existence of life on earth. This notwithstanding, their function in water bodies can have disastrous secondary effects. By their consumption of oxygen, they can endanger the ecosystem more than undecomposed matter

remaining in the water. Furthermore, in the course of decomposition, it can be released toxic substances. In this case, defensive reactions against eutrophication can be directed against the ecosystem itself. Such secondary effects of decomposition are absent in terrestrial habitats.

Similar dyseocisms occur in waterblooms. Before they wash ashore, relieving the water, they cause extreme day-night-alterations of CO_2, O_2 und pH values.

Such dysoecisms can also indicate a transition to organic behaviour. It is well known that the content of prussic acid of waterplants inhibits their defence against pests, instead to protect the plants.

5. The aging of limnetic ecosystems

Limnetic ecosystems age and at any time this aging can lead to the dissolution of the system. Especially for lakes, this process of aging and siltation has been well researched. A lake becomes shallow with dead planktonic and littoral organisms, especially plants. The morphological alterations in lakes lead to an increasing eutrophication and thus to an acceleration of siltation. Eutrophication in the course of aging results in the debilitation of the system and a tendency toward pessimism (*e.g.*, decrease of species diversity, increase of extreme life conditions). In this regard, the aging of lakes is frequently compared with organismic aging.

Aging can be accelerated or retarded. The acceleration is caused, for instance, by clear cutting of border trees, by a permanent nutrient input or when lakes are situated in regions with a nutrient-rich geological underground. Extant oligotrophic lakes can be regarded as perennial young stages. The system cannot reject aging because aging is an irreversible process whereby morphometric relationships are changing. But this process can be retarded by defensive reactions.

Similarly running waters also age. In rivers, the trophic state increases downstream, also under natural conditions. As a consequence of stream continuity, the age stages of running waters remain connected beginning with the brook (young stage), followed by the middle course with meanders (maturity) and ending with the lower course and mouth (old age). Running waters flow into standing waters (for instance a lake, mostly a sea) and end their existence. A shallow, lowland stream with a slow current has little chance to defend against eutrophication, because it can silt up.

In the tropics, the main factor of siltation is the water hyacinth *Eichhornia*. Algal mats also contribute, rising from the stream bed and drifting to the bank where they are deposited by their slow current. This deposition is a siltation process that simultaneously creates a habitat for *Eichhornia*. Unlike as standing water, a water current

erodes a new drain beside the old bed but this new stream represents a new ecosystem.

Other main factors of the siltation in tropic waters are *Salvinia* (water fern) and *Cyperus* grasses. Water bodies that have a dry phase stop their aging process in this dry period because the organic remnants are metabolized by the air at this time, providing a little relief to the aging process.

6. Immigration of foreign species into limnetic ecosystems (neophytes, neozoa)

It is sometimes believed that the immigration of foreign species into an ecosystem causes defensive reactions, comparable to the reaction of organisms to an infection or comparable to defensive reactions against eutrophication. But this is not the case. The immigration of foreign species is a complex process and our knowledge concerning the mechanisms of the integration of the foreign species is deficient.

First, there are situations, in which the ecosystems have enough space for immigrants and therefore no conflicts with the indigeneous species exist. Foreign species penetrate frequently into water bodies which are greatly changed and therefore show significant losses of original species. Recent changes are caused in most cases by anthropogenic influences, *e.g.* eutrophication by wastes, destruction of banks and shores, installation of dams and reservoirs within streams, increased accumulation of fine sediments and so on. Foreign species can compensate species losses and colonize new structures precipitated by the anthropogenical changes. Frequently the immigrants are very mobile euryoecious species that can quickly colonize the new habitats. One example is the Rhine River. It lost nearly 70% of its zoobenthic species in the time from 1900 to 1970. By about 1990, this species deficit was overcome by new species among which 12 were neozoans (KINZELBACH 1982, 1983).

Natural events can also favour such immigrations (*e.g.*, glacial periods, geological relief changes, high water, long dry periods and volcanism). Particularly in streams, foreign species can immigrate after high water events with a strong wash-up effect and can anticipate indigenous recolonisation (TITTIZER 1997).

There are also water bodies – perhaps most – where ecological niches are occupied incompletely, for instance as result of glacial periods. These niches can be filled by foreign species. In all such cases, it does not result in ecosystemic changes. Examples are the neophyte *Bunias orientalis* in the Björka-Kävlinge River in Sweden (KOHLER et al. 2000) and the North American turbellarian species *Dugesia tigrina*, today widely distributed in European lakes. In the last 100 years, many new species arrived in Europe without causing losses of the indigenous flora and fauna.

Such benign immigration notwithstanding, there are also examples of conflicts between the indigenous species and immigrants. The conflicts – eradication or displacement – caused by new predators or competitors (*e.g.*, for food, life space and so on) can be partial or complete. But in the most cases the conflicts are only local, concerning only a certain lake or region (TITTIZER 1997). A well investigated example of eradication of a species by an immigrant is the copepod *Heterocope* in Lake Constance. During a period of eutrophication in Lake Constance, the predatory *Cyclops vicinus* immigrated and has eradicated *Heterocope* by capturing its nauplius larvae within two years.

The most sensational case of the predatory eradication of species by a neozoa is from Lake Victoria, when the predatory Nile perch (*Lates niloticus*) was introduced into the lake. Nearly 200 of the formerly 300 species of endemic cichlids disappeared or are threatened. The whole ecosystem changed dramatically. The disappearance of 13 waste-feeding cichlid species was compensated by the shrimp *Caridina nilotica*. The shrimp was permanently present in the lake in low densities but after the elimination of the cichlids it appeared in masses. Generally, the elimination of primary consumers among the fish species was substituted by pelagic crustaceans. The whole food chain was changed or strongly simplified (WITTE et al. 1992; GOLDSCHMIDT et al. 1993).

Another example of conflict are the 1033 fish species, formerly living in Mexico, U.S.A. and Canada. From these species, nearly 68% have disappeared or are strongly threatened. One of the causes for this drastic change may be the introduction of foreign species (WILSON 1997). As in terrestrial systems, the naturalization of exotic species was an important factor in the extinction of indigeneous species.

Not only foreign predators, but also competitors can significantly effect ecosystemic changes. In Europe, *Dreissena polymorpha* is a well known neozoa. It colonized streams and lakes but has not impaired any species or caused ecosystemic changes. This species occurs mainly as a space competitor on hard substrates that are apparently only weak settled. Stronger changes occurred in Lake Erie, Canada, where *Dreissena bugensis* colonized fine sediments This immigrant has reduced the density of the tube-dwelling amphipod *Diporeia hori* and some small mussels, but it has not eliminated them. Furthermore, the pseudofaeces of *Dreissena* have promoted some indigeneous species (DERMOTT & KERREC 1997).

When a foreign species establishes a key position a total reconstruction of the ecosystem is possible. This applies, for instance, to the water hyacinth *Eichhornia crassipes*. Originally, from the Amazonian region it was

imported to Africa. In Africa it develops dense carpets on the water surface, by darkening the whole water body. The Amazonian region has antagonists of this plant, inhibiting its expansion.

There are a lot of examples of foreign species immigration into water bodies, but no case of an ecosystemic defence reaction which is directed against these species. If there are conflicts, two or more species are confronted, and the superior species wins the interaction. The penetrating species will be eliminated if it is a weak competitor or a preferred prey of indigenous predators.

Another reaction is high densities of a foreign species in the early stages of an immigration, but later these densities retreat and remain at a low level. A well known example is *Elodea*, the waterweed, today a normally niched plant. The mechanism of this elastic reaction is unknown.

Unlike eutrophication which is caused by abiotic factors and concerns all species, immigration is a conflict between two or some species. Eutrophication is a permanent danger for the whole ecosystem. Foreign species which may lack general defensive mechanisms are unpredictable. Evidently the mechanisms of the origin of defensive reactions against eutrophication are not applicable to foreign species. Ecosystems rarely react as an entirety. Mostly only single compartments react "egoistically", but these reactions probably have an "altruistic effect".

Even more unpredictable than a single foreign species that causes only weak changes, is the total reconstruction of an ecosystem by immigrating species. Furthermore, a defensive reaction against these immigrants does not make any biological sense, because the geographic expansion of species is an important factor of evolution.

7. Origin and character of defensive systems. Analogies and differences in regard to organisms

This chapter attempts to examine and theoretically discuss the statements about defensive reactions in limnetic ecosystems given in this paper and to make conclusions based on this examination. Another aim is it to explain the possible origin of defensive systems. Additionally, the nature of defensive systems is made transparent by comparison with organismic defensive reactions to harmful external influences, especially to morbific agents.

7.1. Ecosystemic immunity

Ecosystemic immunity is the activation of microbial and chemical processes (microbial self-purification, calcite precipitation and denitrification) by increasing organic inputs.

These processes seem to respond automatically based on existing chemical and biological potentials. Thus, for instance, as nutrient contents increase, the density of algae is increased. This is connected with a CO_2 deficit and – following chemical laws – leads to calcite precipitation, which takes algae and other particles downward and adsorbes phosphorus. There are dysoecisms which show that not the whole system takes part in these processes. In a way, denitrification in waters also can be regarded as a protective reaction that takes place automatically following bio-chemical laws. It is unknown whether the results of such reactions hide selective mechanisms. Surely these mechanisms exist in microbial self-purification, but they originated in earliest biological evolution.

Because it is necessary that life spaces (including terrestrial) are not filled with caracasses, parts of dead organisms and other organic waste, natural selection has promoted those organisms that contribute to the preservation of life spaces and thus to the basis of their own life. Consequently, selection promoted the origin of saprophytic bacteria, fungi, and such animals as shredders, coprophages, necrophages and detritivores.

Without bacteriovorous animals, decomposition proceeds very slowly. From existing predator-prey relationships, increasing eutrophication automatically stimulates either the food-chain bacteria – ciliates – *Chaetogaster* – *Erpobdella* or analogous chains that effect decomposition activity. It is unknown to what extent natural selection has promoted decomposition and therefore the preservation of life spaces. The above named food chains evolved with regard to their food, but it is not clear if this benefits the whole ecosystem. It could also be that automatism – free from selection – can have euoecistic effects.

7.2. Species-egoistic adaptations with system-altruistic effects

Species-egoistic adaptations with system-altruistic effects are defined as the adaptation of a species to its environment, which simultaneously promotes the preservation of the whole system. This happens in the following ways.

1) Adaptation of a species with the aim to keep the environmental conditions constant in their own interest, but thereby simultaneously benefit the whole system.

   This form of adaptation could be found in algae, but also in the above mentioned saprophytic bacteria and fungi. *Cladophora glomerata* accumulates nutrients in a high degree and is therefore able to colonize oligotrophic stretches of streams. The increasing nutrient level in the water promotes nutrient accumulation in connection with a mass production of

this algae so that the running water might become dammed. Therefore *Cladophora* has developed a detach mechanism that secures its further existence. Much of this detached biomass, including accumulated nutrients and xenobiotics, drifts downstream so that the stretch will be relieved and the production of this green alga will be newly stimulated. The stability of the ecosystem increases, but, as showed above, this increased stability is connected with dysoecisms.

Benthic algae in standing waters show the same pattern. By mass production, they rise from the sediment and drift ashore. Mass production is not only stimulated by direct nutrient supply, but also the CO_2 produced by the decomposition. Drift, caused by wind, leads to a relief of the water body. The same applies for waterblooms and pleuston. In all cases the species or communities, stopping the process of eutrophication, are useful to themselves. LINSENMAIR (1994) makes similar conclusions with reference to the stability of ecosystems. The stability originates indirectly by the selection of populations that have positive effects on the persistence of other populations.

2) Another adaptation mechanism is the filling of a niche with positive effects to the whole system. Tubificids in sediments, for instance, have filled such a ecological niche. The worms are adapted to low oxygen contents by intestinal respiration and possession of haemoglobin. The uptake of sediment and digestion of its microorganisms, as well as the aeration of the sediment caused by its shifting, lead to a stimulation of bacterial production, organic decomposition, and aeration of sediments.

3) Many land animals, both herbivores and predators, are adapted to food seeking within water bodies. The utilization of water bodies as food and common space by terrestrial animals leads – with many contrary processes – to a relief of the water ecosystem. These animals relieve the water bodies because their defecation takes place completely or primarily on land. Probably selection has favoured this form of defecation. In the case of defecation within the water, the transparency would have been considerably decreased, thereby obstructing food seeking. We can say that this relief system was brought into the limnetic ecosystem but it was not developed internally.

4) Euoecisms are also a form of adaptation, although it may be very difficult to understand their origin. Alder zones and zones of emersed plants are polyfunctional, complicated compartments serving the whole system. In the same sense deltas and estuaries are also considered to be gigantic protective systems for the sea.

Plant belts can be considered analogous to the skin of organisms. This protective system seems to be developed by species-egoistic adaptations which have simultaneous system-altruistic effects. Reed grows in shallow waters, therefore in the littoral in large lakes. Its protective effect against eutrophication is probably favoured by selection (*e.g.* growth of densely lying rhizomes, high density of stalk root-aerating, and so on) because a quick eutrophication in connection with siltation would eliminate the life space of reed.

But the reed itself is important to siltation through its mud rich with cellulose (high C/N-ratio) that is difficult to decompose. The decomposers of cellulose, most of all *Cytophaga*, secrete slime which stabilizes the mud of reed and thus favours siltation. During the siltation process, reeds must also compete against not only other macrophytes but also the development of a bog. Therefore, selection favours the protective function of the reed to preserve the water body and simultaneously the inhibition of competeting vegetation.

The function of the alder zone along water's edge can be interpreted similarly to the reed. The selection favours trees with hydrophilic roots, tops closed in a canopy over small bodies of water and fallen leaves with a low C/N-ratio. These mechanisms prevent breakage of banks and fill of brook beds or waterground. Therefore they prevent generally the loss of the living area of trees. The combination of fallen leaves, which are difficult to decompose and intensive solar radiation result in an eutrophication connected with weediness that can finish the existence of smaller running or standing waters relatively quickly.

The fungitoxic substances within the alder leaves protect the crayfish against fungus diseases. Crayfish have an important function in the preservation of the ecosystem "brook", but it is difficult to understand the selective co-evolution between alders and crayfish. Therefore, the positive relationship between alder and crayfish may be only accidentally. In this respect, the alder may be considered to be a weak competitor. Alders are inferior in competition with other trees, primarily because they increase dryness and aerate the soil. But crayfish dig long caves, which they use as hiding places, into the banks and between alder roots and thus provide the alder rhizosphere with water (see Fig. 3).

7.3. Accumulation of xenobiotics

The accumulation of xenobiotics is an acquired defensive reaction against toxic substances and is useful for the preservation of the system in accordance with the principle formulated in chapter 7.2. A toxic substance is removed from the water by accumulation without harm-

ing the accumulator. This makes ecological sense, particularly in plants with a surplus of biomass that drifts downstream or ashore (*Cladophora*). But it applies only during short-term contamination events because permanent loading makes accumulation meaningless in an ecological sense.

It is possible that these mechanisms originally appeared during volcanic eruptions which influened the surrounding waters. Different geological periods (*e.g.*, in the late Cretaceous) experienced high frequecies of eruptions. It is probable that most accumulation mechanisms originated during these times. In this regard, the eruptions of the volcano St. Helens (Washington, U.S.A.) may be considered as an example of the present period (WISSMAR et al. 1982).

7.4. Defensive reactions and stability of ecosystems

Defensive reactions against eutrophication can be interpreted as stabilization mechanisms. In an ecological sense, stability is difficult to define. In our case, stability refers exclusively to the preservation of the trophic level during increasing loading.

After the cessation of nutrient input or the removal of loading substances, waters remain on their trophic level for some time, beause different nutrients are stored differently (*e.g.*, in sediments or organisms). This particularly applies to standing water with a long water-residence time. This concerns the so-called "recovery time" of the water, which cannot be used for a theoretical discussion of stability. Every eutrophication is a wear process of the water body.

The more defensive mechanisms a limnetic ecosystem has at its disposal, the more stable its state. But it could be shown that the defence against a disturbance factor simultaneously effects a detriment to other compartments of the ecosystem, causing instability. As explained above the whole system never reacts to disturbance factors as an entirety, but only in single compartments, that is 'dysoecismically and therefore incompletely'. Even normal microbial self-purification can impair the ecosystem by oxygen consumption and the release of the toxic by-products of decomposition. Despite of the close integration of an ecosystem, only those single populations react that have developed adaptation mechanisms. This is, however, sufficient for the general stabilization of the system. The conditions can be very complicated. According to KALBE (1996), the ranges of stability are broader with increasing trophic status, but the transitions will be instable: oligotrophy – eutrophy – hypertrophy are stable stages; mesotrophy – polytrophy – and all conditions more than hypertrophy are instable stages until finally the ecosystem loses its function.

7.5. The importance of defensive reactions in the preservation of limnetic ecosystems

It seems obvious that without microbial decomposition of organic matter, no life on the earth would be possible, due to the mass of dead bodies. Contrary to the other defensive reactions described in this paper, only the microbial decomposition as a self-purification-mechanism is well studied. These other defensive reactions probably do not reduce the degree of eutrophication, but they make its increase more difficult. This applies mainly to long-term loading processes, as they are commonly found in nature. But short-term loadings can be thoroughly averted. Without these defensive reactions, many water bodies would have a short existence. This applies also to running waters, provided they are shallow and flowing slowly. They can quickly develop weediness and then silt up by depositing algal mats and pleuston plants.

It may be possible to explain defensive reactions and euoecisms by the help of a single species with an "altruistic" effect. DUNBAR (1972) published a theory according to which ecosystems are highly integrated unities that compete jointly and evolve as a unit. This may indeed play a role, but it could be also given another explanation. It may be that those water bodies have longer survived which have had protective features. Accelerated siltation of standing and running water bodies would have catastrophic consequences for the water balance of the inland. Small standing waters – for instance pools and smaller water bodies – can be formed rapidly by changes in the relief of the earth surfaces or by large animals. But it is doubtful whether this process will occur in a shorter time than the physical extinction or ecosystemic destabilization when permanent eutrophication takes place. When flowing water must arode a new way after siltation of a lowland stream, it needs time, but for the formation of really important water bodies, periods of geological folding processes or ice ages may be necessary.

Even the sea puts out by breakers great quantitites of algae and animals. But it is unknown to what extent the wrack-masses relieve the seashore.

7.6. Analogy with organismic defensive reactions

It may be a dubious attempt to draw parallels between ecosystems and organisms, but it is helpful in understanding defensive reactions in limnetic ecosystems. The comparison with the immune system has already been demonstrated. In the case of aquatic ecosystems, there are latent potentialities that are mobilized automatically by eutrophication (chemical processes) and are selectively developed (microbial processes). Another comparison can be made to algal masses washed ashore, the

so-called "algal expectoration". This process is similar to a cough, a head cold, vomitings and expectoration – usually considered as animal or human diseases. These are defensive reactions of the body to get rid of morbic agents. In the case of algae, these are high concentrations of nutrients and xenobiotics.

Like some organisms have a liver, a limnetic ecosystem has "organs" of detoxification in the form of xenobiotics-accumulating plants, most frequently *Cladophora* and water mosses, but also many other plants.

Just as the skin or membranes of organisms serve to protect against foreign influences, reed belts and border trees perform a comparable function in limnetic ecosystems. Like skin that not only protects and demarcates organisms but also enables a selective exchange of matter, the alder belt and belt of emersed plants control not only the uptake of CO_2, the aerating of sediments and the fixation and transport of nitrogen into aquatic systems, but also release of nitrogen by denitrification.

In the same manner as organisms possess special protective mechanisms for entryways into the body (*e.g.*, antibacterial substances in saliva, nose, tears and ears; gastric acid), entryways into limnetic ecosystems are also protected. Springs, for instance, precipitate substances from the earth's interior (calcium, iron, manganes), therefore these minerals reach only a low concentration in streams and lakes. Large lakes and oceans are protected by deltas and estuaries which accumulate many dissolved and particulated substances transported by streams. The origin of such protective systems is difficult to explain [lucky chance or selection in the sense of DUNBAR (1972)?].

The most conspicuous parallelism between organisms and limnetic ecosystems is aging. This relates primarily to lakes but running waters can also age, however in a changed manner in consequence of their kinetic energy or their continuum. Although the aging mechanisms of lakes are totally different in comparison to organisms, over feeding leads, in both systems, to an acceleration of aging. Underfed organisms and oligotrophic lakes live longer than overfed bodies or hypertrophic waters, respectively.

As already described, defensive reactions of ecosystems can impair some compartments of the ecosystem. These so-called dysoecisms also show conspicuous parallelisms to organisms. For instance, the immune system of an organism frequently shows overreactions whereby parts of its own body can be attacked. Examples include multiple sclerosis, rheumatism, arthritis, diabetes and an acceleration of aging. Fever, as a defensive reaction, can harm the body. Allergies are defensive reactions against foreign substances, but the reactions overshoot the mark and can even cause diseases.

Like a cough, sneezing and expectoration are frequently interpreted as autonomous diseases but in reality

are defensive reactions, it is also possible to similarly understand algal masses that wash ashore.

There are no parallelisms between the origin of the defensive reactions of organisms and those of limnetic ecosystems. Both reactions have similar results but are systemspecific.

8. Human support of the defensive reactions of water bodies against eutrophication

Human intervention can support the defensive reactions of water bodies against eutrophication. The most important measures are:

– Algal mats on water surfaces and algae washed ashore should be removed. Drifting *Cladophora* in streams should be caught and removed. For this purpose, special nets for skimming and catching should be constructed.
– Mass developments of neuston and pleuston (*Lemna, Eichhornia* and others) should be removed.
– Support terrestrial outlet systems (protection of otters, ecological management of cormorants; protection of all animals which take part in defence mechanisms).
– Preserve eels and amphibians.
– Induce calcite precipitation in such a way that the sinking crystals do not reach the benthal. There are already artificial calcite treatments of lakes (MURPHY & PREPAS 1990; DITTRICH et al. 1995), but without regard to the benthic zone.
– Protect water mosses (xenobiotics accumulators without drift mechanisms).
– Protection and renaturation of the alder belts and belts of emersed plants in the water bodies and along the banks.
– Reservoirs and other artificial water bodies should be rich in bights and reed habitats.

The removal of plants (mostly algae, neuston and pleuston) that underlie the detach-and-drift mechanisms mimics natural ecosystemic processes. But this does not apply to other plants, for instance a removal of plants from the littoral zone will damage the whole ecosystem.

Summary

– Nutrients and xenobiotics reach the element cycle more quickly in water bodies than in terrestrial systems. Therefore, aquatic ecosystems develop particular defensive mechanisms against organic and toxic loadings.
– Large animals (big game), since about the Mesozoic, have been significant causes of eutrophication in

aquatic systems. Their influence has caused abundant hypertrophy and continues at present in regions with high densities of elephants, buffalos, hippopotamuses and crocodiles.

– Geological periods of increased volcanism may result in higher toxic impacts on water bodies. Freshwater ecosystems have had long time periods to develop defensive reactions against organic and toxic loadings.

– A well known defensive reaction of aquatic ecosystems is microbial self-purification.

– Many benthic algae accumulate nutrients and xenobiotics and tend toward mass production. In running water, they can detach by high current velocities and drift downstream. In standing water, they rise to the surface and drift ashore by wind. These processes unburden (at least) one of the ecosystem compartments (a stream stretch or the open water zone). In standing water in these processes are also involved in the lake bloomings, neuston and pleuston.

– There are important terrestrial outlet mechanisms by food chains from freshwater organism to terrestrial consumer. Examples: Terrestrial consumers of microorganisms, algae, pleuston and small animals (e.g. ducks); consumers of waterplants (many birds and mammals); terrestrial predators capturing (primarily) fish and decapods. Fish and decapods eat a lot of algae. Their accumulated nutrients can be transported out of the aquatic environment. The most important predators are cormorants, certain species of storks and otters. Amphibians also take many material outward after their metamorphosis.

– There are also marine outlet systems, for example eels. But they seem to be not very effective.

– Filtering mechanisms can also unburden water bodies such as the mechanical filtering of seston in interstitial spaces of plant clumps (e.g., Cladophora, Myriophyllum) and the biological filtering of filter feeders (Cladocera, big mussels and other groups). Filter feeders are particularly effective when combined with one of the outlet systems.

– Planktonic calcite precipitation also removes biomass and nutrients (phosphorus) from the open-water zone and seem to be a natural self-purification process.

– Eutrophication leads to a concentration of vegetable biomass and nutrients. This may facilitate their removal. Means of removal are high water discharge (in running water), wind (in standing water), and herbivorous terrestrial animals (through "skimming" or grazing). The effect of this concentration is especially evident in the green alga Cladophora. The mass production of Cladophora yields a centre of primary production and habitats (many animals colonize the clumps, especially larvae of chironomids, which transform the detritus, filtered by a filament network of the clumps in fixed tubes).

– Simultaneously, the leech Erpobdella octoculata develops high densities in the clumps and becomes a centre of predation. Its development stages (3–60 mm) are all carnivorous and control nearly the whole meio- and macrozoobenthos. These processes lead to a centralization of the ecosystem as a response to increasing trophic state. This may lead to a bundling of reactions contributing to self-purification.

– Eutrophication promotes the density of bacteria. It comes to a linear energy-and-matter flow system (e.g., bacteria – ciliates – Chaetogaster – Erpobdella), which keeps the exponential growth phase of the bacterial populations as a stimulation to their production and an intensification of the decomposition of organic matter. This process is a part of centralization, too.

– The accumulation of heavy metals and other noxious matter is another form of defensive reactions. The accumulated matter can be drifted together with the plants or microorganisms (e.g., Cladophora, Sphaerotilus), or isolated, as in the case of the detach- and consume-resistant water mosses.

– Resuspension of sediments and denitrification in water bodies are also part of the disburdening process.

– The zone of alders and emersed plants along running and standing waters protects water bodies from eutrophication comparable to the skin of organisms that protects against penetrating xenobiotic matter. Like the skin, this double protection layer of aquatic systems is also a multifunctional defence system.

– There are features and structures of ecosystem compartments that contribute to the utility and protection of the whole system. This phenomenon can be named "euoecism". On the other hand, there are also "dysoecisms". Mostly they arise when defensive reactions adversely affect other compartments. But inadequacies of defensive reactions are also dysoecisms.

– Aging of water bodies, connected with eutrophication, is an irreversible process (like the aging of organisms) and causes morphometric changes leading to the "death" of the water bodies. But defensive reactions can retard this process.

– There are no defensive reactions against the introduction of foreign species (neophytes and neozoa) into water bodies. The intruder faces one or more resident species. As opposed to situations of eutrophication, most conflicts do not concern the whole ecosystem. But there are cases in which the invasive species catastrophically affect flora and fauna (e.g., Lake Victoria, Africa). Furthermore, the occurrence of foreign species is not foreseeable (eutrophication is a permanent danger), therefore evolution could not effectively operate. An exception is the case in which the invasion is stopped by indigenous predators.

– Microorganisms in particular possess features or activities as well as processes founded on chemical laws that

automatically counteract eutrophication (*e.g.*, self-pu-
rification, calcite precipitation, denitrification). These
processes are comparable to the immune systems of or-
ganisms, but can function only in combination with mi-
croorganisms within a food chain (predator-prey-rela-
tionships). These processes can be the result of selec-
tion in the sense that water bodies with such systems
have slower siltation and are therefore, less prone to ex-
tinction. But this is generally difficult to establish,
exept in the case of saprophytic bacteria which are sure-
ly promoted by selection to save the aquatic system
from being filled by dead organic material.

- Many defensive reactions of water bodies are founded
on species-egoistic adaptations with an (accidentally)
system-altruistic effect. This applies especially to de-
fensive systems based on algae, but also to the self-
purification by saprophytic microorganisms in earli-
est times and also to euoecisms. The adaptation of
species is egoistic because it counteracts the eutrophi-
cation only to keep the species' own favourable living
conditions, or in the case of saprophytic microorgan-
isms to keep their living space. There are also annida-
tions of species with positive effects on the whole sys-
tem (*e.g.*, Tubificidae).

- In most cases, the described defensive reactions could
not be developed from the ecosystem, but it seems
that they have been "caught" by the water bodies,
which is especially clear in the case of terrestrial out-
let systems.

- The accumulation of noxious matter (*e.g.*, heavy met-
als) of certain plant species, which itself is probably
an acquired defensive reaction against toxic loadings,
is primarily an egoistic phenomenon that nevertheless
serves the preservation of the entire ecosystem. The
reaction may have originated in geological periods of
high volcanism.

- Every eutrophic event wears down the ecosystem. In
the course of eutrophication, usually several ecosys-
tems disappear, but without leaving behind corpses.

- The more a freshwater ecosystem possesses defensive
mechanisms, the more stable is its state with regard to
trophism. An ecosystem does not react as a unit, but
by single species (populations) that have a stabilized
efficacy that supports the whole system.

- For the global water balance, it is important that fresh-
waters are not too quickly silted up by sediments
(caused mostly by decomposed waterplants). There-
fore, defensive reactions against eutrophication have
an existential importance for a heritable earth surface,
because these defenses restrain siltation and lead to a
selective advantage.

- Analogies of defensive reactions of freshwater
ecosystems with those of organisms are quite possi-
ble, but only in regard to their effects, not to their
manner of origin.

Examples:
- Self-purification, denitrification and calcite precipi-
tation are comparable to the immune system.
- Concentration of algal masses and their removal (on
banks and shores and in the bights as "sputum
rooms") is comparable to phlegm and expectora-
tion.
- Accumulation of noxious matter by plants is com-
parable to organs of decontamination (*e.g.*, liver).
- Processes in springs and river mouths are compara-
ble to protection of the entrance portals of the body.
- Zones of alders and emersed plants are comparable
to skin.
- Disturbances in the matter cycle by strong eutrophi-
cation (hypertrophy) are comparable to the increase
of diseases by over nutrition.
- Dysoecisms are comparable to overreactions and
inadequacies of organismic defense mechanisms.

The origin and mechanisms of defensive reactions are
completely different from those of organisms.

- Human intervention can support the natural defensive
reactions in freshwaters with the help of relatively
simple techniques.

Zusammenfassung

- Nährstoffe und Schadstoffe gelangen in Gewässern
schneller in den Stoffkreislauf als in terrestrischen
Systemen. Daher haben Gewässer-Ökosysteme gegen
eine Überlastung besondere Abwehrreaktionen ausge-
bildet.

- Großtiere waren und sind extreme Eutrophierungs-
faktoren für die Gewässer, zumindest seit dem Meso-
zoikum. Ihr Einfluß führt noch heute zur Gewässer-
Hypertrophie in Gebieten mit einer hohen Dichte an
Elefanten, Büffeln, Flusspferden und Krokodilen. In
geologischen Zeiten eines erhöhten Vulkanismus
wird es auch zur stärkeren toxischen Belastung der
Gewässer gekommen sein. Die Gewässer-Ökosys-
teme hatten also lange Zeiträume zur Verfügung, um
Abwehrreaktionen gegen die Eutrophierung und
anorganische Belastung zu entwickeln.

- Die bekannteste Abwehrreaktion der Gewässer-
Ökosysteme ist die mikrobielle Selbstreinigung.

- Viele benthische Algen speichern Nähr- und Schad-
stoffe und neigen zur Massenentwicklung. Sie werden
in Fließgewässern bei erhöhten Durchflüssen abgeris-
sen und abgetrieben oder sammeln sich in Stand-
gewässern an der Oberfläche und werden dann vom
Wind an das Ufer oder darüber hinaus gespült. Hier-
durch wird zumindest ein Kompartiment (z. B. Fluss-
strecke, Freiwasser in Standgewässern) entlastet. In
Standgewässern nehmen daran auch Wasserblüten,
Neuston und Pleuston teil.

- Von großer Bedeutung sind auch die terrestrischen Ausleitsysteme mittels Nahrungsketten: Wasserorganismus → terrestrischer Konsument. Zu nennen sind Mikroorganismen, Algen- und Pleustonfresser (z.B. Enten), Wasserpflanzenfresser generell (viele Vogel- und Säugerarten) und terrestrische Prädatoren, die vor allem Fische erbeuten. Fische und auch Großkrebse konsumieren große Mengen an Algen, deren gespeicherte Stoffe durch die Prädatoren nach außen gelangen. Die wichtigsten derartigen Prädatoren sind Kormorane, bestimmte Storcharten und Otterarten. Auch Lurche nehmen über ihre wasserbewohnenden Larven nach der Metamorphose viele Stoffe mit nach außen.

- Weniger ergiebig als terrestrische scheinen marine Ausleitsysteme zu sein, repräsentiert vor allem durch die Aale.

- Auch Filtriersysteme entlasten die Gewässer: mechanische durch Filtration von Seston in interstitialreichen Pflanzenbüscheln (z.B. *Cladophora* und *Myriophyllum*) wie auch organismische durch Aufnahme partikulärer Nahrung aus dem Freiwasser (Cladoceren, Großmuscheln und Vertreter vieler anderer Gruppen). Filtrierer sind besonders leistungsstark für die Entlastung, wenn sie an die genannten Ausleitsysteme gekoppelt sind.

- Bei der planktischen Kalzitfällung wird ebenfalls Biomasse aus dem Freiwasser entfernt, indem sie mit den sinkenden Kristallen abwärts gerissen wird. Auch der sich an den Kristallen adsorbierende Phosphor wirkt für das Pelagial entlastend.

- Die Eutrophierung bewirkt eine Konzentration der pflanzlichen Biomasse und der Nährstoffe und macht sie somit zugleich leichter entfernbar. Medien sind die steigende Wasserführung (Fließgewässer), der Wind (Standgewässer) und die pflanzenfressenden Tiere (Abschöpfer, Abäser). Der Konzentrationseffekt ist besonders infolge ihrer Massenentwicklung an *Cladophora* ausgebildet. Sie wird zu einem Zentrum der Primärproduktion und auch zu einem Habitatzentrum (viele Tiere, vor allem Chironomidenlarven, die den von den Thalli gefilterten Detritus zu festen Röhren umbauen). Gleichzeitig entwickelt sich der Egel *Erpobdella octoculata* durch enorme Dichtezunahme zu einem Prädationszentrum. Alle seine Stadien (3–60 mm) sind räuberisch und kontrollieren fast das gesamte Meio- und Makrozoobenthos. Diese Vorgänge führen zu einer Zentralisation des Ökosystems als Antwort auf die Trophiezunahme, zugleich zu einer Bündelung der an der Selbstreinigung beteiligten Kräfte.

- Mit der Eutrophierung steigt infolge der Konzentration der organischen Stoffe die Dichte der Bakterien an. Sie verbleiben dank der Ausbildung eines linearen Energie- und Stoff-Fluß-Systems (z.B. Bakterien –

Ciliaten – *Chaetogaster* – *Erpobdella*) in der exponentiellen Wachstumsphase ihrer Populationen, wodurch ihre Produktion und Abbauleistung stimuliert wird. Auch diese Vorgänge gehören zur Zentralisation des Ökosystems.

- Die Akkumulation von Schadstoffen durch Pflanzen ist ebenfalls eine Abwehrreaktion. Die akkumulierten Schadstoffe, z.B. Schwermetalle, werden entweder mit den abdriftenden Pflanzen bzw. Mikroorganismen (*Cladophora, Sphaerotilus*) entfernt oder wie im Falle der abflussresistenten und kaum konsumierbaren Wassermoose, isoliert.

- Auch Resuspension von Sediment und Denitrifikation in Gewässern sind entlastende Vorgänge.

- Der Erlengürtel an Fließ- und Standgewässern und die Zone emerser Pflanzen (vor allem Schilf) schützen Gewässer enorm vor der Eutrophierung (vergleichbar der Haut von Organismen gegen eindringende Stoffe). Diese doppelte morphologische Schutzschicht ist ein multifunktionelles Abwehrsystem gegen eindringende Stoffe.

- Es gibt viele Eigenschaften von Teilsystemen, die sich zum Schutz und Nutzen des Gesamtsystems ergänzen. Sie werden als Euökien bezeichnet. Demgegenüber gibt es auch Dysökien. Die meisten von ihnen entstehen, wenn die Abwehrreaktionen eines Kompartiments des Ökosystems zu Lasten eines anderen gehen. Zu den Dysökien gehören auch viele Unvollkommenheiten der Abwehrreaktionen.

- Die Alterung der Gewässer, bei der die Eutrophie zunimmt, ist, wie bei den Organismen, ein irreversibler Vorgang, bei dem sich im Falle der Seen die morphometrischen Relationen ändern. Abwehrreaktionen verzögern diesen Vorgang.

- Gegen das Eindringen von Fremdarten (Neophyten, Neozoen) in ein Gewässer gibt es keine Abwehrreaktionen. Hierbei stehen sich zunächst immer zwei oder mehrere Arten konfliktmäßig gegenüber. Ein Eindringling ist zunächst kein das Gesamtsystem betreffender Faktor wie die Eutrophierung. Überdies sind Eindringlinge stets unvorhersehbar gewesen, so dass sich die Evolution nicht darauf einstellen konnte. Eine Ausnahme machen einheimische Räuber, die die Eindringlinge vernichten. Das Gesamtsystem reagiert fast nie (auch nicht bei der Eutrophierung), sondern es sind immer nur Teilsysteme oder einzelne Arten, die dann (vermutlich meist zufällig) eine "altruistische" Wirkung haben.

- Mikroorganismen besitzen seit langen geologischen Perioden Eigenschaften, die der Eutrophierung (automatisch) entgegenwirken (Selbstreinigung). Ähnliches gilt für Prozesse, die auf chemischen Gesetzmäßigkeiten beruhen, z.B. Kalzitfällung und Denitrifikation. Sie wirken wie ein Immunsystem, das von den Gewässern "eingefangen" wurde. Für das Funk-

tionieren der Selbstreinigung ist allerdings noch eine an die Mikroorganismen sich anschließende Nahrungskette (Räuber-Beute-Verhältnisse) verantwortlich. Dies kann das Ergebnis einer Selektion sein, indem Gewässer mit derartigen Systemen weniger schnell verlandeten, ist aber nicht eindeutig nachzuvollziehen. Daß jedoch die saprophytischen Bakterien in unseren Gewässern selektiv gefördert wurden, ist stark zu vermuten.

– In vielen Fällen beruhen die Abwehrsysteme der Gewässer auf artegoistischen Anpassungen mit zufälligen system-altruistischen Auswirkungen. Dies gilt vor allem neben den genannten saprophytischen Bakterien auch für die auf Algen basierenden Abwehrsysteme. Diese Anpassungen einer Art sind „egoistisch", weil sie der Eutrophierung nur entgegenwirken, um die für die Art günstigen Lebensbedingungen zu erhalten. Es gibt auch Anpassungen einer Art in einer Nische mit positiven Auswirkungen für das Gesamtsystem (z.B. Tubificiden). In vielen Fällen scheinen derartige Verhältnisse aber nicht vom Ökosystem selbst entwickelt, sondern von ihm nur "eingefangen" zu sein. Auch die Euökien sind vermutlich durch eine artegoistische Selektion mit (zunächst zufälliger) system-altruistischer Wirkung entstanden.

– Die Akkumulation von Schadstoffen (z.B. Schwermetallen) ist ebenfalls eine erworbene Abwehrreaktion gegen toxische Stoffe, die dem Erhalt des Ökosystems nutzt, die primär aber artegoistischer Natur ist. Diese Reaktion wird in früheren geologischen Zeiten mit erhöhtem Vulkanismus entstanden sein.

– Jede Eutrophierung ist ein Verbrauchsprozeß des Gewässers. Im Verlauf der Eutrophierung verschwinden meist mehrere Ökosysteme, aber ohne Leichenbildung. Je mehr ein limnisches Ökosystem über Abwehrmechanismen verfügt, um so stabiler ist es, bezogen auf den Trophiestatus. Ein Ökosystem reagiert nie als Ganzes, sondern es sind immer nur Teile von ihm, meist nur einzelne Arten (genauer: Populationen), die dann die stabilisierende Wirkung für das Ganze haben.

– Für den Wasserhaushalt der Erde ist es von Bedeutung, dass die Verlandung der Binnengewässer (v.a. durch sich zersetzende Wasserpflanzen) nicht schneller vonstatten geht als ihre Neubildung. Daher scheinen Abwehrreaktionen gegen Eutrophierung von existentieller Bedeutung für eine bewohnbare Erdoberfläche zu sein, da sie die Verlandung bremsen und somit selektiv im Vorteil sind.

– Eine Analogisierung der Abwehrreaktionen der Gewässer-Ökosysteme mit organismischen Abwehrreaktionen ist durchaus möglich. Beide haben eine ähnliche Wirkung, doch eine andere Entstehungsweise.

Beispiele für solche Analogien:
• Die Selbstreinigung, Kalzitfällung und Denitrifikation sind mit dem Immunsystem vergleichbar.
• Die Ansammlung von Algenmassen und deren Ausstoß – wobei Gewässerbuchten und Ufer als "Sputumkammern" fungieren – sind mit der Schleimbildung und dem Auswurf vergleichbar.
• Schadstoffakkumulierende Pflanzen können mit Entgiftungsorganen verglichen werden.
• Vorgänge in Quellen und Flussmündungen sind mit dem Schutz der Eintrittswege in den Körper vergleichbar.
• Erlen- und Emersengürtel lassen sich mit der Haut vergleichen.
• Störungen im Stoffhaushalt durch Eutrophierung (→ Hypertrophie) können mit der Zunahme von Krankheiten durch Überernährung verglichen werden
• Dysökien sind mit der Überreaktionen und Unvollkommenheiten organismischer Abwehrmechanismen vergleichbar.

– Der Mensch kann durch relativ einfache Verfahren die natürlichen Abwehrreaktionen der limnischen Ökosysteme unterstützen.

Acknowledgements

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