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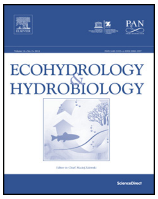

Review Article

Biogeochemistry and biodiversity in a network of saline–alkaline lakes: Implications of ecohydrological connectivity in the Kenyan Rift Valley

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1. Introduction

The interaction among bedrock, surface and ground waters, in aquifers and within deep lake sediments, is a major driver of ecosystem dynamics in lakes worldwide, and particularly in lakes affected by geogenic water inputs with high mineral content (Borch et al., 2009; Christenson et al., 2015). Water–bedrock interactions are further intensified in tropical areas, owing to high average annual temperatures, intense weathering, and frequent hydrological extremes (floods and droughts), which fundamentally contribute to environmental variability. In semi-arid and sub-humid tropical regions, aquatic ecosystems are threatened by intense anthropogenic impact because of urban waste disposal, discharge of industrial effluents, intensive agricultural practices employing fertilizers and pesticides, water abstraction for irrigation and human uses, and hydroelectric energy production. The combined and interacting influence of geogenic and anthropogenic drivers results in biodiversity decline and habitat reduction (Dudgeon et al., 2006); this situation has been recently exacerbated by climate change and demographic growth.

Understanding lake biogeochemical dynamics is essential for interpreting the specificity of human impact and for identifying adequate conservation measures (Vitousek Q3 et al., 1997); this is of great relevance for alkaline lakes where biogeochemical conditions represent a strong environmental filter in the selection of resident lake communities of micro-organisms (prokaryotes as well as algae and micro-crustaceans, Schagerl, 2016). Variable degrees of connectivity (defined as “the strength of interactions across ecotones”, Ward et al., 1999) between separate wetlands bear a significant influence on the composition of fish communities (Bouvier et al., 2009) as well as on aquatic bacteria (Peter and Sommaruga, 2016), thus impacting onto regional biodiversity. We propose that connectivity among adjacent environmentally heterogeneous aquatic ecosystems may have positive implications in terms of contributing to biodiversity protection and to resilience towards various forms of impact, thus enhancing regional environmental stability and overall carrying capacity. This reflects the urgency of collecting scientific data from water bodies at different levels of ecohydrological connectivity. It will support the understanding of ecosystem features and the design of adequate lake management tools for restoring biodiversity, improving water quality and enhancing ecosystem services for the benefit of lake-dependent communities.

Following the concept of ecohydrology, defined on the basis of the mutual interaction between hydrological drivers and biotic processes (*sensu* Zalewski, 2000), this paper reviews existing links between ecohydrological features, hydrological connectivity, and carrying capacity within a lake network. Overall, this review illustrates how

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environmental variability among lakes can support system stability and biodiversity dynamics at regional scale.

We focused on a cluster of lakes aligned from North to South within the Kenyan portion of the East African Rift; they are subject to different levels of hydrological connectivity and represent a discontinuous gradient of water bodies, stretching from freshwater to hypersaline conditions (Schagerl, 2016). Knowledge of these lakes is limited to few accessible ones and research activities that were carried out typically achieved a lifespan no longer than a PhD thesis. Limited long-term studies exist except those few based on satellite image analysis (lake levels and chlorophyll concentrations; Tebbs et al., 2011, 2013) and those on cyanobacteria mass development over a 12-year period (Krienitz et al., 2013a,b,c) and a 15-year period (Krienitz et al., 2016a). This despite the fact that some lakes are under protected area management and could be regularly monitored by conservation management agencies. The harsh biogeochemical setting created conditions for the development of highly selected and diversified microbial communities; very few fish species persist, in particular some cichlids remarkably adapted to alkaline conditions. The target lake network offers a series of stepping stones for migratory birds as well as habitats for sedentary endemic populations, thus retaining a relevant value in terms of regional avian biodiversity.

2. Lakes in the Kenyan portion of the East African Rift Valley

The major 30 volcanic and tectonic lakes of the eastern branch of the African Great Rift Valley are characterised by different ranges of hydrological connectivity and are exposed to multiple natural and anthropogenic stressors. Within the Rift, all catchments, except that of Ewaso Ng'iro North (receiving tributaries from the Nyandarua mountains and from Mt. Kenya) have developed endorheic basins lacking surface outflow. All the lakes are situated in sub-humid to semi-arid savannahs (300–600 mm year^{-1}) subject to high potential evaporation rates (1300–2000 mm year^{-1}) and are fed by drainage from mountain blocks on either side of the Rift Valley. Drastic hydrological changes are rather frequent in the Rift Valley, owing to capricious precipitation patterns originating in distant geographical regions, which are dependent on the variable position of the Inter Tropical Convergence Zone, on the strength of the monsoons and on the temperature of the Indian Ocean. Lake water levels depend upon the balance between water output (e.g. evaporation) and input, controlled by the rate of rainfall that occurs in forested upland portions of the lake catchments. Water levels may vary also under the influence of groundwater pressure, which is connected to tectonic movements below the earth crust and to pressure forces that arise within the mantle. Unusual changes in the water levels of wells are considered common signs of volcanic activity (Tilling, 1989). De Carolis and Patricelli (2003) report that water level in wells had risen in occasion of the Vesuvius volcanic eruption of December 1631; similarly, water levels rose in Taal crater lake in the Philippines just before an eruption (Smith, 2013). Ephemeral streams, from lower altitudes of the catchments and underground springs at the bases of the mountains, can constitute a small proportion of the inflows significantly contributing to the water chemistry. Since 2010, most East African lakes are at high water level despite lacking evidence of an increase in rainfall (Odongo et al., 2015). Upper catchment deforestation and land cover degradation could be an important contributing factor, but there is no clear understanding of the complex hydrology of this Region, where hydrological records disagree with IPPC climate change predictions based upon popular global circulation models, according to which higher rainfall should be expected (Klein et al., 2016; Odongo et al., 2015).

A cluster of these lakes (Table 1) forms a discontinuous gradient of water bodies, from freshwater (Baringo and Naivasha) to hypersaline (Bogoria, Nakuru, Elementeita, Sonachi, Natron). The latter are evaporitic systems (pH from 9.0 to 12.0) representing extreme conditions, characterised by high salinity, high alkalinity and high primary productivity under constant high temperatures. While Nakuru is protected as a National Park, Lake Bogoria is a National Reserve (managed by the County of Baringo), and Lake Elementeita, a Wildlife Sanctuary, is largely within Soysambu Conservancy, a private conservation charity.

Most lakes are primarily of tectonic origin, having developed along linear faults stretching across a geologically ancient volcanic landscape reshaped by recent volcanic activity. Others, such as Sonachi Crater Lake, are entirely within a volcanic caldera and Naivasha, itself a tectonic lake, includes a number of in-filled volcanic craters. Early hydrological studies using stable isotopes highlighted deep water connections below the Rift Valley floor able to transfer groundwater over great distances (Eugster, 1970). In this way, it could be ascertained that water from Lake Naivasha reaches as far as Suswa and up to Lake Magadi, over 100 km South. Recent monitoring of the vertical profile in Lake Sonachi showed a distinct increase in temperature and alkalinity with depth (Pacini, unpublished), indicating that lake level increase in late 2016 (during a dry season) was due to feeding by underground alkaline springs. In some lakes, such as Nasikie Engida and Lake Magadi in southern Kenya, hot spring provide most of the recharge; in other lake basins, thermal springs are minor but sometimes important contributors (Schagerl and Renaut, 2016).

No two lakes have the same limnological characteristics due to their different histories and degrees of hydrological connection within their catchment, and no one lake is stable enough to maintain a consistently high primary production. The most studied lakes have been: Naivasha (limnology, ecology, management), Magadi (microbiology and geochemistry) and Nakuru (ecology and management), whereas Bogoria, Sonachi, Elementeita and Oloidien lakes have been poorly investigated (Table 2). Q4

Kenya's saline–alkaline lakes offer highly prized cultural ecosystem services. They are renowned spots for bird and wildlife tourism, offer magnificent landscape views and include important paleontological sites. Bogoria is visited as much for its hot springs, around the western shore of the lake, as for its flamingos; these springs are reputed to be the most visually impressive and extensive in

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