LAKE AND POND ECOSYSTEMS

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GLOSSARY

ancient lakes Lakes with a persistence of more than 100,000 years are called long-lived or ancient lakes.
eutrophication The process of enrichment of a water body due to an increase in nutrient loading.
species flocks An aggregate of closely related species that share a common ancestor and are endemic to a geographically circumscribed area.

COMPARED TO THE SEA, freshwaters are deficient in major taxa and there are no uniquely freshwater metazoan phyla (May, 1994). In river lakes, aquatic biota is similar to the biota of the river basin. The great majority of existing isolated lakes (around 10,000 exceeding 1 km^2 in extent) are geologically very young and their flora and fauna are usually depauperate compared to ancient lakes that exhibit a rich endemic fauna for several major groups of animals. Species flocks for fish and invertebrates are known from ancient lakes and represent a unique biological heritage to be preserved. Major threats to the lakes biota include habitat alteration, fisheries practice, pollution, and the introduction of exotic species.

I. BROAD CHARACTERISTICS OF THE BIODIVERSITY IN LAKES AND PONDS

Freshwater habitats are widely considered to be transient in time and space in comparison with both terrestrial and marine habitats. This is true for many lakes and ponds. However, depending on the origin of lakes there are great differences in the nature and the diversity of their biota. Three broad categories of lakes may be recognized:

1. *Lakes and ponds that are permanently or frequently connected to large river systems.* This category includes river-lakes (i.e., Lake of Geneva) or lakes that are part of a large floodplain system such as "varzea" lakes. In these lakes, exchanges of flora and fauna occur with the main river system so that their biota is usually greatly similar to the biota of the river system itself with the exception of a few species adapted to still waters. Many endoreic lakes (Lake Chad, Aral Sea) also belong to this group.

2. *Isolated lakes with a limited drainage system.* The biota of the lakes in this category has evolved in isolation from others for a more or less long period of time leading to speciation and endemicity when the period

is long enough. The associated ice ages at higher latitudes and altitudes were the phenomena that created most of the lakes in existence today. Therefore the great majority of existing lakes (around 10,000 exceeding 1 km^2 in extent) are geologically very young and occupy basins formed by ice masses or glacial erosion after the retreat of continental ice sheets some 10,000 years ago. All such lakes are expected to fill slowly with sediment and to disappear in the future, along with any isolated biota. Compared to ancient lakes, they acquired their fauna and flora via the rivers that supply them with water as a result of runoff in their basin and from aerial transport by wind or animals. Only a few existing lakes are known to be much older, and most of them occupy basins formed by large-scale subsidence. They may date back at most 20 million (Lake Tanganyika) or 30 million (Lake Baikal) years. These so-called ancient lakes are of particular interest for biodiversity because they exhibit a rich endemic fauna for several major groups of animals. There is also good evidence that some extinct lakes were also very large and long-lived under different climatic and tectonic conditions.

3. *Temporary lakes and ponds whose water budget is controlled by the climate regime.* The fauna and flora in these lakes exhibit special biological adaptations to seasonal drying.

A. Origin and Peculiarities of Freshwater Biota

It is thought that the early evolution of all the major animal phyla took place in the sea. Most phyla are predominantly marine and benthic: 32 phyla are found in the sea with 11 exclusively marine, whereas 14 are represented in freshwater and only 12 are found on land (May, 1994). Compared to the sea, freshwaters are deficient in major taxa and there are no uniquely freshwater metazoan phyla. The osmotic challenges of life in freshwaters probably discouraged invasion of the habitat by many marine invertebrates. It explains probably the tendency in freshwater invertebrates for larger but fewer eggs than in marine relatives: they must eclose with fully developed osmoregulatory capacities to be at a more advanced stage to cope with the highly dilute surrounding.

Another difference between the species richness of marine and freshwater zooplankton derives from the necessity of diapause or other resting mechanisms as a condition for persistent successful radiation in freshwaters (Lehman, 1988). Freshwater invertebrates developed anabiotic devices: special resistant eggs, cysts, and other resting stages that are produced to tide the animal over periods of desiccation, extreme cold, heat, anaerobic situations, lack of food, and other adverse conditions. In addition to withstanding unfavorable conditions, resistant stages have the further function of making overland transport and geographical dissemination possible. Without such a function, colonization of freshwater areas would be slow and difficult in the discontinuum of isolated lakes and ponds.

B. The Latitudinal Gradient

It is usually assumed that species diversity increases from high to low latitudes for most of the major groups of plants and animals and that highest values occur at low latitudes. Indeed, the diversity of marine plankton decreases from low latitudes to high ones, so that tropical and subtropical ocean waters exhibit rich diversity of zooplankton whereas Arctic and Antarctic waters tend to be dominated by copepods and euphausiids. In freshwaters however, the latitudinal trend in species richness is the opposite. Tropical lakes have abbreviated zooplankton faunas compared with temperate locales (Fernando, 1980); they are depauperate in large-bodied species of copepods and Cladocera, and limnetic rotifers are likewise poorly represented.

It could be assumed that the associated ice ages at higher latitudes and altitudes were the phenomena that created most of the lakes in existence today. They are therefore very young compared to ancient lakes, and they acquired their fauna and flora via the rivers that supply them with water via runoff in their basin and via aerial transport by wind or animals.

For fish, the species richness is actually smaller in north temperate lakes of glacial origin than in long lived lakes from tropical areas. At least the endemicity is much lower in temperate lakes than in tropical lakes.

Dumont (1994), in a review of the species richness of the pelagial zooplankton in ancient lakes, provided also evidence that these water bodies have simple pelagial communities. Among 14 pre-Pleistocene lakes across the world, at least one Cyclopoid copepod species is present, often in the genus Cyclops or Mesocyclops, a group of microraptorial species feeding on rotifers, small Crustacea, and immature stage of other copepods.

The number of species regularly found in the pelagic plankton of ancient lakes (pre-Pleistocene) varies from 3 (Lake Tanganyika) to approximately 15 to 20 (up to 5 copepods, 5 cladocerans, 10 rotifers) in Lakes Victoria, Biwa, and Titicaca. In contrast, "young" lakes may have up to 10 species of copepods, 10 of Cladocera, and 10 to 15 species of rotifers occurring together. In the oldest lakes (Baikal, Tanganyika), which also happen to be the deepest, this simplification has gone extreme and the food web reduces to a linear chain.

The question has been raised as to why Cladocera have been almost completely eliminated from some ancient lakes such as Tanganyika, Baikal, and even Malawi (Dumont, 1994). They are able to eat both large items and microplankton and seem all but competitively inferior to other species for food acquisition. Predation had been advocated as a possible cause. In clear-water lakes such as Tanganyika and Baikal, visual predation by fish is more effective than in turbid lakes, and large clumsy swimmers like big Daphnia are likely to be preyed to extinction before the relative small transparent, agile swimmers like the Calanoids. An experimental demonstration of this hypothesis has been the disappearance of all Cladocera from the pelagial of Lake Kivu, within a decade, after the introduction of the zooplanktivore clupeid Limnothrissa miodon, native from Lake Tanganyika (Dumont, 1986).

C. Vertical Distribution in Lakes

Aquatic organisms are not evenly distributed along depth. Water characteristics are relatively uniform in shallow lakes, which are mixed by winds. However, deeper lakes exhibit patterns of vertical gradients for temperature and light. Briefly speaking, the lake is divided by a thermocline into an upper layer, the epiliminion, and a lower layer, the hypolimnion. Life occurs in the oxygenated upper layer while the lower layer is deoxygenated. In most stratified lakes therefore, biota is very depauperated, except for bacteria, below a few 10 meters in depth. There is an exception, Lake Baikal, which is the deepest lake in the world with a maximum depth of 1620 m. The mechanism of mixing of the deep water zone is still not completely understood, but the entire water column is well oxygenated. Life for fish and invertebrates is therefore possible from surface to maximum depth, which is exceptional for freshwater systems. Lake Baikal is therefore unique among inland systems to the study of bathymetric segregation and includes some of the deepest occurring freshwater animals. Among fishes, the family Abyssocottidae contains 20 species distributed throughout the depths of the lake. Species of the genera *Abyssocottus, Cottinella*, and *Neocottus* are adapted to the deep water way of life in that they do not occur above 400 m, the size of the eyes is reduced, and they are physiologically adapted to resisting high pressures (Sideleva, 1994).

The discovery of a deep sea hydrothermal fauna in the 1980s was a surprise for marine biologists. Similarly, hydrothermal vents have been discovered in Lake Baikal, at a depth of 440 m on the sediment floor of Frolikha Bay (Crane *et al.*, 1991), at the foot of an east-west trending fault. Photographs reveal that the center of the vent field is covered by a near-continuous bacterial mat. A white sponge encrusts small cobbles at the periphery of the vent field. Coiled gastropods and whitish translucent amphipods are found among the sponges and on the sediment at the edge of the bacterial mat.

D. Relationship between Species Richness and Area in Lakes

Community ecologists used to compare isolated freshwater systems to biogeographic islands. The relationship of species number to area containing those species is a well-known empirical observation, and a power function is widely used to describe this pattern mathematically: $S = cAZ$, where S is the number of species, A the area, Z the slope of the regression line, and c a constant. It can also be expressed as $\log S = c + Z\ logA$.

The effect of lake size on species richness of invertebrates has been demonstrated. For crustacean zooplankton, species richness is also significantly correlated with lake surface area (Dodson, 1992). The species area curve for North American lakes is statistically different from and steeper than the corresponding European curve (slopes, respectively, 0,094 and 0,054). The log species richness is also correlated to log of the average photosynthetic flux per cubic meter and log number of lakes within 20 km of the target lake. For 66 North American lakes, the three variables can be combined in a multiple linear regression model, which explains 75% of the variation in log species richness (Dodson, 1992).

Species richness of aquatic birds also increases with lake size. In Swiss lakes, the species number increase steeply with lake size up to 50 km^2 and species richness depends more closely on lake area in fish eaters and diving ducks than in dabbling ducks (Suter, 1994). Actually lake size explains 70 to 85% of the variation of abundance and species richness in fish eaters and diving ducks but only 64% of species richness in dabbling ducks. In Florida lakes, bird species richness was also positively correlated to lake area and to total water column phosphorus concentration value (WCP) for each lake. The multilinear Log (species richness) = 1.12 + 0.56 Log (Lake area) + 0.12 Log (WCP) and accounts for 77% of the variance in species richness (Hoyer and Canfield, 1994).

E. Morphometry and Species Richness

The species diversity in a lake is a function of the diversity of habitats: the more ecological niches in the lakes, the more species may be expected. The lake's morphometry is basic to its structure: deep, steepsided lakes do not offer as many biotops than shallow, flat lakes. For the latter, most of the lake bottom may be colonized by plants and animals (the benthic flora and fauna), while in deep lakes, only a small part of the lake bottom is colonized. Generally speaking, deep lakes are dominated by planktonic organisms, which are floating or weakly swimming organisms, usually associated with suspended particles. In shallow lakes, benthic organisms are dominant and the heterogeneity of lake bottom, as well as the development of macrophytes, may increase the diversity of benthic species.

II. EVALUATING BIOLOGICAL DIVERSITY

Despite the efforts of taxonomists, a good estimation of the total number of species occurring in freshwater lakes and ponds does not exist. We shall provide here some recent findings about aquatic biodiversity.

A. Diversity of Plankton and Microbial Loop

Three major size classes are usually recognized in pelagic plankton: microplankton (20–200 μm), nanoplankton (2–20 μm), and picoplankton (0.2–2.0 μm). In the late 1970, phototrophic picoplankton was discovered in great abundance in both marine and freshwater ecosystems. However, identifying picoplankton causes considerable taxonomic problems due to the very small sizes of these organisms. We do not know how many bacterial species exists in the world, because bacteria cannot be differentiated under the microscope; we do not even know the right order of magnitude. A new way of classification has been proposed, based on the sequences of ribosomal RNA that led to a phylogenetic classification of bacteria. It is becoming apparent that the genetic diversity among bacteria is much wider than that among the animals and plants.

Most heterotrophic nanoplankters are small (2–5 μm), colorless flagellated protists. They grow at about the same rate as bacteria and are capable of consuming the entire bacterial production. Meanwhile, they regenerate significant amounts of nutrients and serve as prey for micro- and mesoplankton.

The importance of bacteria and protozoa activities in the trophic structure of lacustrine food chain has been largely underestimated in the past. The major role played by microorganisms in controlling energy and nutrient fluxes is now better understood following the discovery of the microbial loop and its role as a source or a sink for carbon and energy flow to higher trophic levels in pelagic systems. We know now that these microorganisms can control major fluxes of energy and nutrients. In some cases, 50% of the photosynthetic production does not pass directly to higher trophic level but is diverted into a microbial loop where nutrients are rapidly remineralized and fed back to the dissolved inorganic pools.

B. Diversity in Freshwater Sediments

About 175,000 species of organisms associated with freshwater sediments have been described, but the true number is much higher than this (Palmer *et al.*, 1997). The number of species in most taxa can scarcely be estimated and global estimate of microbial diversity remains controversial. For example, some specialists estimate that there are hundred of thousands of aquatic nematodes and only a small percent of these have been described. Rotifer species diversity is also poorly known for freshwater sediments, but it is estimated that there are thousands of undescribed species.

Most freshwater sediment species are small and concentrated in the upper sediment layers. Availability of light limits the development of plants and photosynthetic bacteria, which are therefore scarce or absent in most sediments. Moreover, oxygen level may influence species richness and the number of species is low in anoxic waters (see Table I).

C. Diversity in Fish

Presently, 25,000 fish species have been described. Some 10,000 species are found only in freshwaters, a large proportion of which occurs in lakes and ponds. The freshwaters are therefore disproportionately rich in species of fishes on the basis of area when compared to oceans. That could be viewed as the result of the patchy nature of inland waters and the resulting high endemicity of the biota. Fish live in almost every conceivable type of aquatic habitat. They exhibit enormous diversity in size, shape, and biology.

Other vertebrates species occur in freshwaters: a few mammals, several reptiles, and many birds and amphibians. There is no quantitative evaluation of the number of vertebrates whose life cycles include lakes or ponds, but it is far from negligible (see Table II).

TABLE I

Species Richness of the Freshwater Sediment Biota for Many Habitat Types

Taxon	Number of species described	Probable number of species	Range of local species richness
Bacteria	>10,000	Unknown	>1,000
Algae	14,000	>20,000	0–1000
Fungi	600	1,000–10,000	0–300
Protozoa	<10,000	10–20,000	20–800
Plants	1,000	Unknown	0–100
Invertebrates	70,000	>100,000	10–1,000
Aschelminthes	4,000	>10,000	5–500
Annelida	1,000	>1,500	2–50
Mollusca	4,000	5,000	0–50
Acarii	5,000	>7,500	0–100
Crustacea	8,000	>10,000	5–300
Insecta	45,000	>50,000	0–500
Others	1,400	>2,000	0–100

Numbers are rough estimates and derived from many sources. Collected by Palmer *et al.* (1997)

TABLE II

Number of Fish Species Recorded from Several Lakes Connected to Rivers Systems

Lake		Latitude	Area	Number of fish
Chad	Africa	13°N	10–20,000	137
Turkana	Africa	3°N	6,750	51
Chilwa	Africa	15°S	675	31
Ngami	Africa	20°S	150	48
George	Africa	0°	270	30
Huron	North America	44°N	59,600	99
Erie	North America	42°N	25,700	113
Michigan	North America	44°N	58,000	114
Superior	North America	47°N	82,400	67
Great Bear	North America	66°N	31,150	12
Great Slave	North America	61°N	27,200	26
Big Trout	North America	54°N	616	24
Chapala	Central America	20°N	1,080	14
Nicaragua	Central America	11°N	8,200	40
Maggiore	Europe	46°N	676	21
Windermere	Europe	54°N	15	9
Ladoga	Europe	61	18,400	48
Aral sea	Europe	45°N	64,500	17

See also Table III for ancient lakes.

III. BIOLOGICAL DIVERSITY AND ECOSYSTEM FUNCTIONING

Energy and nutrients in an ecosystem are transferred through successive trophic levels. Photosynthesis provides the basic food for herbivorous animals, which are eaten by the carnivores. Therefore, knowledge of the role of individual species and their relationships in aquatic systems is critical to understand the functioning of the system as a whole. Limnologists pointed out several key issues to the study of the relationships between species diversity and lake functioning.

A. Food Webs

Food webs are diagrams depicting which species in a community interact in feeding and describing which kinds of organisms in a community eat which other kind. Food webs are thus caricatures of nature, but they give a picture of the processes at work in ecosystems. Connectivity food webs are describing pathways along which feeding interactions occur. These interactions change at least seasonally and not all interactions are equally strong. The interaction web emphasizes connections that appear to have a large effect on the dynamics of the food web structure and function. Food webs occupy a central position in community ecology. Many important interactions (e.g., competition, predation) cannot be isolated from a food web context because the outcome of these interactions can be modified directly and indirectly by other members of the web.

For a long time food webs served principally as heuristic devices, useful in depicting complex ecosystems as diagrams composed of many interactive parts and enhancing our understanding of pathways of energy and material transfer in aquatic ecosystems. However, the recent surge of interest in food webs seems related to the question of the functional role of biodiversity (discussed later).

Few if any of the aquatic food webs are unimpacted by humans both at a local and a global scale. For example, fisheries food webs are complex, involving multiple trophic levels at several spatial and temporal scales. Fish species offer a wide range of body sizes and feeding habits, and thus have a variety of food web roles and interactions with other species. Exploitation of fishes may result in major changes in food webs. However, the consequences of species removal through fisheries are an almost unexplored field of research in most freshwater systems.

B. The Top-Down Control

In the classical limnological approach, it was usual to consider freshwater ecosystems as operating in a physical-chemical milieu that, largely through nutrient availability, conditions the food chain from primary producers to top predators. In this "bottom-up" control, competition between primary producers for limiting nutrients determines the state of higher trophic levels. A reverse viewpoint, the "top-down control" slowly became prominent. It argues that the effects of top predators cascade down the trophic chain and are responsible for controlling the state of the entire ecosystem. The predators, near or at the top of the trophic pyramid, may be fishes but also may be birds, mammals, and so on, as well as invertebrates. Through grazing, for instance, fish have direct effects on the composition and abundance of phytoplankton, periphyton, and macrophytes, as well as on the dynamics of plankton and benthic communities. Size-selective predation by fish may not only play a major role in the population dynamics of prey species, but also result in shifts in the relative abundance of species.

Predation is now considered to be a major driving force in shaping zooplankton communities. A great number of papers emphasized the size-related alterations in zooplankton communities as a consequence of planktivorous fishes, which select the largest available prey and may rapidly reduce the density of large zooplankters, resulting in a shift of the prey community to small species, predominantly rotifers and small cladocerans. Extinction of large zooplankton has been documented in several habitats, usually following the introduction of new species of planktivorous fish.

Trophic cascades from fishes to water quality in lakes are among the clearest examples of feedbacks from population to ecosystem processes (Carpenter and Kitchell, 1993). A shift in the species composition and size distribution of the fish assemblages alters the community composition and size distribution of the herbivorous zooplankton. The impact of herbivory on phytoplankton depends on the relative abundance of certain herbivores with wide diets, high grazing rates, and rapid population growth rates. Population of these keystone herbivores are sensitive to fish predation. In addition, the size distribution of fishes and zooplankton and their migratory behavior largely determine the rate and spatial pattern of nutrient recycling in pelagic ecosystem. In whole-lake experiments, manipulations of fish community structure have caused significant changes in primary production, algal biomass, nutrient recycling, and sedimentation rates.

C. Relationships between Biodiversity and Ecosystem Stability

A major concern for limnologists is to predict response to stress. For a long time, the so-called conventional wisdom in ecology was that increased complexity within a community leads to increased stability. Complexity is used here to mean more species, more interactions between them, and more pathways. The basic assumption is that if the number of pathways increases, any blockage at one point of the network would be compensated for by the opening of another pathway. However, until now this conventional wisdom has not received much support from field or experimental work. Therefore some basic questions remain open and are of particular concern for freshwater lakes:

- How is system stability and resistance affected by species diversity, and to what extent could the integrity and sustainability of ecosystems be maintained in spite of species deletions resulting from degradation of environmental conditions?
- Are rare species an insurance of ecosystem stability? Do these rare species play a role in ecosystem functioning? One hypothesis is that the most stable ecosystems in terms of key functions are those richest in species. However, well documented studies of rare species substituting for declining common species in the maintenance of key freshwater ecosystem functions following disturbance are scant.

D. Role of Intra- and Interspecies Communication Systems in Ecosystem Dynamics

The structure of the biota is determined by complex interactions between individual organisms acting at different trophic levels. It is now becoming clear that besides energy transfer from one trophic level to another, there is an exchange of information between trophic levels through infochemicals. Moreover, sexual pheromones, but also sounds, electric signals, and visual communication play a role in shaping the structure of the biotic community. This diverse communication network has biological consequences and may modify the behavior of aquatic animals, such as migrations. This is a fairly new field of research.

E. Biological Productivity and Biodiversity: The Case of Eutrophication

The biological structure and internal biological control mechanisms of freshwater lakes are highly affected by lake water nutrient level and by the extent of nutrial loading. Limnologists distinguish oligotrophic lakes, which are generally deep with steep slope and are characterized by low nutrient levels and clear water. The biomass at all trophic levels is small. On the opposite, eutrophic lakes are often shallow with gradually sloping edges. The most characteristic features are high nutrients levels, the abundance of plankton, and low water clarity.

One concept of lake succession considers that lakes pass through different trophic states, beginning with low fertility or oligotrophy, gradually moving to a moderately productive or mesotrophic state to reach finally the eutrophic stage. This succession may happen in undisturbed lakes. However, eutrophication (sometimes called cultural eutrophication) is now widespread as a result of human activities. Eutrophication may be defined as the process of enrichment of a water body due to an increase in nutrient loading. The most important nutrients causing eutrophication are phosphates, nitrates, and ammonia. All these chemicals are abundant in waters released from sewage treatment works and from surface and groundwater runoffs in intensive agriculture areas.

The most obvious consequence of eutrophication is the increased aquatic plants and phytoplankton growth, an overall increase in biomass, and a shift in species composition of the lake. For example, at low P-concentrations, north European shallow freshwater lakes are usually in a clearwater stage; submerged macrophytes are abundant, potential piscivores are present in large numbers, and predation pressure on zooplankton is consequently low. At some higher P-concentrations, there is a shift to a turbid stage: submerged macrophytes disappear and the fish stock changes. The fish biomass rises and there is a shift from a system dominated by pike (*Esox lucius*) and perch (*Perca fluviatilis*) to one exclusively dominated by planktivorous-benthivorous fish, mainly bream (*Abramis brama*) and roach (*Rutilus rutilus*).

IV. THE CASE OF ANCIENT LAKES SPECIES FLOCKS

About a dozen lakes in the world are up to three orders of magnitude older than most others (Table III) (Mar-

TABLE III

Summary of Physical and Biological Characteristics of Some of the Larger Extant Ancient Lakes

Lake	Age (My)	Max. depth. (m)	Area (km^2)	Number of animal species	Number of endemic	Number of fish species	Number of fish endemic
Baikal	35–30	1,700	31,500	1,825	982	56	27
Tanganyika	9–12	1,470	32,600	1,470	632	330	241
Malawi	4.5–8.6	785	30,800			>600	>600
Victoria	0,6?	70	70,000			>500	>500
Titicaca	3	284	8,448	533	61	29	23
Ohrid	2–3	295	348			17	2
Biwa	4	104	674	600	54	57	11

In part from Martens, 1997.

tens, 1997). Such lakes have exceptionally high faunal diversity and levels of endemicity.

An important characteristic of ancient lakes biodiversity is the existence of "species-flocks." An aggregate of several species should be identified as a flock only if its members are endemic to the geographically circumscribed area under consideration and are each others' closest living relatives. Briefly speaking, a species flock has to be monophyletic. At present, different rich species flocks for fish and invertebrates have been identified in various ancient lakes, which are therefore exceptional natural sites for the study of speciation patterns.

The processes accounting for these radiations are a matter of debate, but there is more and more evidence that sympatric speciation may occur in isolated water bodies. These species flocks are sometimes considered to be a world heritage that is endangered and has to be preserve from destruction by human activities (Coulter *et al.*, 1986; Nagelkerke *et al.*, 1995) (see Table III).

A. Fish Species Flocks

The most striking feature of the Great East African Lakes (Victoria, Tanganyika, Malawi) is that each has its own highly endemic lacustrine Cichlid fauna. In Lake Victoria, according to our present knowledge, there is a cichlid species flock of more than 500 endemic haplochromine species. The true species number is almost certainly even higher (Seehausen, 1996). The age of this flock was estimated at 200,000 years, but it is most likely that Lake Victoria had entirely dried up as recently as 12,400 years ago, so that most of the endemic cichlid flock would have evolved during the past 12,400 years (Johnson *et al.*, 1996). In Lake Malawi, the diverse cichlid fauna of this lake could also total much more than 500 species. Species flocks are also reported for the clariid catfish *Dinotopterus* (10 species).

The Lake Tanganyika cichlids are slightly less diverse. However, morphological and electrophoretic data both suggest that several lineages of cichlids from Lake Tanganyika are much older than the Lakes Victoria and Malawi lineages and can be traced back to at least seven distinct ancestral lineages. Species flocks also occur in noncichlid families: seven Mastacembelid species, six species of the bagrid *Chrysichthys*, seven species of *Synodontis*, and four species of the Centropomid *Lates* (De Vos and Snoeks, 1994).

Rates of speciation in cichlids can be astonishingly fast. That has been known since the discovery of five endemic species of cichlids in Lake Nabugabo, a small lake less than 4000 years old and separated by a sandbar from lake Victoria. Still faster speciation rates were suggested by the finding that the southern end of Lake Malawi was dry only two centuries ago, while it is now inhabited by numerous endemic species and "color morphs" that are only found there and are believed to have originated during the past 200 years.

The remarkable diversity of the large barbs (genus *Barbus*) in Lake Tana (Ethiopia) constitutes a potential species flock that has been discovered recently. Nagelkerke *et al.* (1995) hypothesized that intralacustrine speciation has occurred among the barbs of Lake Tana and possibly is still going on.

In South America, the native fish fauna of Lake Titicaca includes the genera *Trichomycterus* and *Orestias*, both endemic to the Andean Altiplano. Twenty-four *Orestias* species are presently recognized in Lake Titicaca (Lauzanne, 1992). However it is probably not a monophyletic group but rather an assemblage that includes, in part, several species flocks.

Lake Baikal (East Siberia) hosts a very diverse fauna, with some 2500 described species (most of which are endemic), which might constitute 50% of the total amount. At present, Lake Baikal comprises 56 species and subspecies of fish, which belong to 14 families (Sideleva, 1994), a group of six species and subspecies, belonging to three families (Thymallidae, Coregonidae, and Acipenseridae), which are relatively endemic; another group of nonendemic fauna includes 21 species and subspecies, which belong to Cyprinidae, Percidae, Cobitidae, Esocidae, Gadidae, Salmonidae, Siluridae, and Eleotridae.

In Asia, Lake Lanao was formed by a lava flow that dammed the streams flowing southwest. The cyprinid fauna presents a widely acknowledged example of adaptive radiation. Of the 23 cyprinid species presently known from Mindanao Island, 15 are reported from Lake Lanao (Kottelat and Whitten, 1996). Unfortunately overexploitation and exotic introductions have decimated the fauna, so that now only few endemic cyprinids are still present.

Lake Biwa is the largest and oldest lake in Japan. The deep basin as seen presently is supposed to have been formed 300,000 years ago. Most endemic fishes exist also since that time (Kawanabe, 1996). Some 500 plant and 600 animal species have been recorded. At present there are 71 species and subspecies if freshwater fishes found in Lake Biwa and its tributaries. There are 13 endemic species and subspecies of fish in Lake Biwa.

The only more or less pristine species flocks left in Asia are to be found in the lakes the Malili River drainage of the Sulawesi Island (Celebes) in Indonesia (Kottelat & Whitten, 1996). Malili lakes (lakes Towuti, Matano, Mahalona, Wawontoa, and Masapi) constitute a system of lakes partially isolated from each other and completely isolated from other freshwaters. As a result, most of the animal species known from the lakes are endemic.

B. Invertebrates

Mollusks focus our attention on parts of the world that seem to be hot spots of endemicity, where the resident clades are remarkably more diverse than in other similar environments. Long-lived lakes are prime examples of these evolutionary theaters. Particular clades, such as the hydrobioid and ceratioidean prosobranchs and the planorbid pulmonates, show repeated patterns of diversification in both extant and fossil long-lived lakes, revealing the common patterns that make them prone to speciate (Michel, 1994). The process of diversification is tied to intrinsic characters shared by many of these clades: reproductive and dispersal strategies (brooders and poor dispersers), genetic structure (tightly constrained genetic systems), morphology (often relatively thick and ornamented shells), substrate specificity (hard bottom stenotopy), and physiology (depth tolerance). The most notable examples of these evolutionary theaters are extant lakes Tanganyika, Baikal, Ohrid, Titicaca, and fossil lakes Idaho, Biwa, and Turkana. However, examples of gastropod radiations are also found in river systems (see Table IV).

Among Crustacea, gammarids have also undergone an enormous evolutionary radiation in Lake Baikal, with a total of 259 species, 98% of which are endemic. There are also several species flocks of Ostracods reported from ancient lakes (Martens *et al.*, 1994).

V. MAJOR THREATS TO BIODIVERSITY IN LAKES

The concentration of people around freshwater systems has resulted in a much greater degree of degradation to these systems than most open marine or even terrestrial systems.

A. Competition for Water

Competition for water may result in the total or partial desiccation of lakes and ponds through various diversion and impoundment of tributaries. Water is withdrawn most often from aquatic systems for irrigation, flood control, and urban and industrial consumption. A spectacular example is provided with the Aral Sea, a large saline lake in the terminus of an extensive inland drainage basin in south-central Asia. Water diversion for irrigation purposes of most of the waters in inflowing rivers of the Aral sea, as well as poor agricultural practices, resulted in a marked fall of water level (c. 15 m) and an increase in salinity (from c. 10 to 30 g/l) since the 1960s. This changes have resulted in the degradation of the natural environment. Fish have virtually disappeared from the lake and the diversity of associated bird and wildlife communities has decreased. Many invertebrates also disappeared (Williams and Aladin, 1991).

B. Habitat Alteration

Siltation from erosion of the lake basin has direct adverse effects on fish by covering spawning sites, destroying benthic food sources, and reducing water clarity to

TABLE IV

Endemism in Ancient Mollusk Fauna (ancient lakes and rivers)

Lakes	Baikal	Ohrid	Tangan.	Titicaca	Biwa
Mussels	2	1	12	0	
% end.	0	0	75		
Sphaeridae	10	9	3	4	
% end.	30	22			
Prosobranchs	72	47	52	16	11
% end.	93	91	84	93	72
Pulmonates	61	25	16	3	16
% end.	77	48	6	33	62
Total species	145	82	81	19	27

visual feeding animals. However, the increase turbidity may have also indirect effects on biodiversity in lakes. Seehausen *et al.* (1997) provided evidence that increasing turbidity (as the consequence of deforestation and agricultural practices) by curbing the impact of sexual selection on sexual isolation is responsible for the decline in cichlid diversity in Lake Victoria. Actually, mate choice in these cichlids is determined on the basis of coloration, and strong assortive mating can quickly lead to sexual isolation of color morphs, which is increasing and probably started in the 1920s. By constraining color vision, turbidity interferes with mate choice (Seehausen *et al.*, 1997). The reduced effectiveness of signals causes relaxation of sexual selection for color, with consequent loss of male nuptial coloration and erosion of species diversity due to a breakdown of reproductive barriers. Dull fish coloration, few color morphs, and low species diversity are found in areas that have become turbid as a result of recent eutrophication. This is proof that human activities that increase turbidity destroy the mechanism of diversification and the maintenance of diversity.

C. Species Introductions

The introduction of alien fish into inland waters has occurred all around the world. The main goals of deliberate introductions by fishery officers were initially to improve sport fisheries and aquaculture, or to develop biological control of aquatic diseases, insects, and plants, or else to fill supposed "vacant niches" and improve wild stocks in old or newly created impoundments.

The introduction of alien species has been considered as the main causes of extinction of endemic species flocks in several ancient lakes. In Lake Lanao, the introduction of the white goby (*Glossogobius giurus*) in the early 1960s resulted in the elimination of numerous species of endemic cyprinid fish. In Lake Titicaca the rainbow trout *Salmo gairdneri* was accused of seriously threatening the endemic *Orestias* fauna and for having been responsible for the disappearance of species such as *Orestias cuvieri*. In Lake Biwa, the recent increases in numbers of the exotic bluegill *Lepomis macrochirus*, black-bass *Micropterus salmoides*, and *Channa maculata*, have been mirrored by serious declines in the native species *Onchorhynchus rhodurus rhodurus* (an endemic), *Hemigrammocypris rasborella*, and *Hymenophysa curta*.

Much has been said about the impact of the introduction of the Nile perch on the hundreds endemic haplochromines of Lake Victoria (Lévêque, 1997). In the early 1980s this impact was considered an ecological and conservation disaster (Coulter *et al.*, 1986). However, it was later recognized that predation by *Lates* may not be solely responsible for the depletion of haplochromine stocks, and that the haplochromine stock was already affected by fisheries before the establishment of *Lates*, particularly by unregulated fishing or by trawling techniques introduced in the Tanzanian part of the lake. Lake Victoria is now invaded by water hyacinth, and the remaining fish fauna is therefore more and more threatened.

Transport through ballast water is probably one of the most important pathways for alien species invasions in several places, including the North American Great Lakes (Mills *et al.*, 1993). That is the case for the zebra mussel introduced into the Great Lakes, apparently in 1985 or 1986, which spread dramatically throughout the waterways of both Canada and United States expansion with serious economical and ecological consequences. The recent finding of individual mitten crabs (*Eriocheir sinensis*), a European flounder (*Platichthys* *flessus*), and the establishment of the alien gastropod *Potamopyrgus antipodarum* in Lake Ontario in 1995 demonstrate that the process of invasion is still going on at a fast rate.

One of the major problems in freshwater species introductions is their irreversibility, at least on scale of a human's lifetime. Once introduced and established, it is impossible, given current technology, to eradicate a fish, a mollusk, or a plant species from a large natural water body. As a consequence, we are likely to see a continued reduction in native aquatic biodiversity and an increased homogenization of the world's freshwater biotas.

D. Fisheries Practices

One of the major threats to the unique species flocks of ancient lakes are the fishing practices and particularly overfishing and introduction of new fishing practices. According to Coulter *et al.* (1986), the collective experience in recent years on the African Great Lakes seems to show that large-scale mechanized fishing is incompatible with the continued existence of the highly diverse cichlid communities. Cichlids appear especially vulnerable to unselective fishing because of their particular reproductive characteristics. The structure of endemic cichlid fish communities in the African Great Lakes can change dramatically within a few years when trawlers and other such fishing gear are used. Actually, a number of authors have recorded the effects of overfishing in Lake Victoria, from the decline of some species to the virtual disappearance of others, and the history of the fishery was briefly reviewed by Witte *et al.* (1992).

It has also been suggested that parks should be developed (Coulter *et al.*, 1986) and that fishing should be rendered impossible in certain areas by placing obstructions on the bottom that would snarl trawls. Lake Malawi National Park will very probably afford protection to widespread species, but no data are at present available to confirm this hypothesis. It is unknown yet whether these reserves can adequately preserve the integrity of populations, but that is probably only possible for stenotopic populations whose distribution coincides with the park area. The size of the reserves, the intensity of fishing in nearby areas, and the possible influence of pollution or introduced alien species should also be taken into account.

E. Pollution

Pollution can affect aquatic biota through direct mortality at any life stage or by sublethal effects influencing predation, foraging, and reproduction. The eutrophication of Lake Victoria during the past 25 years is quite well documented. Enhanced quantities of nutrients appear to have been entering this lake for many years, both through rivers and from aerosols as a result of human activities in its watersheds. The eutrophication could lead to increased oxygen demand in the lake's deep water and thus decrease the hypolimnetic volume habitable by fish during seasonal stratification. This phenomenon is partly responsible for the threatening or disappearance of cichlid species belonging to the haplochromine flock.

The release of sulfur and nitrous oxides from the burning of fossil fuels may be transported great distances before being transformed chemically into sulfuric and nitric acids and deposited as rain, snow, or dust. When acid rains occur over areas where waters are poorly buffered, the chemistry and biology of freshwaters can be changed dramatically. Many softwater lakes have been acidified both in North America and Europe, but evidence has accumulated for its occurrence in China, the former Soviet Union, and South America. Monitoring studies indicate a general impoverishment of species numbers in lakes as they become more acidic. Many lakes in the northeastern United States have lost 30% or more of the species in some taxonomic groups. In many northern European countries, acidification strongly modified the fish composition and abundance in lakes.

See Also the Following Articles

ENDANGERED FRESHWATER INVERTEBRATES • EUTROPHICATION AND OLIGOTROPHICATION • FISH, BIODIVERSITY OF • FRESHWATER ECOSYSTEMS • FRESHWATER ECOSYSTEMS, HUMAN IMPACT ON • INVERTEBRATES, FRESHWATER, OVERVIEW • RESOURCE EXPLOITATION, FISHERIES

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