EVOLUTION AND FUNCTION OF FRESHWATER ECOSYSTEMS

Pokorný P.
Academy of Sciences of the Czech Republic, Czech Republic

Keywords: Environmental change, evolution, freshwater, global cycles, nutrients, paleoecology, quaternary, sediments

Contents

Summary

Freshwater ecosystems are undoubtedly one of the most important life-support systems on Earth. Since they record their own history in mineral and organic sediments, their roots can be traced deep into the past. Different timescales are adopted in this article in order to give an overview of the evolution of freshwater biota and their abiotic environments. Attention is drawn to the link between present-day ecology and the paleoecology of lacustrine and fluvial ecosystems. Since they provide us with a long-term record of past climatic and environmental changes, lake and river sediments are invaluable natural archives. To provide an impression of the use of such archives, basic paleoecological approaches and techniques are briefly summarized in the text.

1. Freshwater in the Global Hydrological Cycle

The supply of freshwater on Earth is entirely due to the existence of the global hydrological cycle. The circulation of water from the ocean and land surface into the atmosphere and back again represents the largest matter interchange system on Earth and in its atmosphere. Solar radiation is the primary energy source driving this process. Apart from its role in supplying terrestrial life with freshwater, the global hydrological cycle has another vital role: It is a major transporter of heat over our planet. Moreover, it creates the climate for life by absorbing heat lost by reflection from Earth's surface. Without this "greenhouse effect" of water vapors, surface air temperatures would be 16 °C lower. As the ultimate recycling process, the hydrological cycle washes away waste products in rainfall and runoff and purifies supplies by evaporation. The global hydrological cycle works as an open system that responds to changes in the astronomical, geological, and biotic parameters, as well as to human interference. Change in these parameters alters the proportions held in different water stores and fluxes, not the total volume of water on Earth. The total volume of water within our hydrosphere is estimated at between 1.4 billion km^3 and 1.5 billion km^3. For practical purposes, this amount may be considered constant. However, over the long existence of our planet, the volume of free water has gradually increased by about 1 km^3 every year. This is because Earth's mantle is gradually shrinking as water bound chemically and physically within rocks is released by weathering. Earth's mantle still contains a volume of water about 15 times as much as is presently free in the hydrosphere.

The overwhelming proportion (estimated at 96%) of free water lies in the ocean. About 40 000 km^3 of water per year is transferred from the oceans to the land as precipitation. This is approximately equivalent to the total river flow of the world. The amount of water stored in different stores is shown in Figure 1. The rate of turnover within these individual stores varies considerably, from about 15 000 y for terrestrial ice to about seven d for atmospheric moisture. Turnover is three to five times faster in freshwater stores than in marine ones, with the exception of ice. This reflects the need for rapid turnover to maintain the freshness of water. Of all the terrestrial stores, river channels hold the least, yet are the primary source of freshwater for humankind. We must recognize that it is not the quantity in store but the quantity that passes through the river system that is important for the use of river water as a major resource. Viewed in this way, rivers can supply in one year a volume four to five times greater than that available from lakes. In addition, the rapid turnover tends to make the rivers less vulnerable to pollutant accumulation.

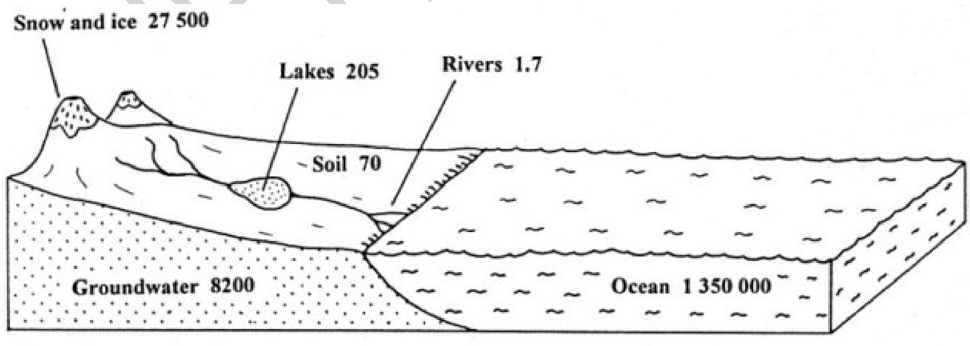

Figure 1. Major stores in the global hydrological cycle (all values are shown as thousands of km^3)

Although storing a relatively small proportion of the freshwater on Earth (particularly compared to groundwater and ice volumes), rivers and lakes are objects of primary interest from several points of view. As important life-support systems they include diverse forms of life. They also can be traced back many millions of years, deep into geological history. Moreover, they are of special interest because they are indispensable resources for the sustainable development of global human culture. For these reasons, focus is directed exclusively to lacustrine and fluvial ecosystems in this article.

2. Age of Freshwater Ecosystems and Evolution of their Biota

Freshwater habitats on land are vastly more varied in physical and chemical features that those in the sea. Also, the transience in time and space of the freshwater environments is often emphasized by biologists and paleoecologists. The duration of individual freshwater bodies is usually assumed to be very short on a geological timescale. From this observation it could be concluded that freshwater ecosystems as a whole are geologically young and only transient compared to marine ones. Such reflections, however, confuse the relatively ephemeral character of individual freshwater bodies with the aquatic habitat as a major ecosystem type. As an ecosystem type, the freshwater habitat may be considered as constant as any other terrestrial or oceanic habitat. There is no reason to believe that all types of continental freshwater bodies have not existed since there was precipitation on land. For that reason, freshwater ecosystems may be considered as old as most life.

If we finally focus attention on individual continental freshwater bodies, at least some of them may display relatively long permanence in time and space. Many river systems have been in continuous existence since far back in geological time. Although rivers may change and evolve, they rarely disappear. In contrast to rivers, lakes usually persist for relatively short periods of time and give less opportunity for development of a purely lacustrine biota. This conclusion can be supported by the example of contemporaneous freshwater fauna composition: running waters include representatives of almost all taxonomic groups found in freshwaters. Several groups of invertebrates occur only in running water and many reach maximum development there. Some primitive groups are restricted to, or are found primarily in streams, demonstrating continuity in time. Lakes are no less capable than rivers of producing evolutionary change, as shown by several ancient lake basins such as those of Tanganyika or Baikal (the latter tectonic lake, or at least the southern part of the basin, was probably formed at the end of the Cretaceous, representing continuity for more than 50 Ma). These lakes have evolved many endemic groups: for example, of the approximately 1 200 animal and 600 plant species in Lake Baikal, over 80% are endemic. But most lakes are much more evanescent phenomena: over the course of some period of time they fill with deposits and disappear, and most of their biota perishes together with them, if it does not move into another lake basin. Characteristic specializations, such as short life cycles, desiccation tolerance, and morphological adaptations for long-distance transport (such as resistant reproduction structures), have evolved in some groups of freshwater organisms to facilitate their dispersal from a water body that is becoming extinct to another body of water.

The freshwater biota is ultimately derivative, taking its origins from marine and terrestrial plants and animals. Four possible sources of origin can be recognized: (a) active invasion from the sea, requiring physiological adaptations to low salinity; (b) passive invasion from the sea by restriction of organisms to habitats that gradually freshened over time; (c) invasion from the land (as in the case of vascular plants and possibly insects); (d) evolution within the freshwater habitat itself (subsequent adaptive radiation of earlier immigrants). Invasion from the sea, either active or passive, appears to be the origin of most living classes of freshwater organisms.

Many freshwater animals do not develop hard body parts and we often deduce their historical presence only from the traces they leave on lake bottoms. In case of fossil plant remains, recognition of their aquatic habit on a morphological basis is sometimes impossible. The fossil record, imperfect though it is, provides the only constraints on the timing with which various habitats were occupied, albeit giving only minimum dates in most cases. Fossil remains of one of the earliest known organisms living on Earth—stromatolites—have been found both in marine sediments and in alluvial and lake deposits in the Middle Precambrian formations of the Canadian Shield. Later in geological history, during the Middle Paleozoic, freshwaters supported the first amphibious vascular plants (found in early Devonian Rhynie Chert beds) and blue-green algae as well as green algae, indicating that the ecosystem had the potential for supporting diverse forms of animal life much earlier than normally anticipated. A summary of the first fossil appearances of important freshwater animal taxa in geological history is given in Figure 2. Because of the scarcity of the fossil record mentioned above, this overview should not be considered definitive. As for freshwater macrophytes, we can conclude only generally that during the Paleozoic and Mesozoic, prior to the diversification of angiosperms, the aquatic niches were filled by pteridophytes whose former diversity is reflected in their abundant megaspore record. Pteridophytes persisted in freshwaters with reduced diversity until the Tertiary, when they were largely substituted by the first freshwater-adapted angiosperms.

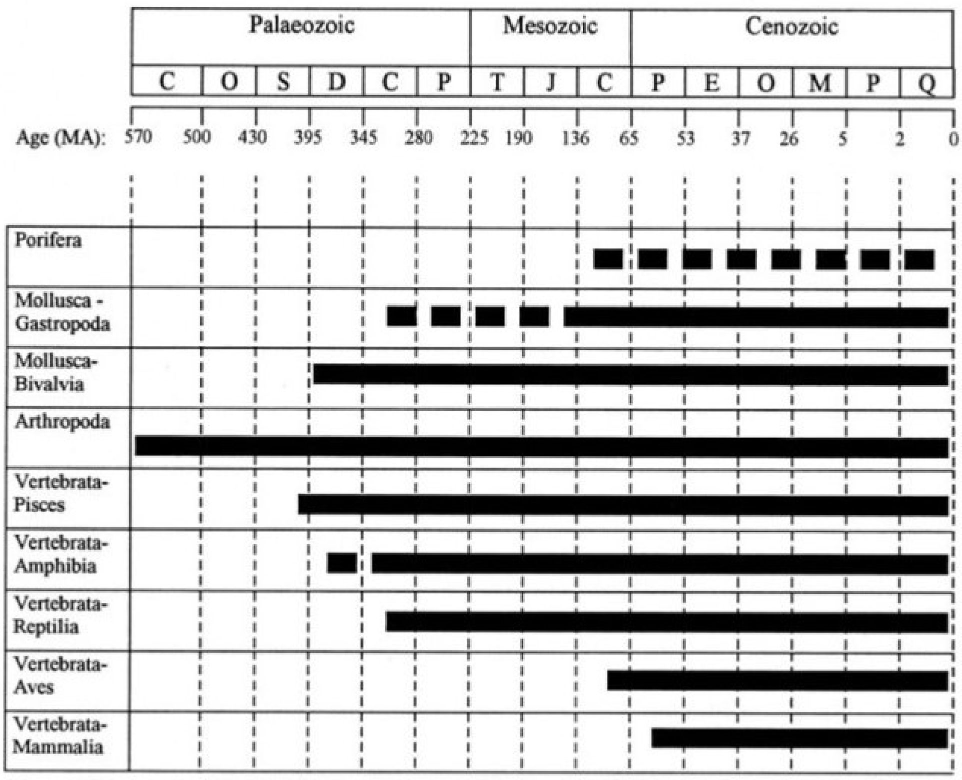

Figure 2. Summary of the first fossil appearances of freshwater animals, exclusive of insects and groups whose fossils preserve poorly. Dashed bars designate a questionable

record.

To summarize, freshwaters not only contain their own ancient and peculiar groups of organisms, some with ancestries as far back as the Middle Paleozoic, but they have been a place of adaptive radiation of more recent immigrants from the land or sea, and a way station for other groups that passed through, both from sea to land (e.g., amphibians) and from land to sea (e.g., some mammals). Although freshwater life is taxonomically impoverished in comparison with marine and terrestrial biotas, it cannot be assumed that freshwater communities are necessarily “immature” or significantly “younger:” they are just specific in many respects. This specificity consists in several important ecological processes and physical characteristics which are briefly summarized in the following section (**see *River and Lake Processes***).

-
-
-

Bibliography

Bradley R.S. (1999). *Paleoclimatology*, second edition, International Geophysics Series, vol. 68, 613 pp. San Diego, London: Academic Press. [This book provides a comprehensive and well-organized overview of different approaches and techniques in the study of past climatic changes.]

Brown A.G. (1997). *Alluvial Geoarchaeology—Floodplain Archaeology and Environmental Change*, 377 pp. Cambridge, UK: Cambridge University Press. [This work provides a synthesis of present-day ecology, paleoecology and archeology of fluvial environments.]

Gray J., ed. (1988). *Paleolimnology—Aspects of Freshwater Paleoecology and Biogeography*, 678 pp. Amsterdam: Elsevier. [This book represents a detailed study of pre-Quaternary lacustrine environments and the evolution of their biota.]

Jones J.A.A. (1997). *Global Hydrology—Processes, Resources and Environmental Management*, 399 pp. London: Longman. [This book presents basic knowledge about global hydrological processes and more detailed discussion of monitoring and managing water resources.]

Wetzel R.G. (1983). *Limnology*, second edition, 767 pp. Philadelphia, London: Saunders College Publishing. [This book presents extensive knowledge in the field of limnology.]

Biographical Sketch

Petr Pokorný, M.Sc., was born in 1972 in Prague, Czech Republic. Since his childhood, Petr Pokorný has been interested in biology. At 1988, during his secondary college studies, he was awarded the first prize in the National Competition of Young Scientists for his work “Physiology and reproduction of Flammulina velutipes (Basidiomycetes).” In the course of his studies at the Faculty of Natural Sciences, Charles University, Prague, he specialized in paleontology (B.Sc. dissertation: paleoecology of Crinoidea communities at Silurian volcanic areas of Central Bohemia), immunology, and developmental biology (M.Sc. dissertation: The role of cytoskeleton in regulation of Xenopus laevis oogenesis). He graduated from Charles University, Prague, in May 1995.

His postgraduate studies have focused on palynology and paleoecology at the Faculty of Biological Sciences, University of South Bohemia, Ceské Budejovice. His Ph.D. thesis concerned high-resolution pollen, macroremains, and paleoalgological analyses from late-glacial and Holocene lacustrine sequences of Svarcenberk Lake, South Bohemia. His Ph.D. degree was defended in May 2000. From June to September 2000, Petr Pokorný was employed as the research staffperson in the Geobotanical Institute, University of Bern, Switzerland. Recently, Petr Pokorny worked as research staff at the Institute of Archaeology, and the Institute of Botany, Academy of Sciences of the Czech Republic. He is now engaged mainly in paleoecology of Central Bohemia, an area with a long history of human impact.